



Taxonomy of coccids (Hemiptera: Coccidae: *Coccus* L.) associated with *Crematogaster* ants (Hymenoptera: Formicidae) in the stems of *Macaranga* plants (Euphorbiaceae) in Southeast Asia

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Abstract

The Southeast Asian soft scale insects (Hemiptera: Coccoomorpha: Coccidae) associated with ants of the *Crematogaster borneensis*-group (Hymenoptera: Formicidae) and living in the hollow stems of *Macaranga* plants (Euphorbiaceae) are revised taxonomically. Ten species of the genus *Coccus* L. are recognised: seven were described previously and three new species are described herein. The species are: *Coccus caviramicolus* Morrison, *C. circularis* Morrison, *C. heckrothi* Gullan & Kondo **sp. n.**, *C. lambirensis* Gullan & Kondo **sp. n.**, *C. macarangicolus* Takahashi, *C. macarangae* Morrison, *C. penangensis* Morrison, *C. pseudotumuliferus* Gullan & Kondo **sp. n.**, *C. secretus* Morrison and *C. tumuliferus* Morrison. All of these species are described or redescribed and newly illustrated based on the adult females, and a key to distinguish the species is provided. We designate a lectotype for *C. macarangicolus*. The first-instar nymphs of all species are morphologically extremely similar and therefore only the first-instar nymph of *C. macarangae* is described and illustrated. Seven of these species currently are known only from *Macaranga*, but *C. macarangae*, *C. secretus* and perhaps *C. pseudotumuliferus* have been recorded from the hollow stems of several other ant-plants and a few non-myrmecophytes. The *Coccus* species from *Macaranga* are closely related to *C. hesperidum* L., the type species of the genus, and therefore are retained

in the genus *Coccus* even though the adult females exhibit a few morphological differences from *C. hesperidum*. The species of *Coccus* from *Macaranga* appear to be parthenogenetic because no male nymphs or adults have been found, despite extensive collecting.

Key words: soft scale, myrmecophyte, mutualism, Coccomorpha

Introduction

Many species of the Southeast Asian *Macaranga* plants (Euphorbiaceae) have an intimate association with ants of the genus *Crematogaster* (Formicidae) (Fiala *et al.* 1989, 1991, 1999; Inui *et al.* 2001; Itino *et al.* 2001b; Quek *et al.* 2004, 2007; Ueda *et al.* 2015). These myrmecophytic or ant-plant species of *Macaranga* provide the ants with nesting sites inside their naturally hollow stems (domatia) or ant-excavated stems, as well as nutrient-rich food bodies (Fiala & Maschwitz 1992a, 1992b; Heil *et al.* 1997, 1998; Davies *et al.* 2001; Itino *et al.* 2001a) and access to honeydew, as explained below. The ants provide their *Macaranga* host plants with protection against herbivores and plant competitors (Fiala *et al.* 1989; Federle *et al.* 2002). Myrmecophytic *Macaranga* species also possess extrafloral nectaries on their leaf margins but their function is not well understood (Fiala & Maschwitz 1991; Davies *et al.* 2001). Myrmecophytism involving varying degrees of plant morphological specialisation has evolved more than once within *Macaranga* but only in the western Malesian lineage of the genus, with myrmecophytic species found in three *Macaranga* sections, namely *Pachystemon*, *Pruinosae* and *Winklerianae* (Blattner *et al.* 2001; Davies *et al.* 2001; Bänfer *et al.* 2004). The relationship is obligate for certain *Crematogaster* ants, which nest only inside these myrmecophytic *Macaranga* species (Fiala *et al.* 1999; Fiala & Maschwitz 1992a; Feldhaar *et al.* 2016). The taxonomy and phylogeny of these specialist ants have been the subject of a number of studies (e.g. Fiala *et al.* 1999; Itino *et al.* 2001; Feldhaar *et al.* 2003; Quek *et al.* 2007; Feldhaar *et al.* 2010; Ueda *et al.* 2015; Feldhaar *et al.* 2016) and currently the majority of the ants are recognised as belonging to the *Crematogaster borneensis*-group (Blaimer 2012), comprising eight species (Feldhaar *et al.* 2016). These ants colonise *Macaranga* hosts in the sections *Pachystemon* (naturally-hollowing stems) and *Pruinosae* (solid stems, excavated by ants), whereas plants in the section *Winklerianae* are colonised only by *C.* morphospecies 8 that belongs to a different *Crematogaster* subclade (Feldhaar *et al.* 2016). The natural history of these ants, including data on the *Macaranga* species inhabited by each ant species, was reviewed by Feldhaar *et al.* (2016).

In addition to the ants, myrmecophytic *Macaranga* species usually house honeydew-producing coccids (Hemiptera: Coccomorpha: Coccidae: *Coccus* L.) inside their hollow stems (Heckroth *et al.* 1998, 2001; Ueda *et al.* 2008; Quek *et al.* 2017). The coccids provide the ants with sugar-rich liquid waste called honeydew, supplementing the food bodies produced by the plants (Heckroth *et al.* 2001; Itino *et al.* 2001a). Coccid honeydew may be especially important to the survival of the *Crematogaster* ants during colony establishment on the *Macaranga* plants (Handa & Itioka 2011). In general for any ant-coccid association, the benefits to coccids of living inside ant nests or under shelters constructed by ants include reduced levels of parasitisation and predation, improved sanitation through removal of honeydew by the ants, and sometimes ant transport to other feeding sites (Sugonyayev 1996; Gullan 1997; Heckroth *et al.* 1998). Although associations of coccids with ants are beneficial for both partners, usually they are facultative, with the ants often existing without the coccids and vice versa (Gullan 1997). In the *Macaranga-Crematogaster-coccid* system, the coccids occur in the ant nest inside the hollow stems of almost all healthy *Macaranga* plants, but the specificity of the coccids for particular ant or plant species is not high, although some associations occur more frequently than expected in relation to partner availability (Heckroth *et al.* 1998; Quek *et al.* 2017). Furthermore, it is common to find two or three coccid species living inside a single *Macaranga* plant (Heckroth *et al.* 1998; Houadria *et al.* 2018). Although most *Macaranga*-associated *Coccus* species have been collected only from inside the hollow stems of myrmecophytic *Macaranga* species, three *Coccus* species, especially *C. secretus* Morrison, have been found occasionally on other unrelated plants, but mostly inside the hollow stems of other ant-plants (Heckroth *et al.* 1998; Moog *et al.* 2005).

In the myrmecophytic *Macaranga* system, coccid first-instar nymphs (called crawlers) disperse between plants either by being carried by the wind or by walking, and then either are carried into the hollow stems by patrolling ants or enter unassisted through an ant-nest exit hole. It has been shown experimentally that *Crematogaster* ants discriminate between symbiotic coccids and non-symbiotic scale insects by generally carrying the former into their nests, but throwing the latter off the plant (Handa *et al.* 2012). Furthermore, ants have been shown to discriminate

among symbiotic coccid species: as noted by Heckroth *et al.* (2001), ants from *M. hypoleuca* generally accepted nymphs of *C. tumuliferus* placed in the internode of their host plant, but threw nymphs of *C. penangensis* off their host plant. Ants of the *Crematogaster borneensis*-group have been shown to solicit honeydew from the coccids, but there is no evidence that the ants ever consume the coccids (Heckroth *et al.* 2001; Houadria *et al.* 2018). Some internodes of the hollow stems contain refuse piles produced by the ants and consisting of amorphous dark brown material usually swarming with nematodes (Maschwitz *et al.* 2016), but no arthropod remains have been found in these piles (Heckroth *et al.* 2001; Houadria *et al.* 2018).

Coccus is a species-rich genus of soft scales (about 90 species are currently recognised) and is also the type genus of the family Coccidae (Ben-Dov 1993; Williams & Ben-Dov 2009). Seven species of *Coccus* have been described from specimens collected inside the hollow stems of *Macaranga* plants in close association with ants (Morrison 1921; Takahashi 1952; García Morales *et al.* 2017). Based on nucleotide sequence data, the type species of *Coccus*, *C. hesperidum* L., has been shown to be closely related to the *Macaranga* coccids (Lin *et al.* 2013, 2017b; Quek *et al.* 2017; T. Kondo and L.G. Cook unpublished data). Thus the coccids from *Macaranga* should be retained in the genus *Coccus*, unless future more extensive gene and taxon sampling suggests otherwise.

The first molecular phylogenetic studies of *Macaranga* coccids were based on mitochondrial data, specifically from *cytochrome oxidase I (COI)* (Ueda *et al.* 2008, 2010), but most of the recovered mitochondrial lineages contained more than one coccid morphospecies. As explained by Quek *et al.* (2017), this latter pattern is consistent either with incomplete lineage sorting or hybridisation, or with the presence of ancient nuclear copies of mitochondrial DNA (NUMTs) that would lead to the *COI* phylogeny being based on both nuclear copies and actual mtDNA sequences and thus not reflecting the true cladogenetic history of the mtDNA. A recent analysis (Quek *et al.* 2017) using the same coccid samples as Ueda *et al.* (2008, 2010) but based on two nuclear genes, *elongation factor 1 α (EF-1 α)* and *wingless (WG)*, recovered clades that are congruent with morphologically defined groups of coccids. In that study, ten clades/lineages of *Macaranga* coccids were recognised—eight of these were well supported clades, while two of them comprised just one morphologically distinct specimen each. These clades/lineages equate to 10 morphological species, which are described or redescribed in this paper. However, geographic and host-plant sampling of coccids for the molecular phylogenetic studies of the coccids was not comprehensive and additional *Coccus* species are likely to be recognised in the future. Although Heckroth *et al.* (1998) recognised more than 20 morphospecies of *Coccus* associated with *Macaranga* plants in Peninsular Malaysia and Borneo, the actual number based on his samples is likely to be fewer because some of those *Coccus* morphospecies were either geographic variants or immature specimens (as discussed in the taxonomic section below under 'Species recognition').

The *Macaranga*-associated species of *Coccus* are almost certainly parthenogenetic because males are unknown (see below under Taxonomy: Male instars). Asexual lineages present a challenge for species delimitation as discussed by Lin *et al.* (2017a), with particular reference to the widespread polyphagous coccid *Parasaissetia nigra* (Nietner). Most species concepts do not apply to asexual organisms, so Lin *et al.* (2017a) defined species as genetic clusters that are ecologically differentiated from other such clusters. All of the *Macaranga* coccids share a similar ecology and none of the well-sampled *Coccus* species have a specific association with particular *Macaranga* or ant species, although some associations are “preferred” or “avoided” (Quek *et al.* 2017). In parthenogenetic species, differing morphological traits can become fixed in different populations, especially those that are geographically separated. There is some evidence for this in the *Macaranga* coccids because two well-sampled and widespread species exhibit some intraspecific genetic diversity (Quek *et al.* 2017, fig. 3) as well as morphological diversity (discussed under individual species).

For this revision, we have examined all available microscope slide preparations of *Macaranga* coccids to assess the morphology of the adult females in light of the recently available nrDNA data used to produce figure 3 of Quek *et al.* (2017). We define species as genetically distinct clusters within which individuals share two or more diagnostic morphological traits. We redescribe the seven previously named species and describe three new species. We provide illustrations of the adult female and record the host-plant species and geographical distribution for each recognised *Coccus* species. We also provide a key to the adult females of the *Coccus* species from *Macaranga* and photographs of the live coccids inside the domatia of *Macaranga* plants.

Materials and methods

Coccid specimens were prepared for microscope examination mostly by PJG and TK, with some slides prepared by S. Ueda and A. Stewart, and always with one female mounted per slide. Many of the specimens used in this revision are DNA voucher specimens and include all of those used in the studies of Ueda *et al.* (2008, 2010) and Quek *et al.* (2017). These voucher specimens frequently were damaged by the extraction procedure and subsequent handling, but documenting their morphology was essential to delimiting species in this study. The DNA voucher specimens of *T. Kondo* are from collections of B. Fiala and the associated molecular data are not published. The gene regions sequenced for TK vouchers were the problematic *COI* region that produced the spurious results published by Ueda *et al.* (2008, 2010) and a *12S* region that has not been used in any other molecular study of these coccids. For slide-mounted specimens prepared by PJG and TK, the mounting method of Williams & Granara de Willink (1992) was used except that xylene was used instead of clove oil. The method involves clearing the body contents in 10% KOH, staining the cuticle in acid fuchsin, then dehydrating in increasing concentrations of ethanol with a final wash in 100% isopropanol or ethanol, then into xylene and finally mounting in Canada balsam on glass slides. Older slide preparations, including sometimes those containing type specimens, often had several individuals mounted under a single coverslip. Identifications were made by PJG and TK using Morrison (1921) and Takahashi (1952), as well as by reference to type specimens of named species and notes on morphological features of some unnamed species prepared by H.-P. Heckroth. All taxonomic decisions relating to the *Macaranga* coccids, including authorship of the new species of *Coccus*, should be attributed to PJG and TK alone. TK prepared the taxonomic illustrations and took most of the measurements; PJG sorted most the specimens to species and prepared the species comparisons and final descriptions.

Measurements of specimens were made using an ocular micrometer on an Olympus phase-contrast microscope. Illustrations of the coccids were prepared by TK and follow the conventional style used for the Coccoidea, with the dorsal surface of the body drawn on the left side and the ventral surface on the right, and with enlargements of important features arranged around the illustration. The morphological terms used in the descriptions follow those used for adult female coccids by Hodgson (1994). All measurements are maximum dimensions (e.g. body width was recorded at the widest point) and are expressed as the range. Setal lengths included the setal base. For each named species, the description is based on type specimens but supplemented by non-type specimens when these were available; any variation encompassed by the addition of recently collected specimens is discussed. The number of specimens from which morphometric and meristic data were taken is indicated as “(n = X)” at the beginning of each description.

In the lists of material studied, the number of slides and specimens on each slide are recorded as the number of slides followed by the total number of specimens and their corresponding stages; for example, 1 slide with 1 adult female and 1 third-instar female would be: 1(1 adult female + 1 third-instar female). If not otherwise specified, the specimens are adult females; for example, 2 slides each with 1 adult female would be listed as 2(2).

The museum depositories for the specimens studied for this revision are as follows:

ANIC	Australian National Insect Collection, C.S.I.R.O., Canberra, Australia
BMNH	The Natural History Museum, London, U.K.
FRIM	Entomology Branch, Forest Research Institute Malaysia, Kepong, Malaysia
FDS	Forest Research Centre, Forest Department Sarawak, Kuching, Malaysia
USNM	The Coccoidea collection of the United States National Museum of Natural History, which is housed at the U.S. Department of Agriculture, Beltsville, Maryland, U.S.A.

Specimens collected at Lambir Hills National Park by Takao Itioka and his colleague Kaori Murase will be returned to Professor Itioka at the Graduate School of Human and Environmental Studies, Kyoto University, Japan, for eventual return to the Forest Department Sarawak, Malaysia, as required by his permit. Unless otherwise specified, the depository for all the non-type specimens listed under 'Other material examined' for each species is the ANIC.

We examined historic coccid specimens from the USNM, which houses the material used by Morrison (1921) to describe six of the named species of *Coccus* from *Macaranga*. Morrison based his descriptions on specimens sent to him by E.E. Green and C.F. Baker, both of whom had received them from I.H. Burkill. All of the

Macaranga coccids used by Morrison were collected by Burkill, who was the Director of the Botanic Gardens in Singapore from 1912 to 1925 (National Library Board Singapore 2018). Morrison's slides of these species in the USNM are labelled as "Holotype" or "Paratype" in his own handwriting, including those for three species for which his descriptions state that each species was described based on a particular number of mounted adults from a single collection but without specific mention of the holotype or paratypes. The status of Morrison's type specimens is clear for these species—*C. macarangae* (only one adult female listed in original description and its slide is labelled as 'holotype'), *C. penangensis* (both slide and envelope labelled as 'holotype') and *C. tumuliferus* (holotype labelled clearly although on a slide with another specimen). Thus, we follow Morrison's type designations for these three species. The Green collection in the BMNH also holds specimens collected by Burkill that have the same collection data, often including the same Burkill collection numbers, as *Coccus* species described at the USNM by Morrison. The BMNH specimens are not types because they were not seen by Morrison and are not listed in Morrison's descriptions. Presumably Green retained some of Burkill's specimens in the BMNH when he sent specimens onwards to Morrison. The BMNH also houses the only specimen of Takahashi's *C. macarangicolus* that we could locate in any museum collection.

The International Commission on Zoological Nomenclature (1999) requires lectotypes designated after 1999 to "contain an express statement of deliberate designation" (amended Article 74.7.3). We use the statement "here designated" to fulfill this requirement. A lectotype has been designated for one species for which an unambiguous syntype was identified. The purpose is to provide stability of nomenclature, and designation is done in a revisionary context in agreement with the amended Recommendation 74G of the ICZN.

We have registered the new species names published in this paper with the Official Registry of Zoological Nomenclature (ZooBank) and cite the Life Science Identifiers (LSIDs) after the heading for each new name. Each LSID is a globally unique identifier for the nomenclatural act of naming a new taxon.

Host-plant species records. Every effort has been made to provide correct names for the *Macaranga* host plants. Care should be exercised when referring to host-plant names used in some of the early literature on the *Macaranga*-ant symbioses, because the taxonomy of *Macaranga* has been updated since. For example, early references to *M. triloba* (e.g. Morrison 1921; Fiala *et al.* 1989; Heckroth *et al.* 1998; Blattner *et al.* 2001; Heil *et al.* 1997, 1998, 2002) actually refer to *M. bancana* (Davies 2001; Murase *et al.* 2003), which is a myrmecophyte, whereas *M. triloba* is not (Davies 2001; Davies *et al.* 2001; Bänfer *et al.* 2004). Additionally, *M. griffithiana* was considered to be a subspecies of *M. motleyana* by Whitmore (1974); however, although closely related, they differ in morphology and ecology and now are treated as distinct (Davies 2001; Fiala *et al.* 2016). *Macaranga pseudopruinosa* is a synonym of the accepted name *M. hosei* (Whitmore 1975; Govaerts *et al.* 2000, Davies 2001). *Macaranga umbrosa* was previously recognised as a subspecies of *M. kingii* (Davies 2001) and may therefore be named *M. kingii* var. *platyphylla* in earlier publications. *Macaranga glandibracteolata* and *M. angulata* were described only in 1999 (Davies 1999) and earlier collections may refer to these species as *M. indistincta* and *M. depressa* respectively. Taxonomic and phylogenetic treatments of *Macaranga* include the following: Davies (1999, 2001), Davies *et al.* (2001), Blattner *et al.* (2001), Bänfer *et al.* (2004, 2006), Kulju *et al.* (2007), Whitmore (1975, 2008), van Welzen *et al.* (2014) and Fiala *et al.* (2016). Host-plant names cited in the material examined sections are as written on the slide labels, but the correct name is given in parentheses if there has been a change of name or identification.

Associated ant species. All the coccid specimens were collected from nests of *Crematogaster* ants inside the hollow stems of *Macaranga* plants, although this usually is not stated either on the slide labels or in the lists of material examined. As explained in the Introduction, all of these plant-ants belong to the *Crematogaster borneensis*-group except those colonising *M. winkleri*. The mtDNA lineages for *Crematogaster* species associated with the coccids from the study of Quek *et al.* (2017) are specified in table S1 (Supporting Information) of that study. The codes for these ant lineages follow the nomenclature of Quek *et al.* (2007). Note S1 in the supporting information of Quek *et al.* (2017) attempts to reconcile these lineages with the ant species described in Feldhaar *et al.* (2016). We have not attempted to list the names of the ant species associated with each of the coccid collections listed in this revision. In a few cases identifications of the ants were not made and, for some collections with ants, these contain mostly worker ants that are difficult to identify to species. All of the ants collected in Brunei by PJG from *M. trachyphylla* were *C. captiosa* Forel, and all from *M. beccariana* were *C. decamera* Forel, based on identifications made by PJG based on queen morphology supplemented by worker ant characteristics as given in Feldhaar *et al.* (2016).

Sampling localities for specimens examined. Coccids and *Crematogaster* ants mostly were sampled from *Macaranga* plants along roadsides or on tracks through forest. Most forests were lowland or hill dipterocarp forests, often very disturbed (secondary), although a few sites were in peat swamp forests. Collections were made by a number of people, especially P.J. Gullan (Brunei only), B. Fiala, H.-P. Heckroth, S.-P. Quek, T. Itioka and K. Murase, as part of long-term research on the *Macaranga-Crematogaster-Coccus* system. The following list explains the collection localities, which often are referred to briefly on labels or using a locality code; also included, where known, is a statement of the forest type at the time of collection (many of the sites have been cleared of forest since, or much altered in condition). The general area of each of the main collecting sites is marked on the accompanying map (Fig. 1), with all localities except for Brunei being the same as those used for ant sampling (see Quek *et al.* (2007, supplementary data) and Feldhaar *et al.* (2016) for details of ant collection sites). A list of collection sites for coccid DNA voucher specimens also is available from the supplementary information supplied by Quek *et al.* (2017) and form a subset of the collection records reported in the present taxonomic revision.

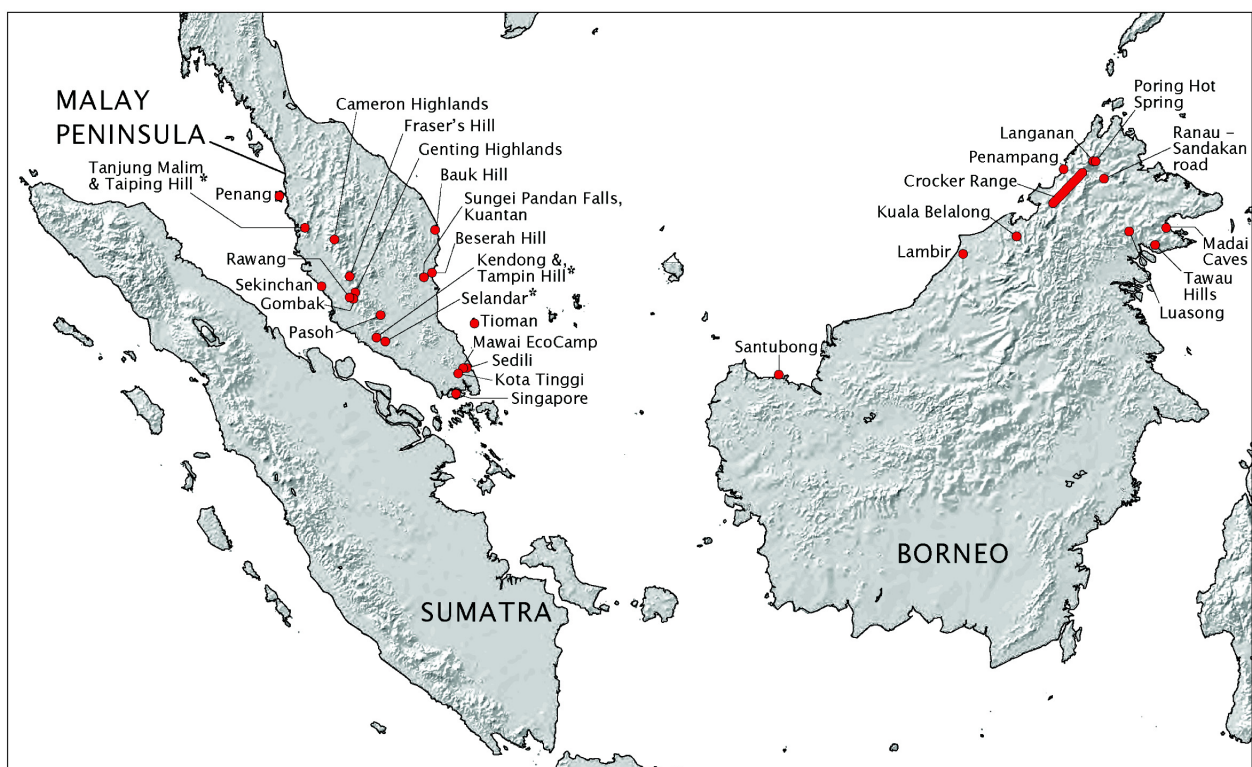


FIGURE 1. Main collecting localities of the coccid specimens used in this revision. The three asterisked locations on the Malay Peninsula denote I.H. Burkill's collections from the early part of the 20th century and should be regarded as gross estimates.

BORNEO: BRUNEI

- Kuala Belalong Field Studies Centre (KBFSC), collections made near tracks and along creeks in primary, lowland forest in the Batu Apoi Forest Reserve in the Temburong district, 4° 32'50" N, 115° 09'30" E, elevation ~30 m; all collections by PJG from August to October 1995.

BORNEO: EAST KALIMANTAN

- Bukit Bangkirai (N of Balikpapan), Tenggarong, road from Samarinda to Kota Bangun, and Wanariset (N of Balikpapan), low lying roadside vegetation, sometimes with soggy soil, fringing plantations or fringing degraded forests or scrubby vegetation.

[In Quek *et al.* (2017), the locality Samarinda was given for the specimens collected near Bukit Bangkirai, Tenggarong and Wanariset. Samarinda is the closest city to these sites.]

BORNEO: NORTH KALIMANTAN

- Long Ampung, 1 42'58" N, 114 57'21" E, elevation ~700 m asl, forests consisting of a mixture of secondary and primary growth and cultivated forest gardens surrounding a village and rice paddies. [Note: all collections at this locality were made in 2005. Until 2012, North Kalimantan was part of the province of East Kalimantan and thus Quek *et al.* (2017, table S1) listed Long Ampung as East Kalimantan.]

BORNEO: SOUTH KALIMANTAN

- Meratus Mountains, Loksado to Kandangan, 2 47'33 " S, 115 26'05" E to 2° 49'50" S, 115° 18'52"E, elevation ~70–200 m, roadside vegetation fringing secondary forest, plantations, or scrubby vegetation.
- Meratus Mountains, Kapayang village to Loksado, 2° 48'59" S, 115° 31'08" E, elevation ~350–500 m, primary forest (in various degrees of disturbance), secondary forest and vegetation along trails and small roads.

BORNEO: WEST KALIMANTAN

- Siduk to Nanga Tayap, 1° 22' S, 110° 12' E, low elevation (<100 m), recently cleared logging trail, unpaved, into primary forest.

BORNEO: SABAH

- Crocker Range, several sites, especially near Keningau, Majora, Senagang, Tambunan and Tikolod, 5° 27' N, 116° 03' E to 5° 51' N, 116° 17' E, elevation 450–1300 m, roadside vegetation fringing primary and secondary forest.
- Langanan, a waterfall area at elevation ~900 m, on upper Langanan trail at 6 03'41" N, 116 41'20" E, near Poring Hot Spring, hill dipterocarp forest.
- Luasong Forest Reserve (Tawau Division), 4 38' N, 117 24' E, elevation ~ 280 m, lowland dipterocarp forest, roadside, fringing mainly secondary forest.
- Madai Caves, Kunak, Lahad Datu-Tawau Highway (89 km from Tawau), 4° 44' N, 118° 08' E, elevation 100–200 m, secondary dipterocarp forest.
- Poring Hot Spring, 6° 03' N, 116° 43' E, lowland and hill dipterocarp forest (elevation up to 900 m), as well as secondary and primary forest [the data labels usually just say "Poring"].
- Road to Sandakan, roadside on road from Ranau to Sandakan, 5 42'59" N, 116 51'51" E, small forest remnant.
- Penampang, roadside, a few km from the village Penampang on the road through the Crocker Range to Tambunan, 5 54' N, 116 05' E, elevation ~300 m, lowland forest.
- Tawau Hills Park (Tawau Division), lowland dipterocarp rainforest, surrounded by secondary forest and plantations, 4° 24' N, 117° 54' E; most samples from elevation 300–500 m, also from disturbed vegetation in an open area between the secondary forest at the foot of Bukit Bombalai and the oil palm plantations close to park entrance.

BORNEO: SARAWAK

- Lambir Hills National Park, 4 12' N, 114 01' E, lowland, secondary and primary forest; also "Lambir"; near the park, on roadside, with sites "2 km Lambir", "3 km Lambir" and "8 km Lambir" referring to sites along the road in the direction of Miri.
- Santubong Park, on slopes of Mt Santubong, 1° 43'60" N, 110° 19'60" E, elevation 150 m, gaps in primary dipterocarp forest remnants.

PENINSULAR MALAYSIA

- Fraser's Hill, 3° 43' N, 101° 40' E, elevation ~1000 m, along tracks in hill and upper dipterocarp forest, primary forest and roadside in secondary forest.
- Genting Highlands, 3 25' N, 101 47' E, elevation 900–1000 m, roadside in hill and upper dipterocarp forest (data labels may just say "Genting").
- Gombak old road and upper and lower logging roads, near Ulu Gombak Forest Reserve, 3 19' N, 101 45' E, along roadside, old logging roads and tracks in lowland, secondary forest.
- Johor area, several sites, elevation <100 m, lowland secondary forest/vegetation; tracks along secondary or primary forest, and roadside vegetation, some fringing oil palm plantations.

- Malacca (a state): Kendong and near Tampin Hill (localities from collections made by I.H. Burkill prior to 1920).
- Pahang (a state), several sites near Kuantan, elevation <100 m, lowland forest and roadside vegetation, some fringing oil palm plantations. Some hill dipterocarp forest (Bukit Beserah: roadside going up mountain/hill along primary forest).
- Penang Island, specific localities unknown (from collections made by I.H. Burkill prior to 1920).
- Perak (a state), Straits Settlement near Tanjong Malim and Taiping Hills (from collections made by I.H. Burkill prior to 1925).
- Perak (a state), Cameron Highlands, S of Tanah Rata on road 59, elevation ~1400 m, roadside, originally hill dipterocarp forest (mostly transformed to tea plantations).
- Terengganu (a state), Bauk Hill, elevation <100 m, secondary forest and roadside vegetation.
- Pasoh Forest Reserve in Negeri Sembilan (a state), 2 59' N, 102 19' E, mainly trails and gaps in the interior of lowland primary forest; also Felda Pasoh, a series of villages very close to the Pasoh Forest Reserve, with partly open fields and areas of swampy natural vegetation.
- Rawang, with sites "6 km Rawang" and "8 km Rawang" referring to distance along the road from Rawang to Gombak, elevation 100–200 m, roadside in disturbed lowland, swampy forest.
- Sekinchan (Sekinchang, on some labels), 3 30' N, 101 06' E, at sea level, lowland peat swamp forest.
- Selandar forest, in Malacca (a state), erroneously listed as Singapore by Morrison (1921) (from collections of I.H. Burkill prior to 1920).
- Tioman Island, Pahang (a state), 2° 48'18" N, 104° 07'01" E, elevation 50–350 m range, along foot trail through primary forest.

RIAU ISLANDS (INDONESIA)

- Bintan Island, lowland, fringes of secondary/disturbed forest.

SINGAPORE

- Several sites associated with water catchment areas, especially Old Upper Thompson Road and Upper Peirce Reservoir, elevation <100 m, roadside along mature secondary forest.
- Bukit Timah Nature Reserve (label from a collection in 1989 says "Bukit Timah Forest Reserve").

SUMATRA

- Gunung Leuser area, including Ketambe (a village), ~3° 50' N, 97° 40' E, elevation <900 m, in secondary vegetation around open areas.
- Medan and Sibolangit areas, ~3° 40' N, 98° 20' E, elevation <100 m, mostly disturbed habitats along roadsides.

Taxonomy

***Coccus* Linnaeus**

urn:lsid:zoobank.org:act:D7AFF012-1B2A-4F9B-BA23-795DCC253C10

Coccus Linnaeus, 1758: 455. Type species: *Coccus hesperidum* L.

Lecanium Burmeister, 1835: 69. Unavailable name.

Taiwansaissetia Tao, Wong & Chang, 1983: 77; synonymy by Lin *et al.* 2013: 259.

A full synonymy for *Coccus* is available from ScaleNet (García Morales *et al.* 2017).

Adult females of all *Coccus* species from *Macaranga* share the features of areolations on the dorsal derm, a cluster of preopercular pores anterior to the anal plates, a broad submarginal band of a ventral tubular ducts, and pregenital disc-pores confined to the area lateral to the vulva. Prior to molecular phylogenetic studies, we considered erecting a new genus for these *Macaranga*-associated coccids but, as discussed in the Introduction above, their close genetic relationship to *C. hesperidum* (the type species of *Coccus*) made this action untenable, despite the morphological distinctness of the *Macaranga* coccid species from *C. hesperidum*. For example, adult

females of *C. hesperidum* lack ventral tubular ducts in the submarginal area of the body (prominent in the *Macaranga* coccids) and possess dorsal tubercles (lacking in the *Macaranga*-associated species).

Diagnosis for *Coccus* species associated with *Macaranga*.

Adult female. Unmounted material (Fig. 2). Insects oval to elongate oval, generally less than 3.0 mm at widest point. Colour in life variable, from white, brown, yellowish-brown to red; covered in a thin layer of wax, with texture either smooth or somewhat finely granulose. Insects rather flat, not becoming convex, often with dorsal elevations. Generally associated with tending ants, and living within hollow stems of *Macaranga* plants.

Slide-mounted material. Body circular, oval or elongate oval, up to 4.5 mm long, 3.1 mm wide at maturity.

Dorsum: Derm membranous, generally with conspicuous areolations covering whole dorsum; derm not becoming heavily sclerotised at maturity. Dorsal tubercles and pocket-like sclerotisations absent. Dorsal setae variable, each sharply spinose, with a clubbed or rounded apex, or very short and about the same length as diameter of its setal socket. Dorsal tubular ducts absent. Dorsal microducts small, appearing bilocular under high magnification, each situated in an areolation, and scattered rather evenly throughout dorsum (since only found in areolations). Simple pores present, scattered evenly on dorsum. Preopercular pores scarce to numerous, generally small (each 5–10 µm diameter), present in a small to large, usually elongate, cluster anterior to anal plates, numbering 1–35 pores. Anal plates together quadrate to pyriform, inner lobes generally well developed, with a membranous fold of tessellated texture; each anal plate with 3–26 dorsal setae, 2 hypopygial setae, 2 ventral fringe setae and 1–4 ventral subapical setae. Anal ring almost entire, bearing a total of 8 or 10 setae, with 1 pair (if 8 setae) or 2 pairs (if 10 setae) thinner than the rest (setae difficult to count as obscured by ano-genital fold and easily confused with anterior margin setae). Sclerotised rim around anal plates absent.

Margin: Eyespots present or absent, when present located on margin or slightly on dorsal submargin. Marginal setae variable, each usually flagellate or sharply spinose with apex either tapering to a point, bifid or fimbriate, present in 1–3 rows. Stigmatic setae distinct from marginal setae, usually well developed, generally totalling 3, rarely 1 but sometimes up to 4 setae per stigmatic cleft; each seta sharply to bluntly spinose, median seta generally longer than lateral setae, but sometimes all setae subequal in length. Stigmatic clefts generally well defined. Spiracular furrow (or stigmatic groove) with a band of spiracular pores 1–4 pores wide, totalling usually 20–40 pores (number of pores difficult to count on most specimens), each pore 4–6 µm wide and with 2–7 (mostly 5) loculi.

Venter: Ventral derm membranous. Ventral setae slender, longest on posterior abdominal segments anterior to vulva. Interantennal setae numbering 2 or 3 pairs. Ventral tubular ducts present in a narrow or broad submarginal band, with tubular ducts also present on both sides of mouthparts (but usually absent anteriorly), across prothoracic and mesothoracic segments, often also present across metathorax or around metathoracic coxae. Ventral microducts present, scattered evenly on venter. Pregenital disc-pores each with 5–10 loculi, restricted to a small area on each side of genital opening. Antennae each 5–8 segmented. Mouthparts normal for coccids; clypeolabral shield with 1 pair of setae; labium with 4 pairs of setae. Legs normal in structure but often small in relation to body size, without tibiotarsal sclerotisation; tarsal digitules thin, one of each pair slightly thicker than the other, each with apex knobbed; claw digitules both knobbed, one thicker than other; claw denticle absent. Spiracles normal, often each set in a spiracular depression. Spiracular pores each with 3–7 (mostly 5, rarely an occasional pore with 2) loculi.

First-instar nymph. We were able to examine the first-instar nymphs of three species of *Coccus*, *C. macarangae*, *C. penangensis* and *C. pseudotumuliferus*, collected from *Macaranga* at one locality in Brunei. These nymphs could not be identified to species, although there may be small differences in body size, but our sample sizes were small and all of the nymphs were from one locality. We identified the first-instar nymphs as belonging to a particular species if they were collected from under the venter of an identified adult female. This was important because often more than one *Coccus* species occurred inside each *Macaranga* plant. Only the first-instar nymph of *C. macarangae* has been described and illustrated in the taxonomic section below. There is no modern and detailed description of the first-instar nymph of the type species of *Coccus*, *C. hesperidum*, although Borchsenius (1957) has a short description and Annecke (1966) provides a taxonomic illustration with reasonable detail. The available first-instar nymphs of *Coccus* species from *Macaranga* resemble the nymph of *C. hesperidum* illustrated by

Annecke (1966) except that the latter is shown with spiracular pores of five loculi (four loculi in *Macaranga* nymphs) and quite straight marginal setae (there is a distinct bend at half-length in the marginal setae of *Macaranga* nymphs).

Slide-mounted material. Body oval to elongate oval, 330–490 µm long, 190–330 µm wide; stigmatic areas distinct, but sclerotised clefts absent.

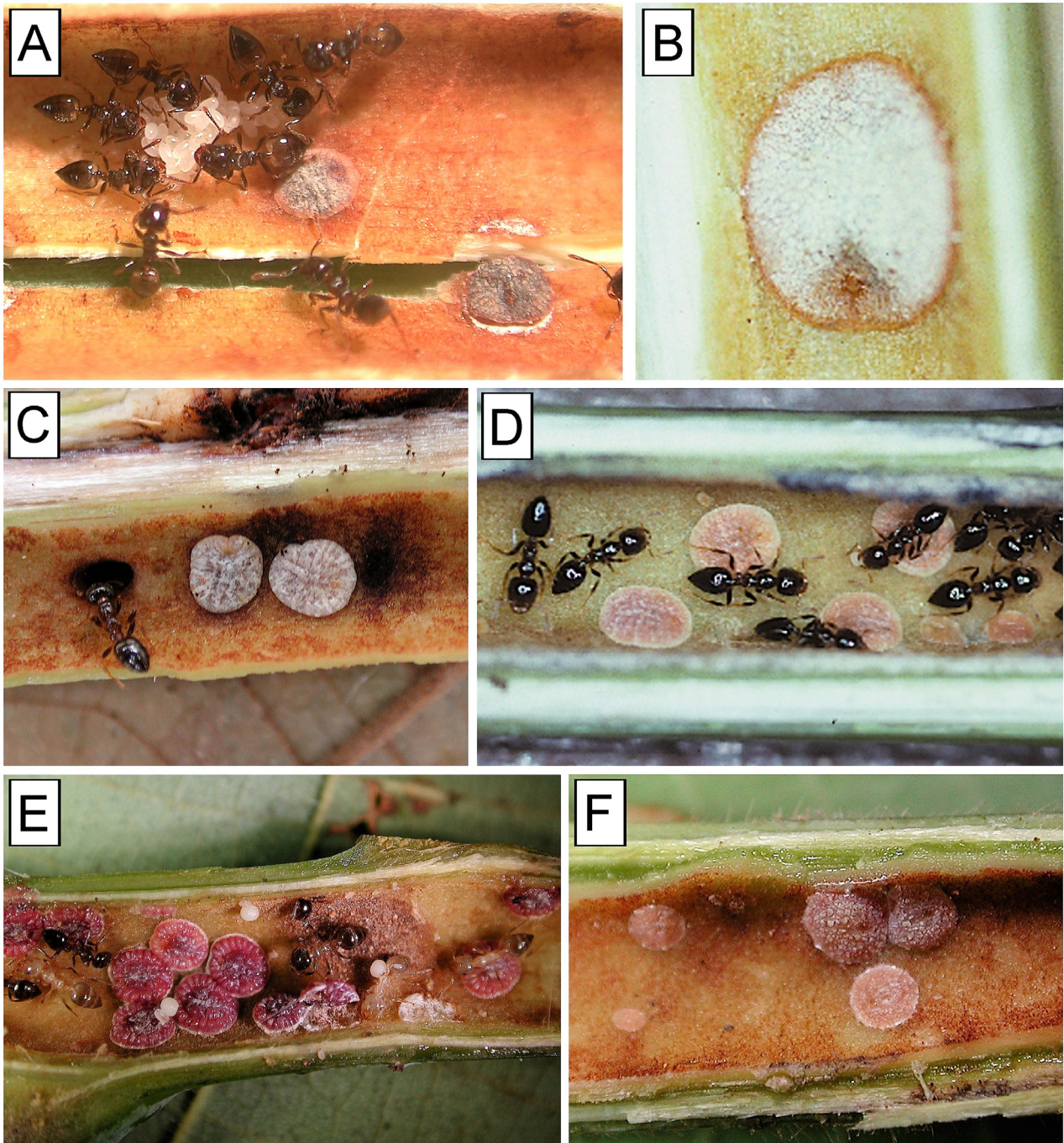


FIGURE 2. Live coccids and ants inside the cut stems of *Macaranga* plants: **A**, *C. macarangae* Morrison, in *M. winkleri*, Luasong, Sabah, Borneo (E. Linsenmair, 2003 BF #96); **B**, *C. macarangae*, in *M. beccariana*, Temburong, Brunei, Borneo (P.J. Gullan, PJG-B16); **C**, *C. penangensis* Morrison, in *M. glandibracteolata*, Poring, Sabah, Borneo (B. Fiala, 2003 BF #2); **D**, *C. penangensis*, in *Macaranga* sp., Temburong, Brunei, Borneo (P.J. Gullan, PJG-B31); **E**, *C. pseudotumuliferus* Gullan & Kondo sp. n., in *M. pearsonii*, Tawau, Sabah, Borneo (B. Fiala, 2003 BF #64); **F**, *C. secretus* Morrison, in *M. indistincta*, Tawau, Sabah, Borneo (B. Fiala, 2003 #95). All photographs taken by the collector specified in parentheses.

Dorsum. Derm membranous. Dorsal setae minute, present in 2 submedial longitudinal rows on thorax and first abdominal segment. Trilocular pores on head not detected, but instead a pair of tiny simple pores present. Dorsal microducts and preopercular pores absent. Anal plates each longer than wide, elongate triangular with anterolateral margin subequal in length to posterolateral margin, and anterior margin rounded; each plate with 2 small dorsal setae near apex, 1 inner margin seta and an apical seta up to 150 µm long. Anal ring bearing 6 setae.

Margin. Eyespots present as pigmented spots on margin. Marginal setae robust flagellate and curved to bend posteriorly, present in 1 row, with always 2 setae between anterior and posterior stigmatic areas, 12 (rarely 11 or 13) on head between anterior stigmatic areas, and 8 on each side of abdomen. Stigmatic setae numbering 3 in each cleft, thicker than marginal setae; median seta longest, 2.0–2.4 µm thick, spinose, slightly curved towards apex and apically rounded; lateral setae small, each ≤5 µm long, apically rounded.

Venter. Derm membranous. Ventral setae slender, 3 pairs of pregenital setae longest, other setae mostly minute, present in a marginal row around body and a submarginal row on each side of abdomen. Interantennal setae numbering 1 pair consisting of a single seta near base of each antenna. Ventral tubular ducts absent. Ventral microducts sparse, present submarginally with each side of body having 1 microduct between ventral setae on most abdominal segments, 2 microducts between anterior and posterior stigmatic areas, and 1 present between base of antenna and body margin. Disc-pores, except spiracular pores, absent. Antennae each 6 segmented; fleshy setae present on last 3 segments. Mouthparts typical of coccid nymphs. Legs normal; tarsal and claw digitules each with a small knobbed apex; claw with small denticle present. Spiracles normal; spiracular furrows each with 3 (anterior furrow) or 4 (posterior furrow) spiracular pores in a line.

Male instars. No adult or immature males were collected. One second-instar male and one pupa with a pharate adult male plus its prepupal exuviae were collected by PJG in Brunei from two different *Macaranga* plants but these belong to an undescribed species of *Myzolecanium* Beccari (Gullan *et al.* 1993; Hodgson 1994). No other collections examined for this study contained any male coccids, and no publications on the *Macaranga* coccids report males; therefore, it is assumed that these *Coccus* species are parthenogenetic.

Species recognition. Delimitation of the *Coccus* species from *Macaranga* is confounded by geographic variation, probably exacerbated by lack of gene flow due parthenogenetic reproduction (as discussed in the Introduction). Several morphological features of adult females that typically are used to separate other *Coccus* species can vary substantially within a species in the *Macaranga* coccids, e.g., the shape and length of the marginal body setae and the number and size of the preopercular pores found anterior to the anal plates. The recent availability of a phylogenetic reconstruction for these coccids based on nuclear genes (Quek *et al.* 2017) greatly assisted in recognising which morphological character states are taxonomically informative; thus, for this revision, we recognise each of the numbered clades presented in figure 3 of Quek *et al.* (2017) as a species, although four of them are based on very limited specimen sampling. In the case of clade 4 (*C.* near *circularis*) and clade 9 (*C.* near *macarangicolus*), we believe that these specimens are geographic variants of their respective species. *Coccus circularis* was described from a few specimens from Singapore (Morrison 1921) and *C. macarangicolus* was based on just a few specimens from Kuala Lumpur (Takahashi 1952), whereas the sequenced specimens are all from Borneo. We describe specimens of clade 3 (*C.* near *tumuliferus*), clade 7 (*C.* sp. Y) and clade 8 (*C.* sp. X) as three new species, below.

Specimens of one new species represented in clade 3 of Quek *et al.* (2017) exhibit morphological variation of cuticular features and their live appearance also varies (see under *C. pseudotumuliferus* below). This may have led H.-P. Heckroth (Heckroth *et al.* 1998; Heckroth, unpublished data) to recognise two morphospecies (*C. tumuliferus* var. C. 84 and C. 214) for specimens that we are assigning to a single species.

As typical for all coccids, species of *Coccus* from *Macaranga* have been described based solely on the morphology of the adult females. Third-instar females of these *Coccus* species can be very difficult to distinguish from their adult females because they can be similar in size and have similar body setae. However, immature female soft scales rarely have multilocular pores near the vulva and their antennae each can have one or more fewer segments than those of adult females.

Morphospecies C. 41. Specimens referred to by this code number in Heckroth *et al.* (1998) were reported as found almost exclusively on the Bornean endemic *M. winkleri* (section Winklerianae), which was inhabited by *Crematogaster* morphospecies 8. This ant species is not part of the *Crematogaster borneensis*-group and its placement is unclear (Feldhaar *et al.* 2016). All specimens of C. 41 (Heckroth collections numbers 41, 153 and 155) were collected in December 1992 in Lambir Hills National Park. All examined individuals of C. 41 are

unusual in having the diagnostic features of a third-instar female (no multilocular pores near the vulva and 6-segmented antennae) but usually a body of the typical size of an adult. We hypothesise that they are probably immature specimens of *C. penangensis*, which may have failed to moult quickly to the adult due to some unsuitability of the host *M. winkleri*. Heckroth *et al.* (1998) reported that *C. 41* never occurred in the same plant as *C. penangensis* (see their table 3, p. 436), although *C. penangensis* did occur on *M. winkleri* (fig. 1b, p. 434), and that *C. 41* was uncommon. An immature female of *C. macarangae* (ID based in 12S DNA) sent by B. Fiala (No. 96) collected from *M. winkleri* at Tawau Hills, Sabah, on 7 April 2001, looks adult-like due to its body size (more than 2 mm long) and well-developed dorsal areolations; however, it also has no multilocular pores near the vulva and has 6-segmented antennae. This suggests that *M. winkleri* may generally be a poor host for the development of these *Coccus* species.

Key to adult females of *Coccus* species associated with *Macaranga*

(Note: this key may be difficult to use unless the specimens are cleared thoroughly of body contents and their cuticle is well stained)

1. Dorsal setae (excluding marginal row) appearing absent but present and very short, most setae less than 2 times as long as width of setal socket, rarely setae near body margin up to 3 times as long as setal socket width, never as long as ventral setae 2
 - Dorsal setae clearly evident, most setae more than 3 times as long as setal socket width, as long or longer than most ventral setae, but may be shorter than long interantennal and pregenital setae 5
2. Marginal setae mostly fimbriate at apices. Anal plates with dorsal setae usually confined to posterior half of each plate *caviramicolus* Morrison
 - Marginal setae mostly tapering to a point, apices rarely bifurcate or fimbriate (except on some individuals of *C. tumuliferus*). Anal plates with dorsal setae usually present on posterior two-thirds of each plate. 3
3. Legs reduced, each smaller than mouthparts, hind trochanter + femur <80 µm long. Dorsum not covered with oval or circular dermal elevations. Anal plate setae robust, often almost cylindrical, and mostly 20–30 µm long. Antennae 6, rarely 5, segmented. *secretus* Morrison
 - Legs well developed, each much larger than mouthparts, hind trochanter + femur >130 µm long. Dorsum covered with oval or circular dermal elevations (Fig. 11), sometimes difficult to see on slide-mounted specimens. Anal plate setae tapered, even if robust, and 8–23 µm long. Antennae 7, rarely 6, segmented 4
4. Dorsal submarginal raised areas (humps) very rounded, almost always numbering 8 on each side of body plus 1 medially on head. Stigmatic clefts often each with just 1 long robust seta (≤25 µm long, frequently damaged or missing), sometimes 2 lateral setae (each 3–8 µm long), rarely 3 subequal very short setae (≤5 µm long). Apical antennal segment with a short (2–8 µm) or often no apical prolongation. *tumuliferus* Morrison
 - Dorsal submarginal raised areas oval or elongate, usually numbering 11, rarely 12, on each side of body plus 1 medially on head. Stigmatic clefts each usually with 3 setae of subequal length (mostly 7–18 µm long, often damaged or missing). Apical antennal segment with an apical prolongation almost always ≥10 µm long on at least 1 antenna. *pseudotumuliferus* Gullan & Kondo **sp. n.**
5. Dorsal setae knobbed, or with rounded apices, not tapering to a point. Marginal setae sharply spinose, apices never bifurcate or fimbriate. Hind trochanter + femur <100 µm long *macarangicolus* Takahashi
 - Dorsal setae with apices not knobbed or rounded, each tapering to a point. Marginal setae spinose, with apices either tapering to a point, bifurcate or fimbriate. Hind trochanter + femur >100 µm long. 6
6. Marginal setae in 2 rows, numerous, with 41–45 between stigmatic areas on each side of thorax, each seta sharply spinose with slightly bent tip. Dorsal setae long and flagellate, each 35–90 µm long. *lambirensis* Gullan & Kondo **sp. n.**
 - Marginal setae in 1 row, not numerous, with <32 setae between stigmatic areas on each side of thorax, at least a few and often most setae with apices fimbriate or bifurcate. Dorsal setae sharply spinose to flagellate but ≤40 µm long, usually much shorter 7
7. Anal plates each with 11–23 dorsal setae 8
 - Anal plates each with 3–11 (very rarely >9 and mostly <7) setae 9
8. Marginal setae mostly sharply spinose, occasionally with slight ‘twigging’ at apices. Lateral stigmatic setae each usually >15 µm long. *heckrothi* Gullan & Kondo **sp. n.**
 - Marginal setae with apices mostly bifurcate or fimbriate, rarely sharply spinose. Lateral stigmatic setae each usually <15 µm long *penangensis* Morrison
9. Dorsal setae rather abundant, sharply spinose, mostly with straight or bent apices, occasionally a few setae with apices bifurcate or fimbriate, each seta 15–40 µm long. Preopercular pores 5–11 µm wide, each generally larger than a pregenital disc-pore *macarangae* Morrison
 - Dorsal setae rather sparse, slender, with a flagellate apex, each 15–30 µm long. Preopercular pores usually ≤6 µm wide, each about same size as a pregenital disc-pore *circularis* Morrison

***Coccus caviramicolus* Morrison**

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(Fig. 3)

Coccus caviramicolus Morrison, 1921: 659.

Type material examined. Holotype: adult female, **SINGAPORE:** in hollow stems of *Macaranga* sp., date not given, coll. I.H. Burkill, 1(1) (USNM). **Paratypes: PENINSULAR MALAYSIA:** Malacca, Kendong, in hollow stems of *Macaranga triloba* [now correctly named *M. bancana*], date not given, coll. I.H. Burkill, 2(2) (USNM; only 1 of these paratypes seen); north of Malacca, foot of Tampin Hill, in hollow stems of *M. triloba* [now correctly named *M. bancana*], date not given, coll. I.H. Burkill, 3(1 adult female, 1 third-instar female, 1 first-instar nymph) (USNM).

Examined non-type material from original collections. PENINSULAR MALAYSIA: Malacca, Kendong, in hollow stems of *M. triloba* [now correctly named *M. bancana*], date not given, coll. I.H. Burkill, 1440, 1(5 adult females + 1 third-instar female; also 1 adult female of *C. secretus* under same coverglass) (BMNH). **SINGAPORE:** Botanic Garden, in hollow stems of *Macaranga*, date not given, coll. I.H. Burkill, No. X-2, 1(4) (BMNH). These two collections have the same data as two of the type collections listed above, but are not type material as explained in the Materials and Methods. Morrison (1921) acknowledges E.E. Green (of the BMNH) for sending him the material upon which he based the description of *C. caviramicolus*.

Other material examined. INDONESIA: Riau Islands, Bintan Island, lowland, ex *M. griffithiana*, 26 Aug. 1999, coll. S.-P. Quek, SPQ.012, DNA voucher 1(1). **PENINSULAR MALAYSIA:** Johor, Mawai camp, ~1.871° N, ~103.954° E, <100 m, ex *M. bancana*, *M. hypoleuca* & *M. griffithiana*, 5 & 7 Sept. 1999, coll. S.-P. Quek, SPQ.020, SPQ.021, SPQ.034 & SPQ.036, DNA vouchers 4(4); Johor, 119 km to Johor Baru from Mersing, <100 m, ex *M. griffithiana*, 16 Sept. 1999, coll. S.-P. Quek, SPQ.069, DNA voucher 1(1); Johor, Sedili, <100 m, ex *M. hullettii* & *M. griffithiana*, 5 Dec. 1999, coll. S.-P. Quek, SPQ.175 & SPQ.178, DNA vouchers 2(3); Negeri Sembilan, Felda Pasoh, <100 m, ex *M. griffithiana* & *M. hypoleuca*, 18 Sept. 1999, coll. S.-P. Quek, SPQ.072: DNA voucher 1(1) & SPQ.075a: DNA vouchers 3(2 adult females & 2 first-instar nymphs); Pahang, near Kuantan, Teluk Chempedak, lowland, ex *M. hypoleuca*, 14 Sept. 1999, coll. S.-P. Quek, SPQ.052-1 & SPQ.052-2, DNA vouchers 2(2); Pahang, near Kuantan, road to Prancing Falls, <100 m, ex *M. griffithiana*, 15 Sept. 1999, coll. S.-P. Quek, SPQ.053 & SPQ.056, DNA vouchers 2(2); 6 km Rawang, ex *M. griffithiana*, Feb. 1993, coll. H.-P. Heckroth, #206 1(1); 8 km Rawang, ex *M. griffithiana*, Feb. 1993 and Mar. 1993, coll. H.-P. Heckroth, #184: 3(3), #185: 4(3 adult females + 4 first-instar nymphs) & #190: 3(3); Terengganu, Bauk Hill, <100–200 m, ex *M. griffithiana*, 12 Sept. 1999, coll. S.-P. Quek, SPQ.044 & SPQ.045, DNA vouchers 2(2). **SINGAPORE:** Upper Peirce Reservoir, <100 m, ex *M. griffithiana*, 4 Oct. 1999, coll. S.-P. Quek, SPQ.092, DNA voucher 1(1); Old Upper Thompson Road, <100 m, ex *M. griffithiana*, 10 Oct. 1999, coll. S.-P. Quek, SPQ.095, DNA voucher 1(1).

Adult female. Unmounted material. “Flat, broad oval, approaching circular, dull brown, central area darker, dull or faintly shining, without or with a very slight secretory coating; ..” (Morrison 1921: 659).

Slide-mounted adult female (n=13, including holotype and 2 adult female paratypes; Fig. 3). Body oval to elongate oval, 1.8–3.4 mm long, 1.4–2.8 mm wide.

Dorsum. Derm (dd) with distinct round-to-oval areolations, with clear area of each areolation usually 10–25 µm in widest dimension and areolations largest towards margin, but rarely with any obvious sclerotised submarginal lines radiating inwards at right angles to margin. Dorsal setae (dset) very short, each about 2 µm long with rounded apex, scattered on dorsum. Simple pores (sp) each 2–3 µm wide, scattered evenly on dorsum. Preopercular pores (pop) each typically 4–6 µm wide, scarce, present in a small group of 4–8 anterior to anal plates. Dorsal microducts (dmic) in areolations each 2.0–2.5 µm wide, appearing bilocular under high magnification. Anal plates (anplt) each triangular with anterolateral margin usually much longer than posterolateral margin, width of each plate about half length, inner lobes well developed, with a tessellated texture, each plate 190–225 µm long, 75–110 µm wide, anterolateral margin 130–200 µm long, posterolateral margin 85–120 µm long; each plate with 16–26 dorsal setae (anpltset), each seta usually short, straight and robust, 5–15 (mostly <12) µm long, and setae usually confined to posterior half of each plate. Anal ring (ar) bearing 10 setae, each seta 60–100 µm long.

Margin. Eyespots situated slightly removed from dorsal margin, mostly not detected. Marginal setae (mset) in 1 row, most setae fimbriate at apices, each 10–43 (mostly about 25) µm long; with 15–28 (rarely <20) setae

between anterior and posterior stigmatic areas on each side of body. Stigmatic setae (stgset) well developed, spinose and tapering to pointed or rounded apices, numbering 3 (rarely 4) per cleft, median setae usually longest, typically 17–33 μm long, lateral setae each 10–29 μm long.

Venter. Derm membranous. Ventral setae (vset) slender, longest on posterior abdominal segments, each 17–90 μm long, elsewhere shorter, each 7–22 μm long. Interantennal setae in 2 pairs. Ventral tubular ducts (vtd) present in a broad submarginal band; each duct with outer ductule 15–20 μm long, inner ductule 15–23 μm long, and duct opening about 2 μm wide. Ventral microducts (vmic) each about 2 μm wide, scattered fairly evenly on venter. Pregenital disc-pores (pgp) each with 6–8 (mostly 6–7) loculi, each pore 6–7 μm wide. Antennae (ant) mostly 7 segmented (rarely 5 or 8 segmented), each 235–290 μm long; fleshy setae present on last 3 segments when 7 segmented, and on last 2 segments when 6 segmented. Clypeolabral shield 218–268 μm long, 183–238 μm wide; labium 85–108 μm long, 115–153 μm wide. Legs with hind trochanter + femur 160–190 μm long; hind tibia + tarsus 165–193 μm long; all tarsal digitules each 35–43 μm long; claw digitules each 22–28 μm long, claws each 22–26 μm long. Spiracles normal: anterior peritremes each 48–68 μm wide; posterior peritremes each 50–75 μm wide. Spiracular pores (spp) each 4–6 μm wide, with 3–7 (mostly 5) loculi.

Comments. Adult females of *C. caviramicolus* can be distinguished from all other species of *Coccus* known from *Macaranga* by having the combination of (i) extremely short dorsal setae (appearing absent); (ii) marginal setae ≤ 40 μm long and each with a fimbriate apex; (iii) anal plates together pyriform in shape; and (iv) the numerous (≥ 15), very short (5–8 μm) setae on each plate. They are most similar to the adult females of *C. pseudotumuliferus*, *C. secretus* and *C. tumuliferus* in having very short dorsal setae of length mostly less than two times width of setal socket, but differ in that their marginal setae are apically fimbriate (mostly tapering to a point in the other three species) and their anal plates together are pyriform (anal plates together are quadrate to subcircular in other three species).

Coccus caviramicolus has been recorded only from Singapore, Peninsular Malaysia and herein also from the Riau Islands of Indonesia. Our records for *C. caviramicolus* are mostly from *M. griffithiana*. Heckroth *et al.* (1998) recorded this species almost exclusively from secondary forest in Peninsular Malaysia and from five species of *Macaranga*, although most commonly on *M. griffithiana* (identified then as *M. motleyana* subspecies *griffithiana*). The host plants of *C. caviramicolus* are from both section *Pachystemon* and section *Pruinosae*.

***Coccus circularis* Morrison**

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(Fig. 4)

Coccus circularis Morrison, 1921: 665.

Type material examined. Holotype: adult female, **SINGAPORE:** in hollow stems of *Macaranga* sp., date not given, coll. I.H. Burkill, Holotype 1(1) (USNM). **Paratypes: SINGAPORE:** same data as holotype, 2(1 adult female + 1 first-instar nymph) (USNM); in hollow stems of *Macaranga triloba* [now correctly named *M. bancana*], date not given, coll. I.H. Burkill, 1396, 1(1) (USNM).

Examined non-type material from original collection. SINGAPORE: in hollow stems of *Macaranga griffithiana*, date not given, coll. I.H. Burkill, 1389, 1(2 adult females + 2 nymphs) (BMNH). These four BMNH specimens have similar data to the type collections listed above and one of the same Burkill collection numbers as provided by Morrison (1921) in his original description of this species, but they are not type specimens, as explained in the Materials and methods.

Other material examined: PENINSULAR MALAYSIA: Negeri Sembilan, Felda Pasoh, <100 m, ex *M. hypoleuca*, 18 Sept. 1999, coll. S.-P. Quek, SPQ.076, 1(1). **SINGAPORE:** Lower Peirce Reservoir, <100 m, ex *M. hypoleuca*, 10 Oct. 1999, coll. S.-P. Quek, SPQ.094, 1(1).

Other material examined. Coccus near circularis: BORNEO: Brunei, Batu Apoi Forest Reserve, 4° 33' N, 115° 09' E, 24 Aug. 1995, coll. P.J. Gullan, PJG-B47, 3(1 adult female & 13 first-instar nymphs); Sabah, Crocker Range, Keningau to Ulu Kimanis trail, 5.28° N, 116.05° E, 900 m, ex *M. glandibracteolata*, 19 Oct. 1999, coll. S.-P. Quek, SPQ.136a, DNA voucher 1(1); Sabah, Crocker Range, Tambunan to Kota Kinabalu Rd, 1000? m, ex *M. puberula*, 15 Oct. 1999, coll. S.-P. Quek, SPQ.098, DNA voucher 1(1); Sabah, Crocker Range, Tambunan to Kota

Kinabalu Rd, 1300 m, ex *M. petanostyla*, 24. Oct. 1999, coll. S.-P. Quek, SPQ.163, DNA voucher 1(1); Sabah, Poring, ex *M. glandibracheolata*, 17 Apr. 2001, coll. B. Fiala, #106, 6(6); Sabah, Poring Hot Springs, ex *M. depressa*, *M. motleyana* & *M. petanostyla*, no dates, coll. H.-P. Heckroth, #552, 573, 640, 1140 & 1410, 5(18) (FRIM); Sabah, Poring Hot Springs, ex *M. indistincta*, no date, coll. H.-P. Heckroth, #589, 1(1 on slide with 1 adult female of *C. pseudotumuliferus*) (FRIM); Sabah, Ranau, roadside, ex *M. beccariana*, no date, coll. H.-P. Heckroth, #539, 1(3) (FRIM).

Note. Specimens referred to as *Coccus* near *circularis* are all from Borneo and three of these specimens form Clade 4 in Quek *et al.* (2017, fig. 3). At our present state of knowledge, we consider these three specimens from the Crocker Range in Sabah (listed above) together with other specimens from Sabah and a specimen from Brunei, to be geographic variants of *C. circularis* (discussed below under Comments).

Adult female. Unmounted material. “Nearly to quite circular, dull grayish, appearing as if sprinkled with gray powder or dust; flat, but slightly ridged transversely about the middle and with low radiating ridges around the margin; anal cleft a little less than one-third the body length; extreme margin of body slightly elevated all the way around, forming a more or less distinct marginal ridge; ..” (Morrison 1921: 665).

Slide-mounted adult female (n=6, based on adult females from Singapore, including all 5 collected by Burkill; Fig. 4). Body circular to oval, 3.0–3.1 mm long, 2.6–3.1 mm wide.

Dorsum. Derm (dd) with numerous oval to circular areolations and with lightly sclerotised submarginal lines radiating inwards at right angles to margin. Dorsal setae (dset) slender, each with a flagellate apex, 15–30 µm long, scattered on dorsum. Simple pores (sp) each 2.5–3.0 µm wide, scattered evenly on dorsum. Preopercular pores (pop) each 4–6 µm wide, scarce (7 on holotype), present anterior to anal plates (not counted on most Singapore females but numbering 6–10 pores in non-Singapore females). Dorsal microducts (dmic) in areolations each about 2.0–2.5 µm wide, appearing bilocular under high magnification. Anal plates (anplt) each triangular with anterolateral margin either equal to or slightly longer than posterolateral margin, length of each plate 1.5–1.8 times width, inner lobes well developed, with a tessellated texture, each plate 170–185 µm long, 100–145 µm wide, anterolateral margin 110–160 µm long, posterolateral margin 115–130 µm long; each plate with 4–7 dorsal setae [females from Sabah with 6–11 setae; see Comments], each seta 15–30 µm long. Anal ring (ar) bearing 10 setae, each 85–113 µm long.

Margin. Eyespots present on dorsal margin. Marginal setae (mset) in 1 row, each seta sharply spinose, with a pointed or bifurcate or fimbriate apex, 17–38 µm long. Marginal setae between anterior and posterior stigmatic areas on each side of body totalling 6–12 [females from Sabah with 19–27 setae; see Comments]. Stigmatic setae (stgset) well developed, spinose with pointed apices, numbering 3 per cleft, median setae usually longest, each 17–40 µm long, lateral setae each 10–28 µm long.

Venter. Derm membranous. Ventral setae (vset) slender, prevulvar pairs longest, each 17–60 µm long, elsewhere shorter, each 10–23 µm long, with submarginal setae each 10–15 µm long. Interantennal setae in 2 or 3 pairs, each seta 10–25 µm long. Ventral tubular ducts (vtd) present in a broad submarginal band; each duct with outer ductule about 15 µm long, inner ductule 17–20 µm long, and duct opening about 2 µm wide. Ventral microducts (vmic) each about 2 µm wide, scattered fairly evenly on venter. Pregenital disc-pores (pgp) each with 5–8 (mostly 6 and 7) loculi, each pore 5–6 µm wide. Antennae (ant) each with 7, rarely 8, segments, 225–290 µm long; fleshy setae present on distal 3 segments. Clypeolabral shield 230–263 µm long, 230–255 µm wide; labium 90–100 µm long, 105–130 µm wide. Legs with hind trochanter + femur 165–185 µm long; hind tibia + tarsus 145–190 µm long; all tarsal digitules each 26–33 µm long; claw digitules each 20–30 µm long, each claw 20–25 µm long. Spiracles normal: anterior peritremes each 52–55 µm wide; posterior peritremes each 57–70 µm wide. Spiracular pores (spp) each 4 µm wide, with 3–5 (mostly 5) loculi.

Comments. Adult females of *C. circularis* can be distinguished from all other species of *Coccus* known from *Macaranga* by having the combination of (i) slender dorsal setae each >10 µm long and with a flagellate apex; (ii) marginal setae in a single row and with each seta spinose, 17–38 µm long and with a pointed, divided or fimbriate apex; and (iii) anal plates each with 4–7 setae, each seta ≤30 µm long. Adult females of *C. circularis* are most similar to the adult females of *C. macaranga* in having fewer than 10 setae on each anal plate and some or many marginal setae that are apically fimbriate or bifurcate, but differ from *C. macaranga* in that the dorsal setae are sparser, generally shorter (≤30 µm long) and more slender, and the preopercular pores are usually smaller (5–6 µm wide) and scarce (≤10) in *C. circularis* (*C. macaranga* with some dorsal setae up to 40 µm long and 20–50 preopercular pores each 5–11 µm wide).

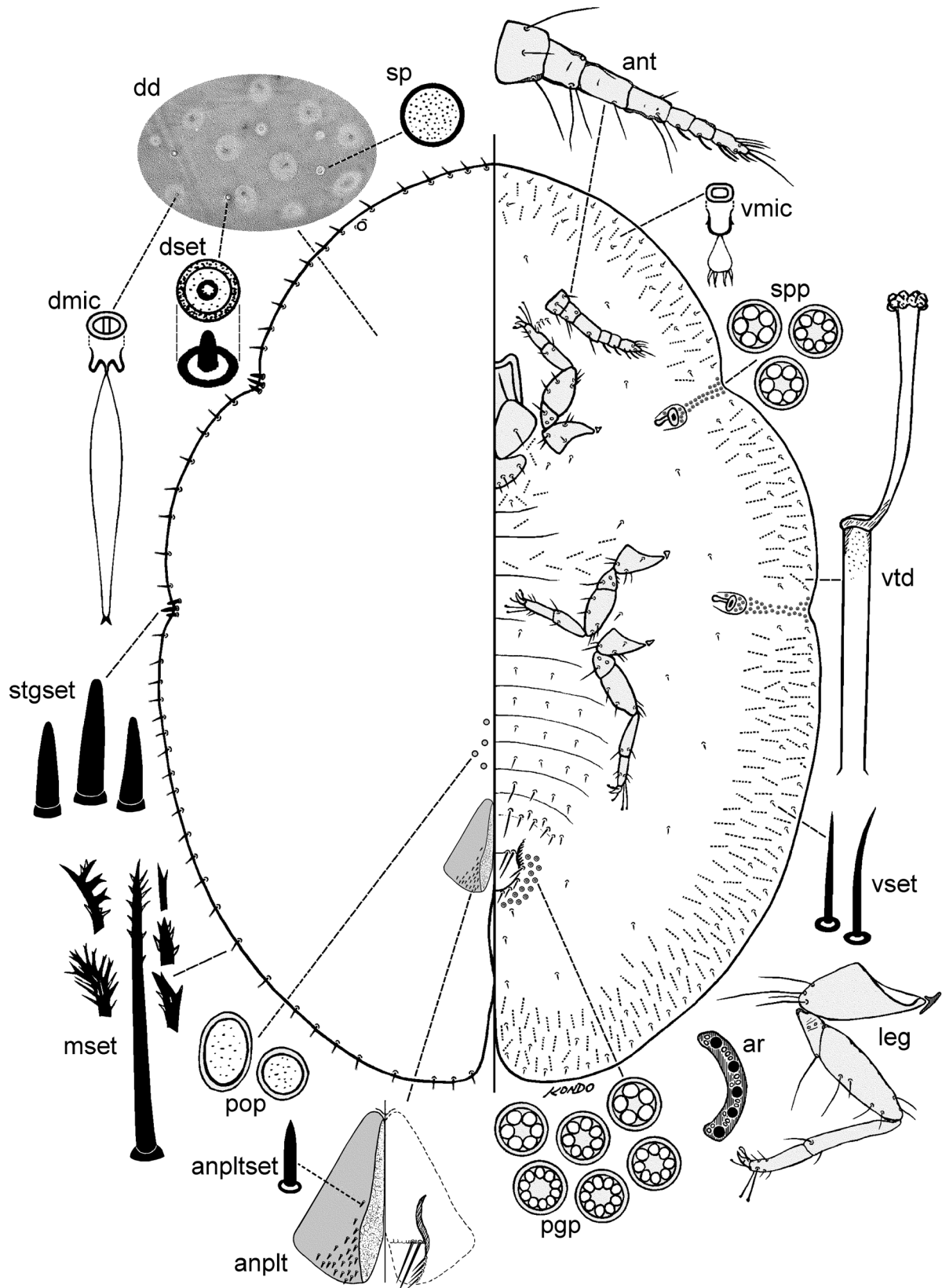


FIGURE 3. Adult female of *Coccus caviramicolus* Morrison. Abbreviations for enlargements: ar—anal ring, only right half illustrated (this ring lies medially under the anal plates and thus is not visible on the main illustration); anplt—anal plates; dd—dorsal derm; dmic—dorsal microduct; dset—dorsal seta; mset—marginal setae; pop—preopercular pores; pgp—pregenital disc-pores; sp—simple pore; spp—spiracular pores; stgset—stigmatic setae; vmic—ventral microduct; vset—ventral setae; vtd—ventral tubular duct.

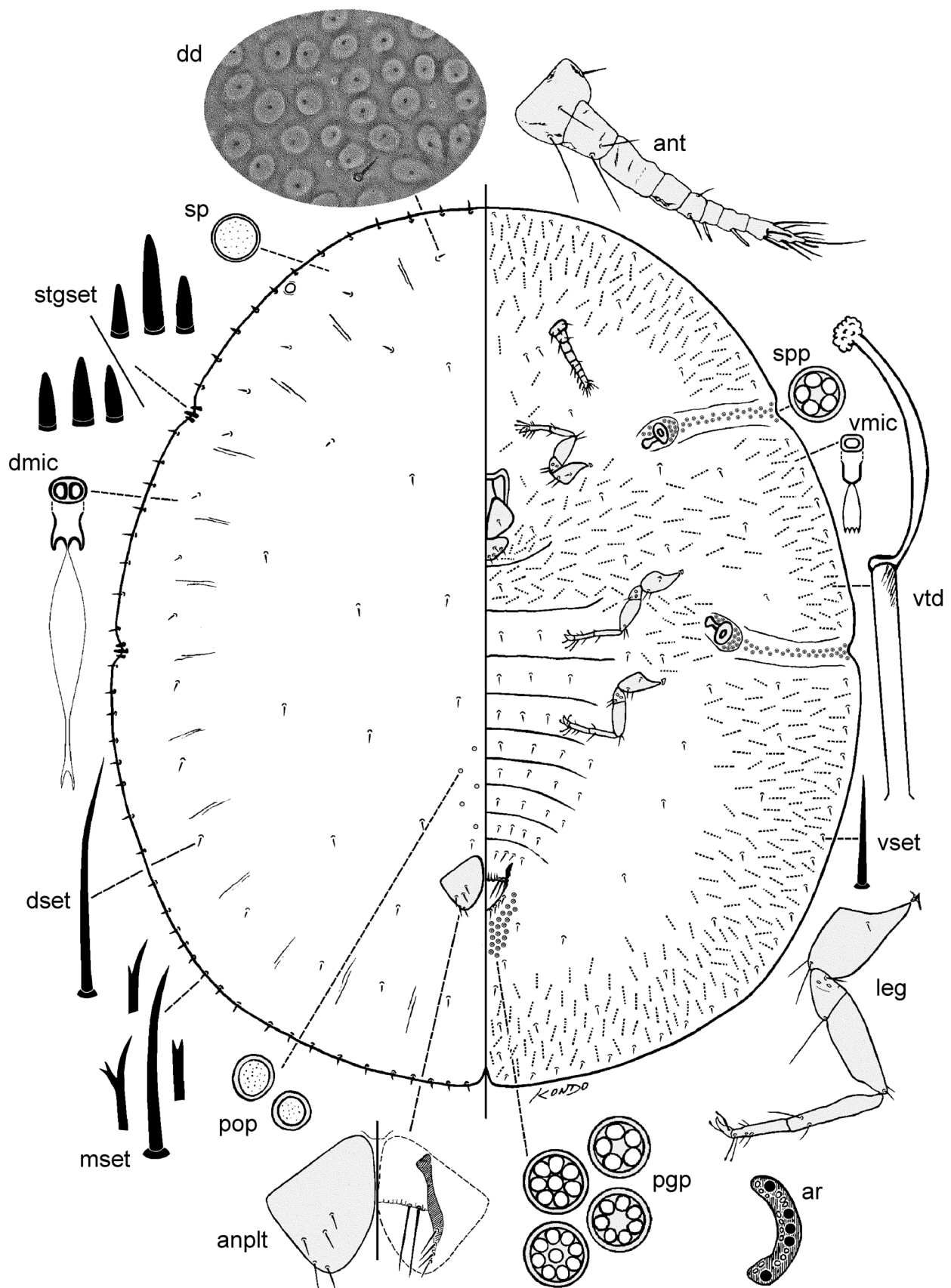


FIGURE 4. Adult female of *Coccus circularis* Morrison. Abbreviations as in Fig. 3.

Burkill's collections of this species were from two *Macaranga* species from Singapore. No specific locality was provided on the labels but, during Burkill's time, collections may have been made at various places on the island because there would have been more native vegetation present. Heckroth *et al.* (1998) mentioned only a single specimen of this species and provided no further information on it. Only specimens from three collections from the Crocker Range in Sabah on Borneo were sequenced for the phylogenetic reconstruction of Quek *et al.* (2017, fig. 3, Clade 4). These three adult females, referred to as *C.* near *circularis*, are very similar morphologically to specimens from Singapore and one from Peninsular Malaysia, but have a greater number (19–27) of marginal setae between the anterior and posterior spiracular clefts on each side of the body compared with the Singaporean and Peninsular Malaysian specimens (5–12 setae), generally shorter marginal setae (12–25 µm long, but mostly 13–20 µm, versus 17–38 µm long), shorter dorsal setae (10–15 µm versus 15–30 µm long) and often more dorsal setae on each anal plate (6–11 versus 4–7). The specimens from the Crocker Range were collected at higher altitude and are geographically separated from populations found in Singapore and Peninsular Malaysia. There are a number of other specimens from Sabah (from Poring Hot Springs and near Ranau) that seem to be *C.* near *circularis*, but most of the specimens are mature, damaged or heavily stained. The latter, however, appear similar to the three females from the Crocker Range, although their marginal setae appear shorter (generally 10–18 µm long). The single specimen from Brunei is also morphologically similar to the type specimens of *C. circularis* except that it has very few ventral tubular ducts on the head or the posterior abdomen. More samples are required for molecular analysis to determine the extent of any genetic variation among the regions.

***Coccus heckrothi* Gullan & Kondo sp. n.**

urn:lsid:zoobank.org:act:86F500BF-88D0-44F0-AE47-F4E76687E9AB

(Fig. 5)

“*Coccus* sp. Y”, Quek *et al.* 2017: 823.

Type material examined. Holotype: adult female, **BORNEO:** Sarawak, 2 km from Lambir Hills National Park in direction of Miri, in hollow stem of *Macaranga hosei*, Dec. 1992, coll. H.-P. Heckroth, #85, 1(1) (FRIM). **Paratypes: BORNEO:** same data as holotype, 12(12) and 2(2 third-instar females) (ANIC except 4 adult females to FRIM); Sarawak, 2 km Lambir NP, ex *M. hosei*, Dec. 1992, coll. H.-P. Heckroth, #47, 1(1 on slide with 1 adult female of *C. pseudotumuliferus*) (FRIM); Sarawak, 3 km Lambir, in hollow stem of *Macaranga trachyphylla* with *C. secretus*, Dec. 1992, coll. H.-P. Heckroth, #92, 3(3) (ANIC); Sarawak, 3 km Lambir, in hollow stem of *Macaranga hosei*, Feb. 1993, coll. H.-P. Heckroth, #50, 1(4) (FRIM); Sarawak, Lambir, ex *M. rufescens* & *M. hosei*, 3 Sept. 2001, coll. K. Murase, KM.s11 & KM.s22, DNA vouchers 2(2) (FDS); Sarawak: Lambir, ex *M. rufescens* (TI.s42 only) & *M. hosei*, 2–4 Aug. 2003, coll. T. Itioka, TI.s42, TI.s49, TIs.50, TI.s51 & TI.s52a, DNA vouchers 5(5) (FDS).

Other material examined. BORNEO: Sabah, Crocker Range, Keningau, 1100 m, ex *M. puberula*, 17 Oct. 1999, coll. S.-P. Quek, SPQ.113, DNA voucher 1(1); Sabah, Crocker Range, ex *M. pearsonii*, 13 Apr. 2001, coll. B. Fiala, #8 (TK0016), DNA voucher 1(1); North Kalimantan, Long Ampung, Sungai Anai trail, 700 m, 1° 42.964' N, 114° 56.943' E, ex *M. aëtheadenia* & *M. bancana*/*M. indistincta*, 9 Feb. 2005, coll. S.-P. Quek, SPQ.701, SPQ.704 & SPQ.705, DNA vouchers 3(3).

Note. Specimens of this new species form Clade 7, which is referred to as “*Coccus* sp. Y” in Quek *et al.* (2017, fig. 3). This clade has two very closely related subgroups, which are considered to be geographically separated populations—one from Sarawak and Sabah, and the other from North Kalimantan. This species appears to be common in and near Lambir Hills National Park in Sarawak.

Etymology. During his Ph.D. studies, Hans-Peter Heckroth recognised this species as *Coccus* morphospecies 85, but did not specifically refer to it in his publications on the *Macaranga* coccids (Heckroth *et al.* 1998, 2001). Here we name the species after him in recognition of his pioneering research on the *Macaranga* coccids.

Adult female. Unmounted material. Not seen.

Slide-mounted adult female (n = 10, all from Lambir and including holotype; Fig. 5). Body elongate oval, 1.9–3.5 (holotype 1.9) mm long, 1.4–2.9 (holotype 1.4) mm wide.

Dorsum. Derm (dd) with circular to oval areolations, mostly each 10–40 µm in greatest dimension, and with lightly sclerotised submarginal lines radiating inwards at right angles to margin, often obvious only on more mature

females. Dorsal setae (dset) slender, each 6–23 (mostly 10–15) μm long, sparsely scattered on dorsum. Simple pores (sp) each 2.5–3.2 μm wide, scattered evenly on dorsum. Preopercular pores (pop) each 4–7 (mostly 5) μm wide, present in an elongate cluster of 8–16 pores anterior to anal plates. Dorsal microducts (dmic) in areolations each 1.8–2.2 μm wide, appearing bilocular under high magnification. Anal plates (anplt) each triangular and typically with slightly convex margins, anterolateral margin always slightly longer than posterolateral margin, length of each plate 1.5–1.9 times width, inner lobes swollen, with a tessellated texture, each plate 165–183 μm long, 85–118 μm wide, anterolateral margin 125–158 μm long, posterolateral margin 105–133 μm long; each plate with 12–23 dorsal setae, each 18–25 μm long. Anal ring (ar) with 10 setae, each 90–120 μm long.

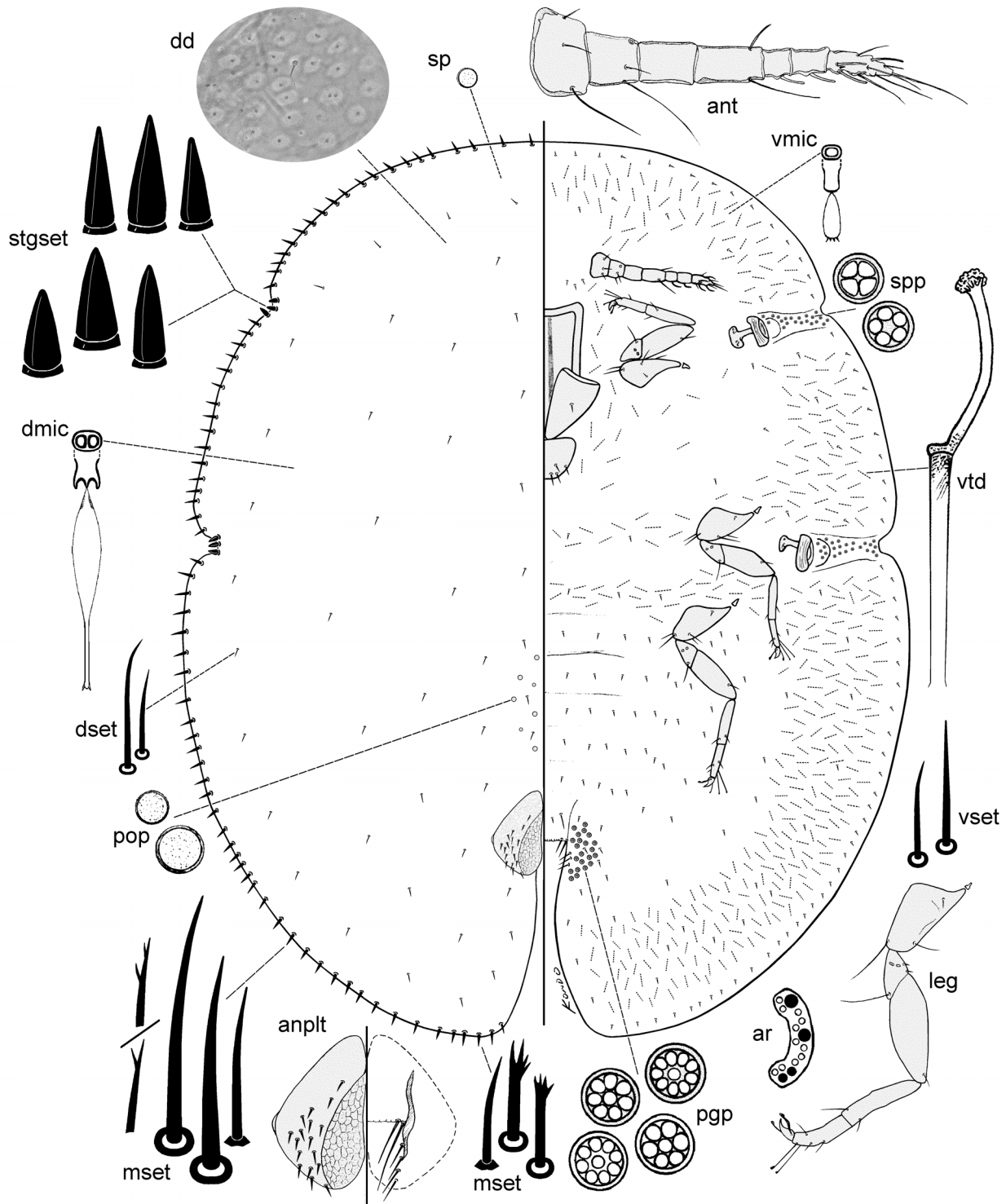


FIGURE 5. Adult female of *Coccus heckrothi* Gullan & Kondo sp. n. Abbreviations as in Fig. 3.

Margin. Eyespots, if visible, each 20–35 µm in maximum dimension, on margin but difficult to discern. Marginal setae (mset) in 1 row, most setae sharply spinose, rarely with apices fimbriate or bifurcate, each 12–45 (mostly 20–40) µm long, setae near anal cleft with tendency to be shorter and more fimbriate at apices than setae of rest of margin; with 10–21 setae between anterior and posterior stigmatic areas on side of body. Stigmatic setae (stgset) well developed, sharply spinose, typically numbering 3 per cleft, median setae longest, each 22–43 µm long, lateral setae each 12–28 (mostly >15) µm long.

Venter. Derm membranous. Ventral setae (vset) slender, with posterior-most prevulvar pair longest (each seta up to 55 µm long), elsewhere shorter, each 7–20 µm long. Interantennal setae numbering 3 pairs, each seta ≤20 µm long. Ventral tubular ducts (vtd) present in a broad submarginal band; each duct with outer ductule 15–20 µm long, inner ductule usually 15–18 µm long, and duct opening about 2 µm wide. Ventral microducts (vmic) each about 2 µm wide, scattered fairly evenly on venter. Pregenital disc-pores (pgp) each with 8–10 loculi, each pore 6–7 µm wide. Antennae (ant) 7 (rarely 6 or 8) segmented, each 225–270 µm long, fleshy setae present on last 3 segments. Clypeolabral shield 258–280 µm long, 205–255 µm wide; labium 110–120 µm long, 130–150 µm wide. Legs with hind trochanter + femur 150–185 µm long; hind tibia + tarsus 150–190 µm long; all tarsal digitules each 30–40 µm long; claw digitules each 20–30 µm long, claws each 24–32 µm long. Spiracles normal: anterior peritremes each 60–80 µm wide; posterior peritremes each 70–88 µm wide. Spiracular pores (spp) each 4–5 µm wide, typically with 5 loculi.

Comments. Adult females of *C. heckrothi* can be distinguished from all the other species of *Coccus* known from *Macaranga* by having the combination of (i) anal plates each with 12–23 dorsal setae, each seta 18–25 µm long; (ii) short, slender dorsal setae, each mostly 10–15 µm long and tapering to apex; and (iii) marginal setae in a single row and with each seta sharply spinose, mostly 20–40 µm long and rarely with apex fimbriate or bifurcate. The adult females of *C. heckrothi* are most similar to those of *C. penangensis* in the number of dorsal setae on each anal plate (11–23 in *C. penangensis*) and in having short and slender dorsal body setae (mostly <20 µm long in *C. penangensis*), but differ in that the marginal setae of *C. heckrothi* mostly have sharply pointed apices (mostly bifurcate or fimbriate in *C. penangensis*) and the lateral stigmatic setae are mostly >15 µm (usually <15 µm long in *C. penangensis*).

Coccus heckrothi has been collected only on the northern half of Borneo in North Kalimantan, Sabah and Sarawak, at a range of altitudes. The three adult females from North Kalimantan and the two from Crocker Range in Sabah differ from the females collected in the area of Lambir Hills in having shorter (10–17 µm) setae on the anal plates and, for two Kalimantan specimens, more numerous (20–40) preopercular pores. *Coccus heckrothi* has been found inside the hollow stems of seven *Macaranga* species belonging to both sections *Pachystemon* (three species) and *Pruinosae* (four species). Specimens of a species very similar to *C. heckrothi* were collected from *Crypteronia ?macrophylla* (Crypteroniaceae) in association with *Cladomyrma* ants in the Lambir Hills area (Achim Moog, #95/83, 23 Feb. 1995). The adult females of the coccids from *Crypteronia* differ from those of *C. heckrothi* in having longer (~25 µm) and more slender setae on the anal plates, shorter (~20 µm long) marginal setae, and smaller (~3 µm diameter) and more numerous (>20) preopercular pores. Mealybugs (Pseudococcidae) and coccids have been reported associated with *Cladomyrma* ants in the hollowed-out stems of *Crypteronia griffithii* in Peninsular Malaysia (Maschwitz *et al.* 1991) but the identity of those coccids is unknown.

***Coccus lambirensis* Gullan & Kondo sp. n.**

urn:lsid:zoobank.org:act:CBBDC76D-0BBC-4E83-86C3-9BB452F41D79

(Fig. 6)

“*Coccus* sp. X”, Quek *et al.* 2017: 823

This species was referred to as “*Coccus* sp. X” in Quek *et al.* (2017) (use of this name is not intended to be for nomenclatural purposes). The holotype listed below is the only known specimen and is a DNA voucher. Its nucleotide sequence data place it as sister to a specimen identified as *Coccus* near *macarangicolus* in figure 3 of Quek *et al.* (2017). *Coccus* X is sufficiently distinct morphologically to be described below as a new species.

Type material examined. Holotype: young adult female, **BORNEO:** Sarawak, Lambir Hills National Park, ex *Macaranga beccariana*, 11–15 Aug. 2002, coll. T. Itioka, TI.s39, DNA voucher 1(1) (FDS).

Etymology. This species is named after its collection locality, “Lambir”, referring to a site in primary forest in Lambir Hills National Park, called Taman Negara Bukit Lambir in Malay.

Adult female. Unmounted material. Unknown.

Slide-mounted adult female (n=1; Fig. 6). Body oval, 2.83 mm long, 2.56 mm wide.

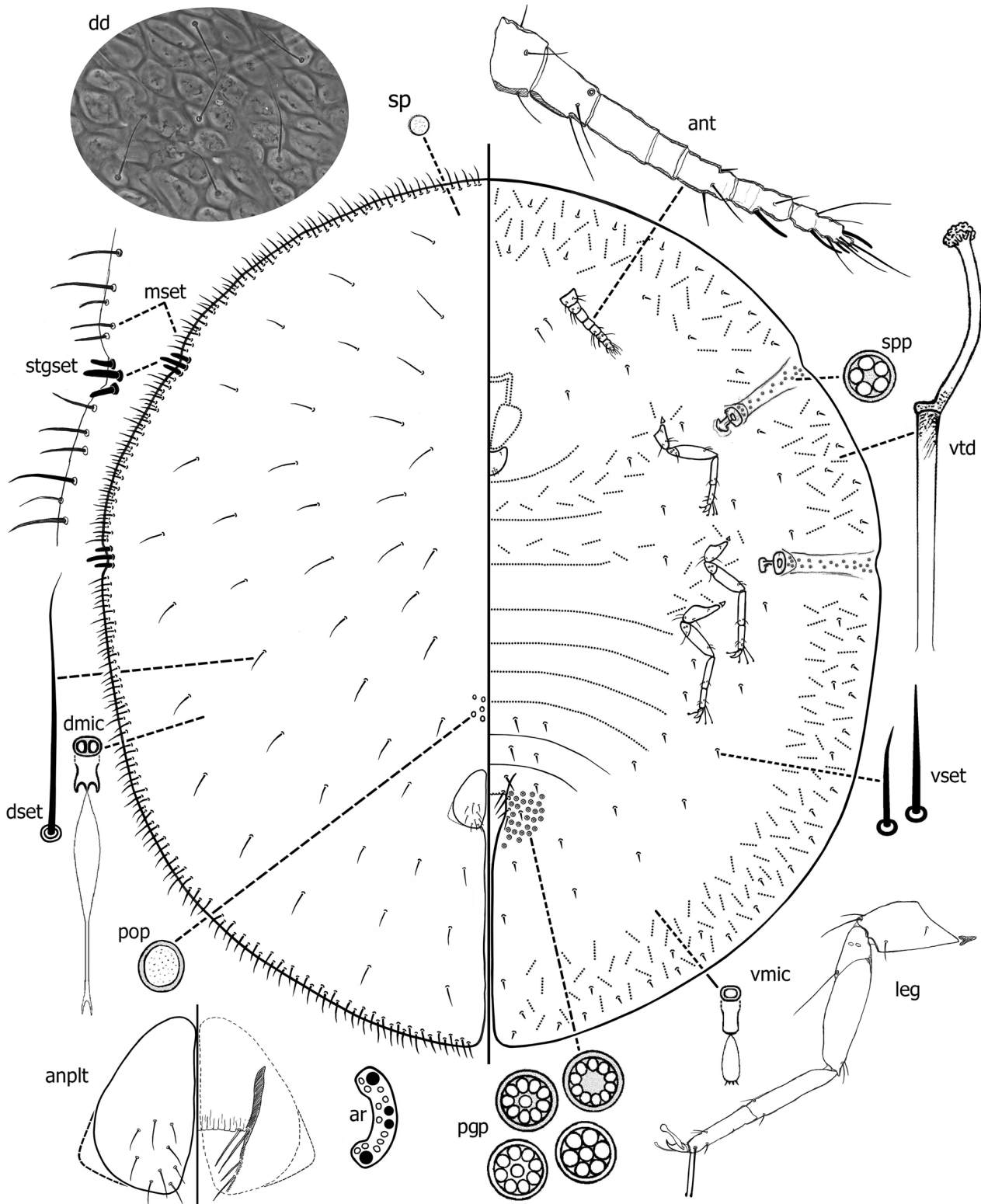


FIGURE 6. Adult female of *Coccus lambirensis* Gullan & Kondo sp. n. Abbreviations as in Fig. 3.

Dorsum. Derm (dd) membranous, with irregular polygonal areas abutting each other, each with a central areolation, and with faint submarginal wrinkle lines radiating inwards from margin. Dorsal setae (dset) slender, flagellate, each 35–88 μm long, longest from head to anterior abdomen and shortest on area lateral and posterior to anal plates. Simple pores (sp) each about 2.5 μm wide, scattered evenly on dorsum. Preopercular pores (pop) each 3.8–7.5 μm wide, 5 in number, present in a medial cluster anterior to anal plates. Dorsal microducts (dmic) in areolations each about 2.0–2.5 μm wide, appearing bilocular under high magnification. Anal plates (anplt) each triangular but outer apex of each plate distorted (perhaps during slide preparation), anterolateral margin 1.3 times longer than posterolateral margin and both margins slightly convex, length of each plate 1.8 times width, inner lobes normal, each plate 200 μm long, 110 μm wide, anterolateral margin 162–163 μm long, posterolateral margin 125 μm long; each plate with 9 flagellate dorsal setae, each 10–40 μm long. Anal ring (ar) probably bearing 10 setae (difficult to see), each 75–90 μm long.

Margin. Eyespots not detected. Marginal setae (mset) in 2 rows, each seta fairly robust and almost always flagellate at apex, 27–58 μm long, with 41–45 setae between anterior and posterior stigmatic areas on each of body. Stigmatic setae (stgset) well developed, spinose with rounded apices, apparently 3 in number, median setae longest, each 25–45 μm long, lateral setae each 15–35 μm long.

Venter (partially missing on holotype). Derm membranous. Ventral setae (vset) slender, mostly each 10–25 μm long, except prevulvar setae each up to 88 μm long. Interantennal setae missing due to damage to ventral cuticle. Ventral tubular ducts (vtd) present in a broad submarginal band; each duct with outer ductule 17–18 μm long, inner ductule about 20 μm long, and duct opening about 2 μm wide. Ventral microducts (vmic) each about 2 μm wide, scattered fairly evenly on venter. Pregenital disc-pores (pgp) each 6–8 μm wide and mostly with 10 (occasionally 6, 8 or 9) loculi. Antennae (ant) 7 segmented, each 320 μm long; fleshy setae present on last 2 segments. Clypeolabral shield missing; labium ~100 μm long, ~100 μm wide. Legs with hind trochanter + femur 172–175 μm long; hind tibia + tarsus 195–200 μm long; all tarsal digitules each 47–58 μm long; claw digitules each 20–23 μm long, claws each 27–28 μm long. Spiracles normal: anterior peritremes each 62–63 μm wide; posterior peritremes each 72–73 μm wide. Spiracular pores (spp) each 4–5 μm wide, usually with 5 (rarely 3 or 4) loculi.

Comments. The adult female of *C. lambirensis* can be distinguished from all other species of *Coccus* found on *Macaranga* by its possession of numerous marginal setae in two rows and its long flagellate dorsal setae, each mostly 40–80 μm long, that are longer than the dorsal setae of all other *Macaranga* coccids. Although adult females of *C. pseudotumuliferus* and *C. tumuliferus* group can have marginal setae in two rows, these two species have very short dorsal setae, each of about the same length as the diameter of its setal socket. In addition, in *C. lambirensis*, each dorsal areolation (clear area with microduct at centre) is situated on an irregularly shaped polygonal area with the abutting polygonal areas giving a cellular appearance to the derm, whereas in other species of *Coccus* from *Macaranga* the dorsal areolations are situated on uniform derm. Although molecular data placed *C. lambirensis* as sister to a specimen (SPQ.392 from Siduk in West Kalimantan) identified as *C. near macarangicolus*, it differs from that specimen and the examined syntype of *C. macarangicolus* (from Kuala Lumpur) in the length and shape of its dorsal setae as well as in the number of marginal setae (one row in *C. macarangicolus*). An unidentified adult female from Poring in Sabah (B. Fiala No. 30a) is similar to *C. lambirensis* in having a double marginal row of setae but its dorsal setae are shorter and slightly more robust and it has more than 30 preopercular pores anterior to the anal plates. The single adult female most similar to the holotype of *C. lambirensis* is from Panga in Thailand (probably Phang Nga province) on *Xylocarpus granatum* (Meliaceae), collected 8 March 2006 by Numakura and sent to TK. The latter unidentified specimen has similar dorsal and marginal setae to the holotype of *C. lambirensis*, with 45–57 marginal setae between the anterior and posterior stigmatic furrows on each side of body, but has more than 30 preopercular pores anterior to the anal plates. It is possible that *Macaranga* is not the usual host-plant genus of *C. lambirensis*.

***Coccus macarangae* Morrison**

urn:lsid:zoobank.org:act:30644D80-511B-4645-9BB3-FBFD0D4AC770

(Figs 2A & B, 7, 8)

Coccus macarangae Morrison, 1921: 663.

Type material examined. Holotype: adult female, **PENINSULAR MALAYSIA:** Selandar forest, in hollow stem

of *Macaranga*, date not given, coll. I.H. Burkill, Holotype 1(1) (USNM). **Paratypes:** same data as holotype, 1(6 first-instar nymphs) (USNM).

Examined non-type material from original collection. PENINSULAR MALAYSIA: Selandar forest, in hollow stem of *Macaranga triloba* [now correctly named *M. bancana*], date not given, coll. I.H. Burkill, 5-a or 6, two slides also with "1319" in pencil, 3(10) (BMNH). These three BMNH slides have similar data to the type collection listed above and one slide has the same Burkill collection number as provided by Morrison (1921) in his original description of this species, but they are not type specimens, as explained in the Materials and methods.

Other material examined: BORNEO: Brunei, Batu Apoi Forest Reserve, 4° 33' N, 115° 09' E, ex *M. beccariana*, *M. trachyphylla* & *Macaranga* sp., 3–30 Aug. & 1 Sept. 1995, coll. P.J. Gullan, PJG-B7: 12(8 adult females, 3 third-instar females & 8 first-instar nymphs), PJG-B10: 8(4 adult females, 1 pharate adult female, 1 third-instar female & 14 first-instar nymphs), PJG-B14: 4(4), PJG-B15: 5(5), PJG-B16: 9(9), PJG-B21: 8(8), PJG-B22: 2(2 adult females & 1 third-instar female on slide with *C. pseudotumuliferus*), PJG-B23: 1(1) (coll. P.S. Cranston), PJG-B25: 2(2), PJG-B29: 7(7), PJG-B46: 2(1 adult female & 1 third-instar female), PJG-B47: 7(3 adult females, 3 third-instar females & 1 third-instar female pharate in second-instar cuticle), PJG-B50: 1(1), PJG-B52: 3(2 adult females & 4 first-instar nymphs), PJG-B55: 1(1), PJG-B56: 1(1), PJG-B58: 4(3 adult females & 1 third-instar female) & PJG-B70: 3(3); Sabah, Crocker Range, Keningau to Ulu Kimanis trail, ~5.28° N, ~116.05° E, 1100 m, ex *M. angulata*, 19 Oct. 1999, coll. S.-P. Quek, SPQ.133, DNA voucher 1(1); Sabah, Crocker Range, near Majora, ~500 m, ex *M. indistincta*, 16 Oct. 1999, coll. S.-P. Quek, SPQ.108a, DNA voucher 1(1); Sabah, Crocker Range, Tambunan to Kota Kinabalu Rd, Rafflesia Reserve, 1200 m, *M. angulata*, 15 Oct. 1999, coll. S.-P. Quek, S.-P. Quek, SPQ.099, DNA voucher 1(1); Sabah, Crocker Range, forest behind Tambunan, 600 m, *M. indistincta*, 18 Oct. 1999, coll. S.-P. Quek, S.-P. Quek, SPQ.123, DNA voucher 1(1); Sabah, Crocker Range, Tambunan to Trusmadi trail, 1200 m, *M. angulata*, 23 Oct. 1999, coll. S.-P. Quek, S.-P. Quek, SPQ.156, DNA voucher 1(1); Sabah, Crocker Range, ex *M. hullettii*, 13 Apr. 2001, coll. B. Fiala, #13 (TK0017), DNA voucher 1(1); Sabah, Luasong, ex *M. winkleri*, 4 Sept. 2003, coll. B. Fiala, #96, 5(5) (2 ANIC, 3 FRIM); Sabah, Ranau, Langanan [waterfall], ex *M. depressa* [now correctly named *M. angulata*], Feb. 1992, coll. B. Fiala, #23a, 2(2); Sabah, Penangpang [=Penampang], roadside, ex *M. bancana*, 28 Mar. 2002, coll. B. Fiala, #135 (TK0095), DNA voucher 1(1); Sabah, Poring, ex *M. angulata*, 25 Mar. 2002, coll. B. Fiala, #110 (TK0100), DNA voucher 1(1); Sabah, Poring, ex *M. winkleri*, 18 Apr. 2001, coll. B. Fiala, #161 (TK0045), DNA voucher 1(1); Sabah, Poring, ex *M. ?indistincta*, 20 Feb. 1992, B. Fiala, #32a, 2(1 adult female & 1 third-instar female); Sabah, Tawau, road to Madai Caves, ex *M. motleyana*, 11 Mar. 2002, coll. B. Fiala, #4 (TK0108) & #5 (TK0107), DNA vouchers 2(2); Sabah, Tawau Hills, ex *M. kingii* [now identified as *M. lamellata*] & *M. winkleri*, 4 & 7 Apr. 2001, coll. B. Fiala, #62 (TK0024) & #96 (TK0032), DNA vouchers 2(2); Sarawak, Lambir, ex *M. near kingii* [now identified as *M. lamellata*], 14 Feb. 1992, B. Fiala, #37a, 2(2) (1 ANIC, 1 FRIM); Sarawak, Lambir, ex *M. beccariana*, Feb. 1992, coll. B. Fiala, #51a, 2(2); Sarawak, Lambir, ex *M. hullettii*, 26 Feb. 1992, coll. B. Fiala, #70a, 3(3); Sarawak, Lambir, ex *M. hypoleuca*, Feb. 1992, coll. B. Fiala, #71a, 3(3); Sarawak, 8 km Lambir NP, ex *M. lamellata*, Dec. 1992, coll. H.-P. Heckroth, #109, 2(2); Sarawak, Miri, Lambir Nat. Park, ~400 m, ex *Macaranga* sp. [now identified as *M. lamellata*], 27 Sept 1993, coll. A. Moog, #93/172, 3(3). **PENINSULAR MALAYSIA:** Fraser's Hill, ex *M. hosei* & *M. hullettii*, Mar. 1993, coll. H.-P. Heckroth, #274, #281 & #289, 6(6) (4 ANIC, 2 FRIM: #281); Pasoh, ex *M. hosei*, Mar. 1992, coll. B. Fiala, #132a & #168a, 3(3); Pasoh, ex *M. hypoleuca*, 6 Feb. 1992 & Mar. 1992, coll. B. Fiala, #105a: 4(1 adult female & 3 third-instar females) & #193a: 1(1). **SUMATRA:** Sibolangit, ~3° 40' N, ~98° 20' E, ex *M. bancana*, 23 Oct. 1992, coll. U. Maschwitz, sent by B. Fiala, #7a, 2(2).

Material examined from non-Macaranga host plants: BORNEO: Sabah, Ranau, Poring Hot Springs, ~700 m, in domatium of *Myrmeconauclea* sp. (Rubiaceae), 24 Mar. 1995, coll. A. Moog, #95/149, 1(1). **PENINSULAR MALAYSIA:** Selangor, Ulu Gombak, ex hollow stem of *Ryparosa fasciculata* (Achariaceae) in association with *Cladomyrma ?petalae*, 20 Sept. 1993, coll. A. Moog, #93/161, 4(4); Selangor, Ulu Gombak, ex hollow stem of *Strychnos vanprukii* (Loganiaceae) in association with *C. ?petalae*, 7 Mar. 1993, coll. A. Moog, #93/111, 2(2); Selangor, Ulu Gombak, in *Lepisanthus tetraphylla* (Sapindaceae) in association with *Crematogaster* ants, 28 Mar. 1994, coll. G. Riedel, #94-125.2, 1(1); Selangor, Ulu Gombak, in *Saraca thaipingensis* (Fabaceae) in association with *Crematogaster* ants, 25 Apr. 1994, coll. G. Riedel, #94-160.2, 3(3).

Adult female. Unmounted material. "Short oval, pale reddish brown, darker in middle, flat, with faint radiating ridges near margin; dorsal surface appearing naked, possibly with a very thin film of secretion; .." (Morrison 1921: 663). Morrison's description of probably dried adult females from Singapore agrees fairly well

with live specimens photographed in Borneo (Fig. 2A & B). Adult females from *M. winkleri* in Sabah (Fig. 2A) were orange-brown with some whitish waxy dorsal secretion and ridges radiating inwards from the margin. The amount of dorsal waxy secretion appears to increase as females age but the body margin remains largely devoid of wax, as shown by a mature female from *M. beccariana* in Brunei (Fig. 2B).

Slide-mounted adult female (n=18, including holotype and 4 of Burkill's specimens from Selandar forest; Fig. 7). Body oval to elongate oval, body often truncated anteriorly on head, 2.0–4.4 mm long, 1.3–3.1 mm wide.

Dorsum. Derm (dd) membranous, areolated and with faint submarginal wrinkle lines radiating inwards at right angles to margin. Dorsal setae (dset) mostly sharply spinose, occasionally with a few setae with open divided apices, each 15–40 (mostly 25–35) μm long, scattered on dorsum. Simple pores (sp) each 2.0–2.5 μm wide, scattered evenly on dorsum. Preopercular pores (pop) each 5–11 μm wide, present in a group of 20–50 anterior to anal plates. Dorsal microducts (dmic) in areolations each about 2–3 μm wide, appearing bilocular under high magnification. Anal plates (anplt) each triangular, anterolateral margin subequal to posterolateral margin (ratio 0.9–1.2) and posterolateral or both margins usually slightly convex, length of each plate 1.4–1.9 times width, inner lobes swollen, with a tessellated texture, each plate 130–145 μm long, 80–103 μm wide, anterolateral margin 85–120 μm long, postero-lateral margin 85–115 μm long; each plate with 3–4 dorsal setae, each 20–40 mm long. Anal ring (ar) bearing 10 setae [Morrison (1921: 664) said apparently 8 setae, but these setae are difficult to see], each 100–135 μm long.

Margin. Eyespots present slightly removed from dorsal margin, each 17–23 μm in maximum dimension, often not detected or hard to detect. Marginal setae (mset) fimbriate to sharply spinose, present in 1 row, each seta 10–30 μm long, with 7–30 (mostly 12–24) setae between anterior and posterior stigmatic areas on each side of body. Stigmatic setae (stgset) well developed, numbering 3, lanceolate to tapered spinose with rounded apices, much thicker than marginal setae, bases often swollen, median setae longest, each 18–43 μm long, lateral setae each 7–25 (mostly 12–20) μm long.

Venter. Derm membranous. Ventral setae (vset) slender, with most posterior prevulvar pair longest (each seta 50–70 μm long), elsewhere shorter, each 7–35 μm long. Interantennal setae numbering 2 pairs, each seta ≤ 20 μm long. Ventral tubular ducts (vtd) present in a broad submarginal band; each duct with outer ductule 16–19 μm long, inner ductule 13–20 μm long, and duct opening about 2 μm wide. Ventral microducts (vmic) each about 2 μm wide, scattered fairly evenly on venter. Pregenital disc-pores (pgp) each with 5–10 (mostly 7 and 8) loculi, and each pore 6–7 μm wide. Antennae (ant) 7–8 (mostly 8) segmented, each 200–275 μm long; fleshy setae present on last 3 segments. Clypeolabral shield 240–290 μm long, 180–230 μm wide; labium 80–100 μm long, 135–155 μm wide. Legs with hind trochanter + femur 113–145 μm long; hind tibia + tarsus 120–163 μm long; all tarsal digitules each 25–37 μm long; claw digitules each 17–25 μm long, claws each 20–25 μm long. Spiracles normal: anterior peritremes each 60–93 μm wide; posterior peritremes each 65–100 μm wide. Spiracular pores (spp) each 4–5 μm wide, with 3–5 (mostly 5) loculi, with an occasional pore with 6 or more loculi.

Comments. Adult females of *C. macaranga* can be distinguished from all other species of *Coccus* known from *Macaranga* by having the combination of (i) sharply spinose dorsal setae each mostly 25–30 μm long but a few can be up to 40 μm long; (ii) marginal setae in a single row, with each seta 10–30 μm long with apex fimbriate to sharply spinose; and (iii) anal plates each with 3 or 4 setae, each mostly 20–30 (rarely up to 40) μm long. Adult females of *C. macaranga* are most similar to the adult females of *C. circularis* in having fewer than 10 setae on each anal plate and many marginal setae that are apically fimbriate or bifurcate, but differ from *C. circularis* in that the dorsal setae are sparser, generally longer (up to 40 μm long) and less slender and the preopercular pores are more numerous (20–50) and usually larger (5–11 μm wide) in *C. macaranga* (dorsal setae 15–30 μm long with flagellate apices and preopercular pores scarce (≤ 10) and 5–6 μm wide in *C. circularis*).

Coccus macaranga was poorly represented in the molecular phylogeny of Quek *et al.* (2017), although it appears to be a common and widespread species that is found inside the hollow stems of *Macaranga* species belonging to each of the three myrmecophytic sections of the genus. It also occurs in the hollow stems of several other myrmecophytic genera, namely *Lepisanthus*, *Myrmeconuclea*, *Ryparosa*, *Saraca* and *Strychnos*, each belonging to a different plant family (refer to 'Material examined' list above). Adult female coccids from these different hosts showed no consistent differences from females collected from the hollow stems of *Macaranga*. Morphological variation in the number and size of the preopercular pores was noted among *Macaranga*-associated adult females of *C. macaranga*. The length of the dorsal setae also sometimes varied, with a few females having slightly shorter (15–20 μm) and others slightly longer (often 30–40 μm) setae than the typical length of 25–30 μm .

One female from Tawau Hills in Sabah collected from *M. winkleri* (DNA voucher TK0032, coll. B. Fiala, #96) is unusual in having 6-segmented antennae and few pregenital disc pores near the vulva but was confirmed as *C. macarangae* based on *12S* sequences (T. Kondo & L.G. Cook, unpublished data).

First-instar nymph. Slide-mounted material (n=10, all from Brunei, Borneo; Fig. 8). Body oval to elongate oval, body often truncated anteriorly on head, 370–460 µm long, 205–280 µm wide.

Dorsum. Derm membranous. Dorsal setae (dset) extremely difficult to see and appearing absent except under x100 objective under oil; each seta very short, at most 1 µm long, in perhaps 4 pairs submedially on thorax and first abdominal segment. One pair of minute simple pores (sp) present on head, but difficult to see except with x100 objective under oil. Preopercular pores and dorsal microducts absent. Anal plates each elongate triangular, 42–58 µm long, 20–33 µm wide, anterolateral margin 25–40 µm long, posterolateral margin 27–40 µm long; each plate with 2 dorsal setae each 10–12 µm long, positioned one each side of long apical seta, 110–124 µm long, plus 1 short inner margin seta. Anal ring (ar) 17–20 µm wide, bearing 6 setae, each 48–62 µm long.

Margin. Eyespots present as pigmented spots on margin, each 9–12 µm in maximum dimension. Marginal setae (mset) flagellate and with distinct bend at about half-length, each seta 10–15 µm long, present in 1 row, with always 2 setae between anterior and posterior stigmatic areas on each side of body, 12 (rarely 13) on head between anterior stigmatic areas and 8 on each side of abdomen with most posterior seta always straight. Stigmatic setae (stgset) numbering 3 in each cleft, thicker than marginal setae, median seta longest, 13–20 µm long, and spinose with rounded apex, lateral setae very small and rounded at apices, each 2–5 µm long.

Venter. Derm membranous. Ventral setae (vcs) as follows: short setae, each 2–3 µm long, present in a marginal and a submarginal longitudinal row of 7 setae on each side of abdomen, with 3 pairs of longer setae (called prevulvar setae on adult female), each 20–35 µm, submedially on posterior abdominal segments; a few setae similar to those on margin of abdomen present marginally on each side of mesothorax and metathorax; 1 pair of ventral cephalic setae (vcs), each 2–4 µm long, situated near apex of head; 1 pair of interantennal setae, each about 30 µm long, between bases of antennae. Ventral tubular ducts absent. Ventral microducts (vmic) each about ~1 µm wide, very few, present submarginally around body, between each pair of setae on abdomen, 2 located submarginally between anterior and posterior stigmatic areas, and 1 present between base of antenna and body margin, on each side. Abdominal disc-pores absent. Antennae 6 segmented, each 95–112 µm long; fleshy setae present on last 3 segments. Clypeolabral shield 65–90 µm long; labium 25–30 µm long, with 2 pairs of apical setae. Legs normal; hind trochanter + femur 50–62 µm long; hind tibia + tarsus 53–65 µm long; tarsal digitules each 15–27 µm long, one of each pair slightly thicker than other, each with a small knobbed apex; claw digitules each 10–14 µm long, both knobbed, one thicker than other; claws each 10–14 µm long, with small denticle present (only easily visible with x100 objective). Spiracles normal: peritremes each 4–6 µm wide. Spiracular pores (spp) each ~2 µm wide, with 4 loculi; spiracular furrows each with 3 or 4 pores in a line.

***Coccus macarangicolus* Takahashi**

urn:lsid:zoobank.org:act:9873F7EA-9473-4B56-B276-4B26D519309F
(Fig. 9)

Coccus macarangicolus Takahashi, 1952: 14.

Type material examined. Lectotype (here designated): adult female, **PENINSULAR MALAYSIA**: Kuala Lumpur, ex *Macaranga*, 26 Mar. 1944, coll. R. Takahashi, BMNH 1955-812, 1(1) (BMNH). Originally, this slide was deposited in the Selangor Museum, Kuala Lumpur, Malaysia, but after the loss of that institution, the remaining insect collections were sent to the BMNH in 1955, as documented by Williams (2017). Takahashi did not specify how many slides were prepared, but his description appears to have been based on a single adult female, which almost certainly is the one now in the BMNH. We believe that no other syntypes of *C. macarangicolus* exist. We have checked for other Takahashi specimens of this species in the Department of Agriculture Malaysia in Kuala Lumpur, where some of Takahashi's mealybug specimens are deposited (Sartiami *et al.* 2017), as well as in the Forest Research Institute Malaysia in Kuala Lumpur and in digital databases at the Taiwan Agriculture Research Institute in Taiwan and the University of Hokkaido in Japan. The envelope of the BMNH syntype has a handwritten note: “Probably young of *C. macarangae* Morr.”; TK determined this specimen to be an adult female as it has multilocular pores near the vulva.

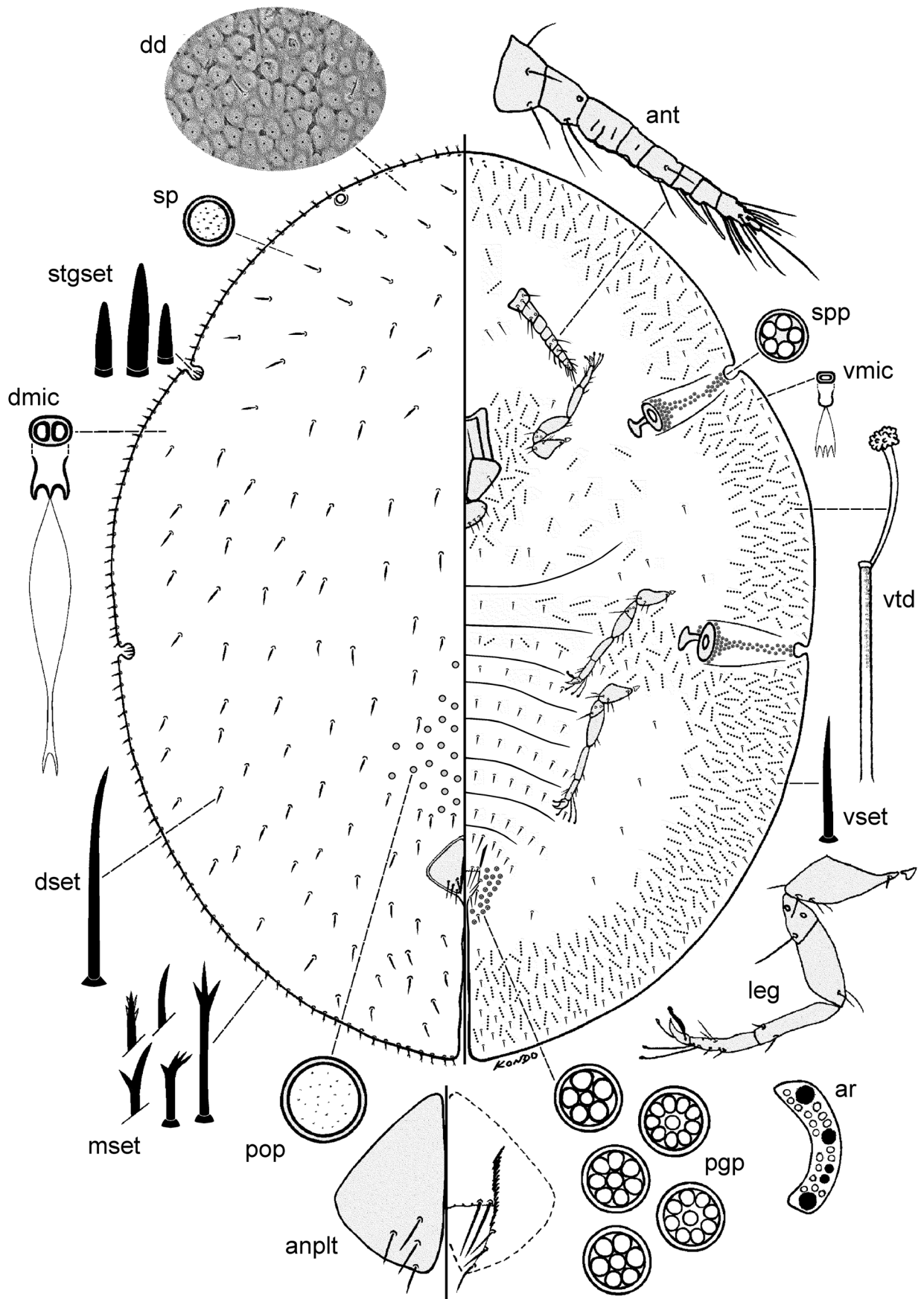


FIGURE 7. Adult female of *Coccus macarangae* Morrison. Abbreviations as in Fig. 3.

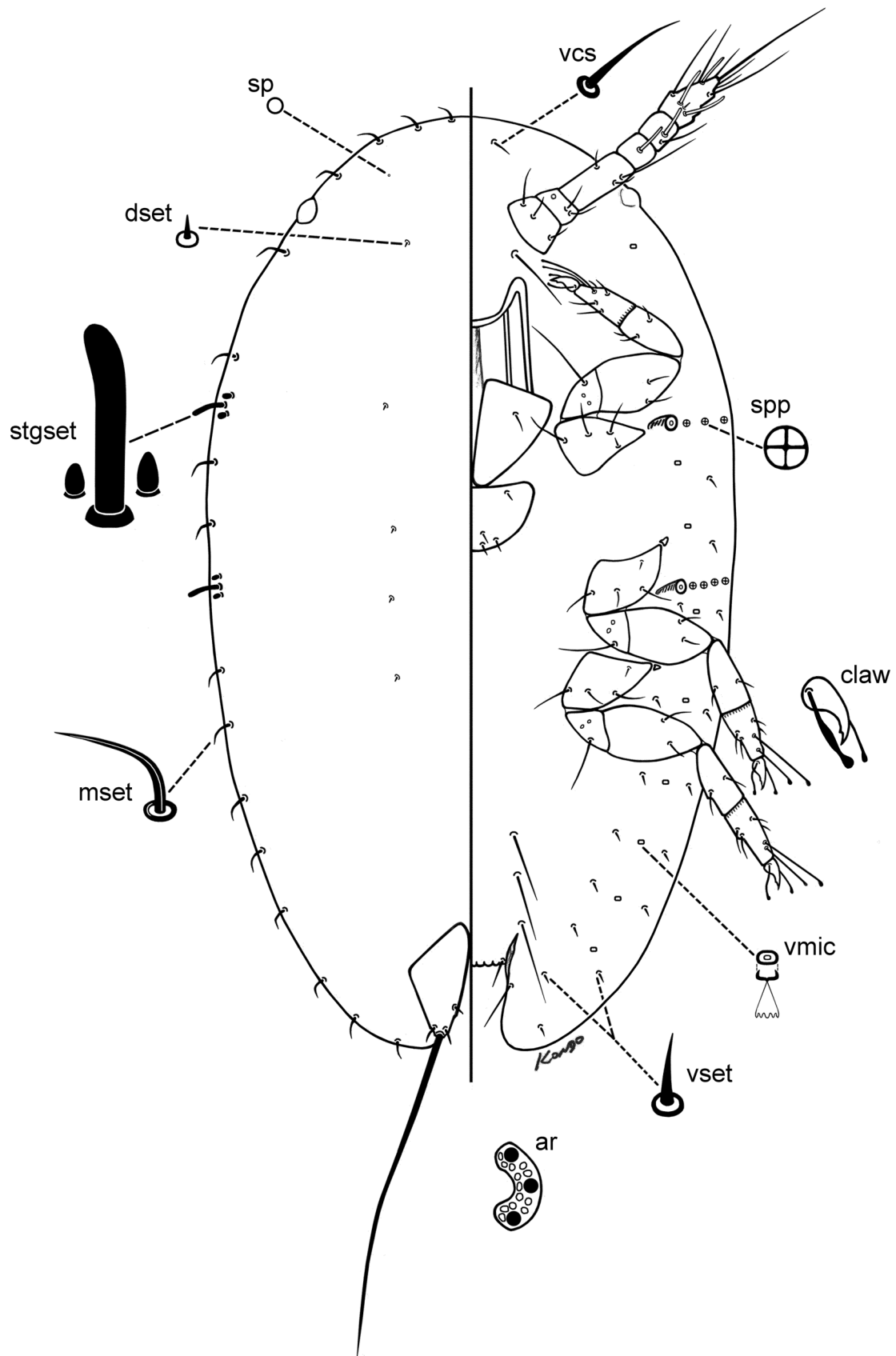


FIGURE 8. First-instar nymph of *Coccus macaranga* Morrison. Abbreviations for enlargements: ar—anal ring; dset—dorsal seta; mset—marginal setae; sp—simple pore; spp—spiracular pore; stgset—stigmatic setae; vcs—ventral cephalic seta; vmic—ventral microduct; vset—ventral seta.

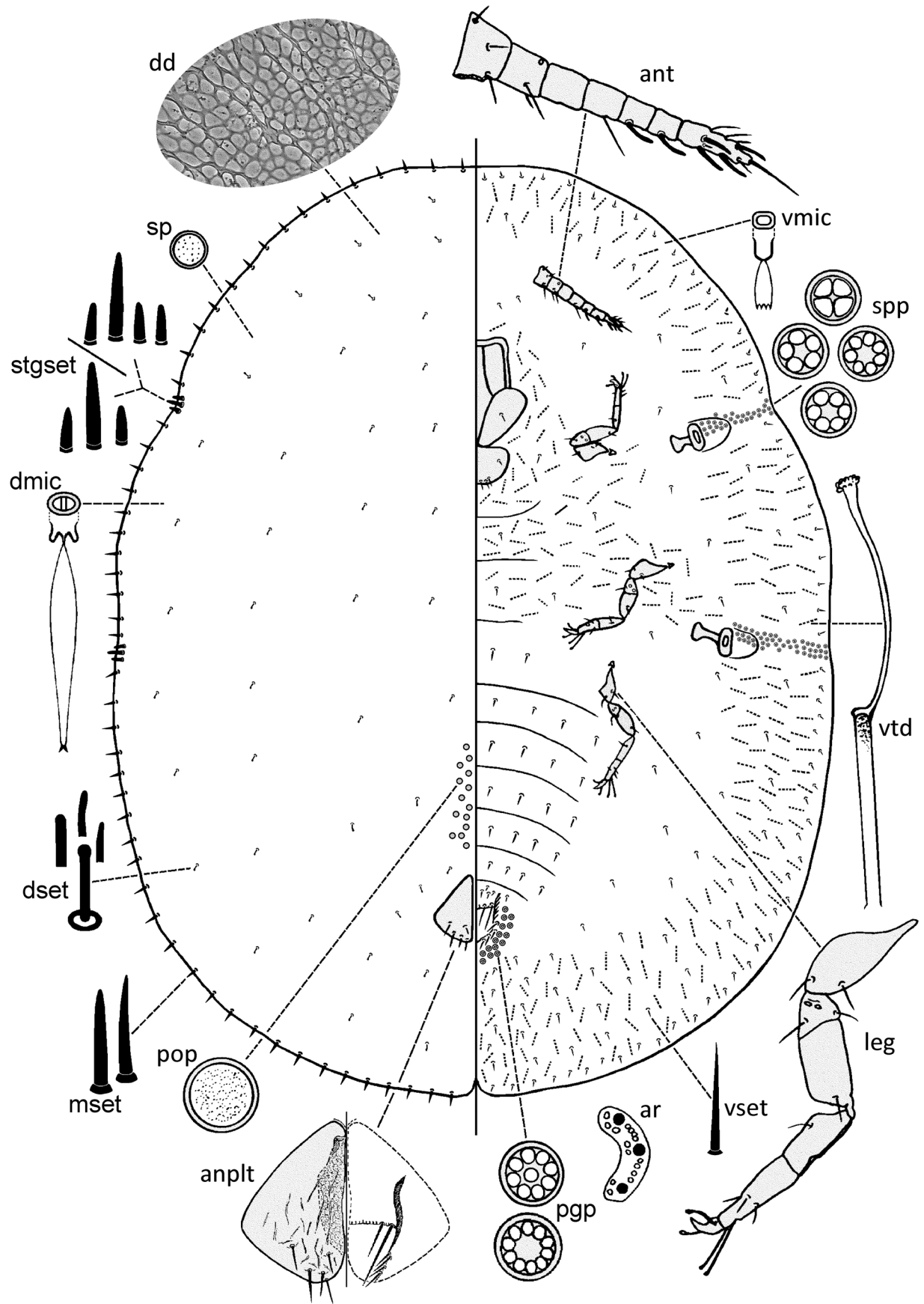


FIGURE 9. Adult female of *Coccus macarangicolus* Takahashi. Abbreviations as in Fig. 3.

Other material examined. PENINSULAR MALAYSIA: Selangor, Ulu Gombak, ex durian, 11 May 1944, coll. R. Takahashi, BMNH 1955-812, 1(19) (BMNH). Even though this slide as a small circular BMNH label with the word "Type", the specimens are not part of the type series because they were not mentioned in Takahashi's original description.

Coccus near *macarangicolus*: BORNEO: West Kalimantan, Siduk to Nanga Tayap, low elevation, ex *Macaranga velutiniflora*, 21 June 2002, coll. S.-P. Quek, SPQ.392, DNA voucher 1(1); Sarawak, 8 km Lambir, ex *M. havilandii*, Dec. 1992, coll. H.-P. Heckroth, #170, 2(2).

Note. The original description (Takahashi 1952: 15) refers to "Kuala Lumpur, a few specimens, in hollow of the stems of *Macaranga triloba* (26.III.1944). Associated with *Crematogaster* inhabiting the host plant." The correct identity of the host should be *M. bancana* (refer to M&M). One slide from the BMNH has specimens, which were collected by Takahashi from durian (*Durio* sp., Malvaceae), that were determined to belong to *C. macarangicolus* by TK and PJG. The latter specimens are not mentioned by Takahashi (1952). There are no recent collections of this species from near the type locality of Kuala Lumpur. Specimens identified as *C. near macarangicolus* are all from Borneo and they are discussed below under 'Comments'. The description of the adult female is here based on the one available Takahashi specimen, which is designated here as the lectotype.

Unmounted material. "Yellow in life. Circular, a little convex dorsally, but oval and distinctly longer than wide when mounted on slides." (Takahashi 1952: 14).

Slide-mounted adult female (n=1; Fig. 9). Body elongate oval, 1.8 mm long, 1.4 mm wide.

Dorsum. Derm (dd) membranous, areolated, with lightly sclerotised irregular submarginal lines radiating inwards at right angles to margin. Dorsal setae (dset) slender, each 7–10 µm long, with apex rounded to slightly knobbed, scattered on dorsum. Simple pores (sp) each 2.0–2.5 µm wide, scattered evenly on dorsum. Preopercular pores (pop) each 5–8 µm wide, 30 in total number, present in a longitudinal line anterior to anal plates. Dorsal microducts (dmic) in areolations each about 2 µm wide, appearing bilocular under high magnification. Anal plates (anplt) each triangular, anterolateral margin 1.1 times longer than posterolateral margin and posterolateral margin slightly convex, length of each plate 1.3 times width, inner lobes normal, with a tessellated texture, each plate 130 µm long, 78 µm wide, anterolateral margin 100 µm long, posterolateral margin 88 µm long; each plate with 4–5 dorsal setae, each seta up to 20 µm long. Anal ring (ar) probably bearing 10 setae [Takahashi (1952: 15) said "6 stout setae" but he probably only saw the 3 pairs of robust setae], each 80–95 µm long.

Margin. Eyespots not detected. Marginal setae (mset) sharply spinose, present in 1 row, each seta 10–18 µm long, with 12–14 setae between anterior and posterior stigmatic areas on each side of body. Stigmatic setae (stgset) well developed, sharply spinose with pointed to rounded apices, numbering 3 (rarely 4), median setae longest, each 27–30 µm long, lateral setae each 12–18 µm long.

Venter. Derm membranous. Ventral setae (vset) slender, with some medial to submedial abdominal setae longest, each 17–38 µm long, elsewhere shorter, each 7–18 µm long. Interantennal setae in 2 pairs, each seta up to 18 µm long. Ventral tubular ducts (vtd) present in a broad submarginal band; each duct with outer ductule 15–18 µm long, inner ductule up to 18 µm long, and duct opening about 2 µm wide. Ventral microducts (vmic) each about 2 µm wide, scattered fairly evenly on venter. Pregenital disc-pores (pgp) each with 8–10 loculi, each pore 6–7 µm wide. Antennae (ant) 7 segmented, each ~200 µm long; fleshy setae present on last 3 segments. Clypeolabral shield ~210 µm long and ~208 µm wide; labium not measured. Legs with hind trochanter + femur 87–95 µm long; hind tibia + tarsus 92–115 µm long; all tarsal digitules each 25–27 µm long; claw digitules each 12–15 µm long, claws each ~18 µm long. Spiracles normal: anterior peritremes each 50–58 µm wide; posterior peritremes each 62–68 µm wide. Spiracular pores (spp) each 5–6 µm wide, with 4–7 loculi.

Comments. Adult females of *C. macarangicolus* can be distinguished from all other species of *Coccus* known from *Macaranga* by the presence of short (7–10 µm) dorsal setae each with a rounded or knobbed apex. The adult females of *C. macarangicolus* are most similar to the adult females of *C. circularis* and *C. macarangae* in having fewer than 8 setae on each anal plate and having the marginal setae in a single row, but differ in that the marginal setae of *C. macarangicolus* never have fimbriate apices.

Adult females identified as *C. near macarangicolus* are from Borneo (lowland, near coastal localities in Sarawak and West Kalimantan) and we consider them to represent disjunct populations of *C. macarangicolus*. One of the latter females is DNA voucher specimen SPQ.392 that was placed as sister to the holotype of *C. lambirensis* in figure 3 of Quek *et al.* (2017), but the two specimens are quite distinct morphologically. The Bornean specimens of *C. near macarangicolus* are very similar to the lectotype of *C. macarangicolus* but differ in having fewer (4–8)

preopercular pores that are of two sizes (5–6 μm and 2.5–3.0 μm). Given the very few specimens of *C. macarangicolus* available to allow study of variation, we have restricted the redescription to Takahashi's type specimen.

Heckroth *et al.* (1998, table 2) listed *C. macarangicolus* almost entirely from secondary forest in Borneo and Peninsular Malaysia, although there were very few records of it and we have not seen any of the specimens that Heckroth identified as this species.

***Coccus penangensis* Morrison**

urn:lsid:zoobank.org:act:D8A35CBE-4EB3-4492-9C2C-38AD45B77D04

(Figs 2C&D, 10)

Coccus penangensis Morrison, 1921: 657.

Type material examined. Holotype: adult female, **PENINSULAR MALAYSIA:** Penang Island, in hollow stems of *Macaranga triloba* [now correctly named *M. bancana*], date not given, coll. I.H. Burkill, (USNM). **Paratypes:** same data as holotype, 2(2 adult females + 3 first-instar nymphs) (USNM). Morrison (1921: 659) states that this species was "described from two mounted adults, three mounted larvae, and few unmounted specimens, ...". One of his three slides has a single adult female and is labelled "Holotype" in Morrison's handwriting (on both the slide and its envelope). Another slide has two adult females and includes the word "Paratype". We assume that Morrison's overlooked the fact that there were two adult females on the paratype slide when he stated that the description was based on two mounted adults. It seems that this species originally was to be named "Lecanium inquilinum" by Green as this name is crossed out on the slide labels and replaced by "Coccus penangensis". The slide envelope for the holotype also includes the words: "Green, ms: (Part of type material)".

Examined non-type material from original collections. PENINSULAR MALAYSIA: Penang Island, in hollow stems of *Macaranga triloba* [now correctly named *M. bancana*], coll. I.H. Burkill, No. 2693-b, also labelled: "(type material)", 4(6) (BMNH); Penang Island, in hollow stems of *Macaranga*, coll. I.H. Burkill, 1(8) (BMNH). These two specimen lots have the same data as the type collection listed above and the same data as provided by Morrison (1921) in his original description of this species, but they are not type specimens, as explained in the Materials and methods.

Other material examined. BORNEO: Brunei, Batu Apoi Forest Reserve, 4° 33' N, 115° 09' E, ex *M. beccariana*, *M. trachyphylla* & *Macaranga* sp., 2–31 Aug. & 1 Sept. 1995, coll. P.J. Gullan, PJG-B1: 6(6 adult females), PJG-B6: 16(14 adult females & 2 second-instar females), PJG-B9: 6(4 adult females & 2 third-instar females), PJG-B14: 5(4 adult females & 5 first-instar nymphs), PJG-B28: 1(1), PJG-B30: 21(18 adult females, 1 pharate adult female, 5 first-instar nymphs), PJG-B33: 7(7), PJG-B43: 5(4 adult females & 1 third-instar female), PJG-B45: 5(4 adult females & 5 first-instar nymphs), PJG-B48: 7(7), PJG-B51: 9(9), PJG-B58: 3(3), PJG-B59: 5(5), PJG-B64: 6(6), PJG-B70: 8(7 adult females & 2 first-instar nymphs); Brunei, Batu Apoi Forest Reserve, near KBFSC, 4° 33' N, 115° 09' E, ex *Macaranga* sp., 23 Aug. 1995, coll. P.S. Cranston, PJG-B44: 5(5 adult females); Brunei, Batu Apoi Forest Reserve, near KBFSC, 4° 33' N, 115° 09' E, ex *Macaranga* sp., 12 Aug. 1995, coll. C. Maycock, PJG-B31: 3(2 adult females & 1 pharate adult female); North Kalimantan, Long Ampung, Sungei Ampung trail, 1° 43.367' N, 114° 59.838' E, 700 m, ex *M. hullettii* & *M. indistincta*, 8 Feb. 2005, coll. S.-P. Quek, SPQ.689 & SPQ.691, DNA vouchers 2(2); North Kalimantan, Long Ampung, Sungei Selungei trail, 1° 42.266' N, 114° 58.898' E, 700 m, ex *M. indistincta*, 10 Feb. 2005, coll. S.-P. Quek, SPQ.712, DNA voucher 1(1); Sabah, Crocker Range, Keningau, 1200 m, ex *M. angulata*, 17 Oct. 1999, coll. S.-P. Quek, SPQ.114, DNA voucher 1(1); Sabah, Crocker Range, Keningau to Ulu Kimanis trail, 5.28° N, 115.05° E, 280–1100 m, ex *M. angulata*, *M. bancana* & *M. indistincta*, 19 Oct. 1999, coll. S.-P. Quek, SPQ.130, SPQ.137a, SPQ.141 & SPQ.145, DNA vouchers 4(4); Sabah, Crocker Range, near Majora, 500? m, ex *M. indistincta*, 16 Oct. 1999, coll. S.-P. Quek, SPQ.105, DNA voucher 1(1); Sabah, Crocker Range, Senagang, past Keningau, \leq 450 m, ex *M. glandibracteolata* & *M. indistincta*, 20 Oct. 1999, coll. S.-P. Quek, SPQ.149 & SPQ.151, DNA vouchers 2(2); Sabah, Crocker Range, forest behind Tambunan, 600 m, ex *M. hypoleuca*, 18 Oct. 1999, coll. S.-P. Quek, SPQ.119, DNA voucher 1(1); Sabah, Crocker Range, Tambunan to Kota Kinabalu road, 200–1300 m, ex *M. angulata*, *M. bancana*, *M. petanostyla* & *M. trachyphylla*, 24 Oct. 1999, coll. S.-P. Quek, SPQ.162, SPQ.164, SPQ.165, SPQ.166, SPQ.168,

SPQ.170, SPQ.172, SPQ.173a & SPQ.174a, DNA vouchers 9(9); Sabah, Crocker Range, Tambunan to Trusmadi trail, 1300 m, ex *M. angulata*, 10 Oct. 1999, coll. S.-P. Quek, SPQ.158 & SPQ.158b, DNA vouchers 2(2); Sabah, Crocker Range, Tikolod, 650 m, ex *M. indistincta*, 18 Oct. 1999, coll. S.-P. Quek, SPQ.127, DNA voucher 1(1); Sabah, Crocker Range, ex *M. angulata*, 14 Apr. 2001, coll. B. Fiala, #20 = TK0020, DNA vouchers 2(2); Sabah, Crocker Range, ex *M. angulata*, 14 Apr. 2001, coll. B. Fiala, #31, 4(4, including DNA voucher NH5) (2 ANIC, 2 FRIM); Sabah, Crocker Range, Rafflesia Centre, ex *M. angulata*, 28 Mar. 2002, coll. B. Fiala, #126 (TK0097) & #134 (TK0096), DNA voucher 2(2); Sabah, Poring, ex *M. ?depressa* [now identified as *M. angulata*], Feb. 1992, coll. B. Fiala, #29a, 4(4); Sabah, Poring, ex *Macaranga* sp. [now identified as *M. motleyana*], 16 Apr. 2001, coll. B. Fiala, #36 (TK0034), DNA voucher 1(1); Sabah, Poring, ex *Macaranga indistincta*, 12 Apr. 2001, coll. B. Fiala, #137 (TK0037), DNA voucher 1(1); Sabah, Poring, ex *Macaranga glandibracteolata*, 24 Mar. 2002, coll. B. Fiala, #103b (TK0101), DNA voucher 1(1); Sabah, Poring, ex *M. glandibracteolata*, 24 Aug. 2003, coll. B. Fiala, #2, 3(3) (1 ANIC, 2 FRIM); Sabah, Poring Hot Springs, Kipungit waterfall, ex *M. beccariana*, Dec. 1994, coll. H.-P. Heckroth, #598, 1(5 adult females plus 2 adult females of *C. pseudotumuliferus*); Sabah, Poring Hot Springs, ex *M. indistincta*, no date, coll. H.-P. Heckroth, #550, 1(2 adult females, probably *C. penangensis* but poorly cleared, + 2 nymphs) (FRIM); Sabah, Tawau, ex *M. umbrosa* [now identified as *M. lamellata*], 15 Mar. 2002, coll. B. Fiala, #19 (TK0106) & #65b (TK0103), DNA vouchers 2(2); Sarawak, Lambir, ex *M. bancana*, 20 Jan. 1999, coll. K. Murase, KM.s27, DNA voucher 1(1) (FDS); Sarawak, Lambir, ex *M. kingii* [now named *M. umbrosa*] & *M. winkleri*, 2–4 Aug. 2003, coll. T. Itioka, TI.s56, TI.s57a & TI.s57b, DNA vouchers 3(3) (FDS); Sarawak, Lambir, ex *M. lamellata*, 24 Feb. 1992, coll. B. Fiala, #38a, 2(2); Sarawak, Lambir, ex *M. kingii* var. *platyphylla* [now named *M. umbrosa*], 24 Feb. 1992, coll. B. Fiala, #44a, 3(3); Sarawak, 8 km Lambir NP, ex *M. lamellata*, Dec. 1992, coll. H.-P. Heckroth, #106, #107 & #138, 5(5); Sarawak, 10 km Lambir NP, ex *M. hulletti*, Dec. 1992, coll. H.-P. Heckroth, #148, 1(2) (FRIM); South Kalimantan, Meratus Mts, Loksado area, 2° 48.856' N, 115° 30.695' E, 380 m, ex *M. bancana*, 18 June 2001, coll. S.-P. Quek, SPQ.345, DNA voucher 1(1); South Kalimantan, Meratus Mts, Loksado to Kandangan, 2° 47.670' N, 115° 28.712' E, 170–200 m, ex *M. hullettii*, *M. indistinct/velutina* & *M. motleyana*, 18 June 2001, coll. S.-P. Quek, SPQ.351, SPQ.352, SPQ.353, SPQ.354, SPQ.356b & SPQ.361a, DNA vouchers 6(6); West Kalimantan, Siduk to Nanga Tayap, 1° 14.672' S, 109° 59.184' E to 1° 22.360' S, 110° 13.686' E, <100 m, ex *M. aethadenia* & *M. indistinct/velutina*, 21 & 22 June 2002, coll. S.-P. Quek, SPQ.393, SPQ.396, SPQ.420 & SPQ.412b, DNA vouchers 4(4). **PENINSULAR MALAYSIA:** Genting, 900 m, ex *M. hullettii*, Mar. 1993, coll. H.-P. Heckroth, #222, 2(1 adult female & 1 first-instar nymph); Gombak Field Studies Centre, ex *M. triloba* [now correctly named *M. bancana*], Mar. 1993, H.P. Heckroth, #269, 1(1) (BMNH); Gombak, ex *M. triloba* [= *M. bancana*] & *M. hullettii*, 22 Mar. 1992, coll. B. Fiala, #174a & #175a, 4(4); Gombak, lower logging road, ex *M. triloba* [= *M. bancana*], Feb. & Mar. 1993, coll. H.-P. Heckroth, #251, 5(5) (3 ANIC, 2 FRIM) & #298, 2(2) (ANIC); Johor, Mawai camp, Ginger Hill, ~1.871° N, ~103.954° E, <100 m, ex *M. bancana*, 7 Sept. 1999, coll. S.-P. Quek, SPQ.031, DNA voucher 1(1); Pahang, Beserah Hill nr Kuantan, ~3.867° N, ~103.347° E, <300 m, ex *M. bancana*, 14 Sept. 1999, coll. S.-P. Quek, SPQ.047, DNA voucher 1(1); Pahang, Tioman Island, Tekek-Juara trail, 2.805° N, 104.117° E, ex *M. bancana*, 21 Sept. 1999, coll. S.-P. Quek, SPQ.084, DNA voucher 1(1); Terengganu, Bauk Hill, 200–300 m, ex *M. bancana*, 12 Sept. 1999, S.-P. Quek, SPQ.037, SPQ.037b, SPQ.040 & SPQ.041, DNA vouchers 4(4); Perak [state], Taiping Hills, in stems of *M. triloba* [now correctly named *M. bancana*], attended by *Crematogaster bouensis* [sic], 2.iv.1924 (letter), coll. I.H. Burkill, Singapore Field No. 13055, 1(3) (USNM); Perak [state], Straits Settlement, near Tanjong Malim, on *Macaranga triloba* [now correctly named *M. bancana*], 5.vii.1924 (letter), Singapore Field No. 13489, coll. I.H. Burkill, 1(3) (USNM). **SINGAPORE:** Central Catchment, Sime Road, 1° 21'35" N, 103° 48'30" E, ex *M. bancana*, 18 Mar. 2009, coll. P.S. Cranston, 3(3); Old Upper Thompson Road, ~1.381° N, ~103.813° E, <100 m, ex *M. bancana*, 4 Oct. 1999, coll. S.-P. Quek, SPQ.088 & SPQ.089, DNA vouchers 2(2); in hollow stems of *Macaranga*, coll. I.H. Burkill or C.F. Baker, 3(17 adult females & 1 nymphal female) (BMNH). **SUMATRA:** Ketambe, ~3° 50' N, 7° 40' E, ex *M. triloba* [now correctly named *M. bancana*], 30 Oct. 1992, coll. U. Maschwitz, sent by B. Fiala, #8a, 2(2); Medan, ~3° 40' N, 98° 20' E, ex *M. triloba* [= *M. bancana*], 20 Oct. 1992, coll. U. Maschwitz, sent by B. Fiala, #4a, 3(3); Sibolangit, ~3° 40' N, 98° 20' E, ex *M. hullettii*, 20 Oct. 1992, coll. U. Maschwitz, sent by B. Fiala, #5a & #9a, 8(6 adult females, 1 pharate adult female & 1 third-instar female); Sibolangit, ~3° 40' N, 98° 20' E, ex *M. triloba* [= *M. bancana*], 23 Oct. 1992, coll. U. Maschwitz, sent by B. Fiala, #6a, 2(2).

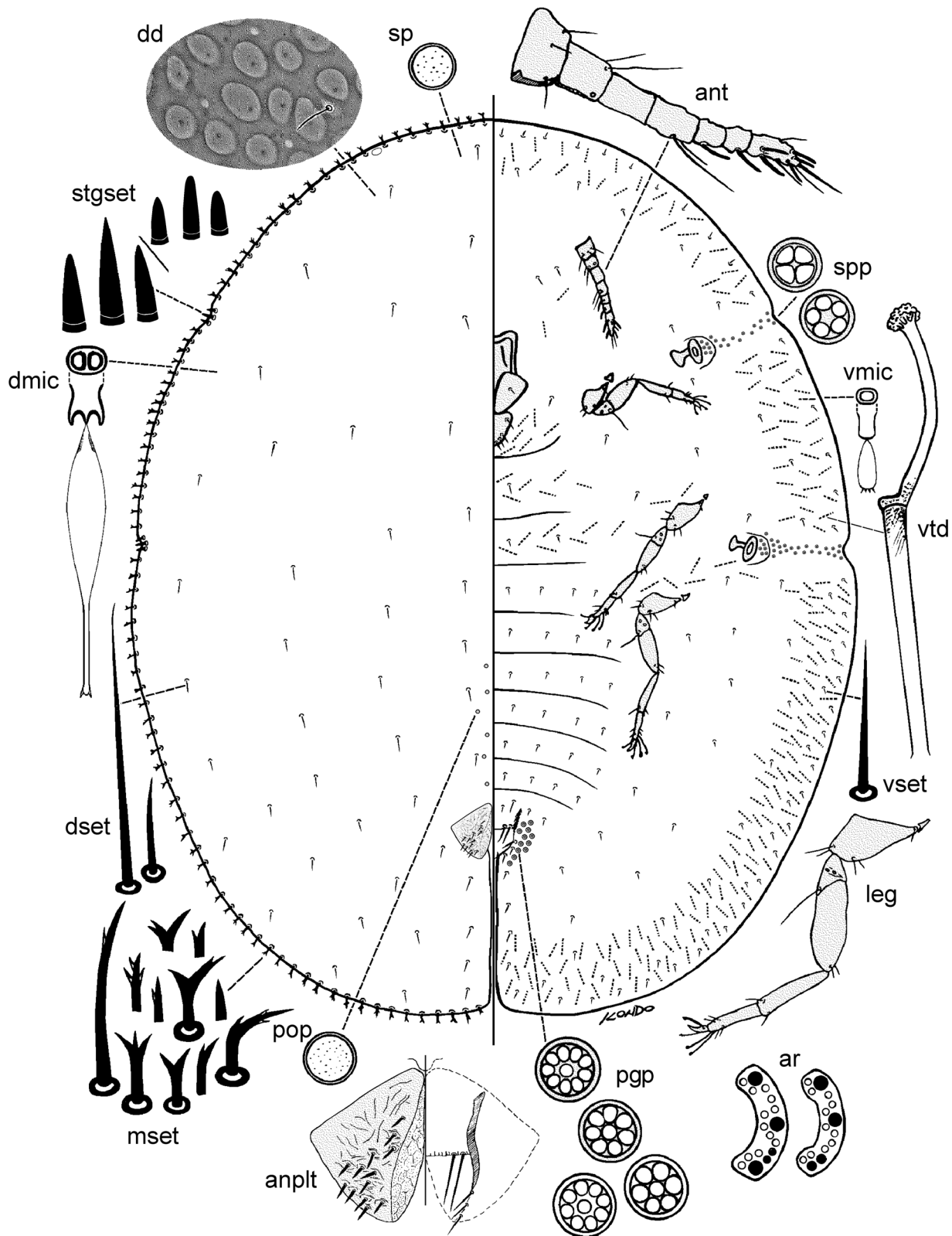


FIGURE 10. Adult female of *Coccus penangensis* Morrison. Abbreviations as in Fig. 3.

Adult female. Unmounted material. “Normally short oval, flat, dorsal surface dull, naked, wrinkled radially near margin, outer portion light brown, central disk usually much darker brown to blackish; ..” (Morrison 1921: 657). Morrison’s description of adult females from Penang Island differs in body colour from specimens

photographed in Borneo (Fig. 2C & D) probably because Morrison's specimens were dead and dried. Females from both Brunei and Sabah were pale ochre to salmon pink with a thin dorsal secretion that varied in whiteness among females from different collections. Ridges radiating inwards from the body margin were apparent in all specimens.

Slide-mounted adult female (n=27, including holotype and paratypes; Fig. 10). Body oval to elongate oval, 1.6–3.0 mm long, 1.2–2.5 mm wide.

Dorsum. Derm (dd) membranous, with numerous areolations and lightly sclerotised irregular submarginal lines radiating inwards at right angles to margin. Dorsal setae (dset) slender, each 7–38 (mostly ≤ 20) μm long, scattered on dorsum. Simple pores (sp) each 2.5–3.0 μm wide, scattered evenly on dorsum. Preopercular pores (pop) each 3.5–7.5 (rarely up to 10) μm wide, scarce, present in an elongate group of 6–25 (usually 10–17) anterior to anal plates. Dorsal microducts (dmic) in areolations each 2.0–2.5 μm wide, appearing bilocular under high magnification. Anal plates (anplt) each broadly triangular with anterolateral margin usually slightly longer than posterolateral margin and latter often slightly convex, length of each plate 1.2–1.7 times width, inner lobes well developed, with a tessellated texture, each plate 120–170 μm long, 85–125 μm wide, anterolateral margin 95–140 μm long, posterolateral margin 85–115 μm long; each plate with 11–23 dorsal setae, each seta 8–20 μm long (12–18 μm long on holotype). Anal ring (ar) probably always bearing 10 setae [Morrison (1921: 659) said 8 setae, but the thinner ones are difficult to see], each 75–120 μm long.

Margin. Eyespots indistinct, present on dorsal margin, each 15–28 μm wide, but not detected on some specimens. Marginal setae (mset) in 1 irregular row, each seta short and usually fairly stout, sometimes slender, each usually 7–20 (rarely up to 40) μm long, with apex bifurcate or fimbriate, rarely sharply spinose, with 12–31 setae between anterior and posterior stigmatic areas on each side of body. Stigmatic setae (stgset) well developed, spinose and tapering to pointed or rounded apices, usually numbering 3, median setae usually longest, each 10–28 (mostly 13–20) μm long, lateral setae each 5–18 (mostly 7–15) μm long.

Venter. Derm membranous. Ventral setae (vset) slender, with prevulvar setae each 18–75 μm long, elsewhere shorter, each 8–18 μm long. Interantennal setae numbering 2 or 3 pairs, each seta 7–15 μm long. Ventral tubular ducts (vtd) present in a broad submarginal band; each duct with outer ductule 15–22 μm long, inner ductule 17–20 μm long, and duct opening about 2 μm wide. Ventral microducts (vmic) each 2.0–2.5 μm wide, scattered fairly evenly on venter. Pregenital disc-pores (pgp) each with 5–9 (mostly 7 and 8) loculi, each pore 5–6 μm wide. Antennae (ant) 7 or 8 (mostly 7, very rarely 6) segmented, each 200–265 μm long; fleshy setae present on last 3 segments. Clypeolabral shield 180–258 μm long, 165–210 μm wide; labium 75–100 μm long, 103–140 μm wide. Legs with hind trochanter + femur 140–170 μm long; hind tibia + tarsus 145–185 μm long; all tarsal digitules each 27–42 μm long; claw digitules each 23–33 μm long, claws each 25–30 μm long. Spiracles normal: anterior peritremes each 45–77 μm wide; posterior peritremes each 55–83 μm wide. Spiracular pores (spp) each 4–5 μm wide, with 3–6 (mostly 5) loculi.

Comments. Adult females of *C. penangensis* can be distinguished from all other species of *Coccus* known from *Macaranga* by having the combination of (i) anal plates each with 11–23 setae, each seta ≤ 20 μm long; (ii) short, slender dorsal setae, each mostly ≤ 20 μm long and tapering to apex; and (iii) marginal setae in a single row with apex of each seta usually bifurcate or fimbriate, and mostly 7–20 μm long. The adult females of *C. penangensis* are most similar to those of *C. heckrothi* in the number of dorsal setae on each anal plate (although the setae of *C. heckrothi* are often slightly longer) and in the shape and length of the dorsal body setae, but differ in that the marginal setae of *C. penangensis* mostly have bifurcate or fimbriate apices (mostly with sharply pointed apices in *C. heckrothi*) and the lateral stigmatic setae are usually < 15 μm long (mostly > 15 μm in *C. heckrothi*).

Two of five adult females of *C. penangensis* from Poring Hot Springs in Sabah, all mounted on one slide prepared by H.-P. Heckroth (slide also with 2 adult females of *C. pseudotumuliferus*), have extremely few and very short (≤ 5 μm long) dorsal setae. The other three females are poor mounts but a few slightly longer dorsal setae are visible on two of them. Thus at least two of these females could erroneously key to the *C. tumuliferus* group or *C. secretus* because of these very short and sparse dorsal setae.

Coccus penangensis is a very widespread species, occurring in Borneo, Peninsular Malaysia, Singapore and Sumatra. Heckroth *et al.* (1998) recorded this species as common in both primary and secondary forest on Borneo (inside the stems of 17 *Macaranga* species) and Peninsular Malaysia plus Sumatra (in five *Macaranga* species). There is a large amount of morphological variation among adult females of *C. penangensis* from different localities, but there do not appear to be consistent differences related to geography. However, specimens from Burkill's collections on Penang Island appear to have longer dorsal setae than specimens from most other localities.

Coccus penangensis was well represented (over 40 specimens) in the molecular phylogeny of Quek *et al.* (2017), with specimens from Bauk Hill on the east coast of Peninsular Malaysia and from near Siduk in West Kalimantan each forming a small cluster distinct from the remainder of the specimens. The adult females of these two groups did not appear to differ morphologically from specimens collected elsewhere but, unfortunately, the condition of molecular vouchers often makes detailed morphological comparisons difficult.

***Coccus pseudotumuliferus* Gullan & Kondo sp. n.**

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(Figs 2E, 11A–C, 12)

Coccus "tumuliferus var. C. 84", Heckroth *et al.* 1998: 431, 432, 434, 436, 438 & 440.

Morphospecies C. 214, Heckroth *et al.* 1998: 431, 433, 436, 437 & 440.

Coccus "near tumuliferus", Quek *et al.* 2017: 823.

Type material examined. Holotype: adult female, **BORNEO:** Sabah, Crocker Range, Tikolod, 650 m, ex hollow stem of *Macaranga indistincta*, 18 Oct. 1999, coll. S.-P. Quek, SPQ.125b, DNA voucher 1(1) (FRIM). **Paratypes:** **BORNEO:** same data as holotype except ex *M. pearsonii* & *M. glandibracteolata*, SPQ.126a & SPQ.129b, DNA vouchers 2(2) (ANIC); Sabah, Crocker Range, Keningau to Ulu Kimanis trail, ~5.28° N, ~116.05° E, 900–1200 m, ex *M. angulata*, *M. puberula* & *M. glandibracteolata*, 19 Oct. 1999, coll. S.-P. Quek, SPQ.131b, SPQ.136b, SPQ.139 & SPQ.147, DNA vouchers 4(4) (3 ANIC, 1 FRIM: SPQ.147); Sabah, Crocker Range, past Keningau, Senangang, 450 m, ex *M. glandibracteolata* & *M. indistincta*, 20 Oct. 1999, coll. S.-P. Quek, SPQ.148 & SPQ.150, DNA vouchers 2(2) (1 ANIC, 1 FRIM: SPQ.148); Sabah, Crocker Range, Mahua camp, 1000 m, ex *M. puberula*, 16 Oct. 1999, coll. S.-P. Quek, SPQ.101a, DNA vouchers 2(2); Sabah, Crocker Range, near Majora, Apin Apin, 500 m, ex *M. motleyana*, 16 Oct. 1999, coll. S.-P. Quek, SPQ.102 & SPQ.103b, DNA vouchers 2(2); Sabah, Crocker Range, near Majora, 500? m, ex *M. glandibracteolata* & *M. indistincta*, 16 Oct. 1999, coll. S.-P. Quek, SPQ. 108b, SPQ.110a & SPQ.111, DNA vouchers 4(4) (3 ANIC, 1 FRIM: SPQ.110a); Sabah, Crocker Range, Tambunan to Kota Kinabalu road, Rafflesia Reserve, 1200 m, ex *M. petanostyla*, 15 Oct. 1999, coll. S.-P. Quek, SPQ.100b, DNA voucher 1(1); Sabah, Crocker Range, Tambunan to Kota Kinabalu road, 200 m, ex *M. bancana*, 24 Oct. 1999, coll. S.-P. Quek, SPQ.174b, DNA voucher 1(1); Sabah, Crocker Range, Tambunan to Ranau road, 15 km from Ranau, ex *M. indistincta*, 22 Oct. 1999, coll. S.-P. Quek, SPQ.155, DNA voucher 1(1) (FRIM); Sabah, Crocker Range, Tambunan to Trusmadi trail, 1200–1300 m, ex *M. angulata*, *M. indistincta* & *M. puberula*, 23–24 Oct. 1999, coll. S.-P. Quek, SPQ.157, SPQ.159, SPQ.160 & SPQ.161, DNA vouchers 4(4).

Note. The holotype is not a perfect specimen but was chosen for three reasons: (1) it shows the diagnostic features of the species, (2) it is a DNA voucher specimen included in the analysis of Quek *et al.* (2017), and (3) it is from northwest Borneo, a region where this species is well sampled. The collection site probably was along Jalan Kampung Tikolod at about 5° 38'18" N and 116° 16'15" E. Although the description below is based on measurements of specimens from a range of localities in Borneo, our type series is restricted to specimens from the Crocker Range in Sabah, for the following reasons. Subsequent, especially molecular, research on further samples of these coccids may show cryptic species or subsequent authors may have a more restrictive species concept. Species delineation is problematic because of parthenogenesis (as explained in the Introduction) and thus deciding whether there is one variable species or several more tightly defined species is highly subjective.

Other material studied. BORNEO: Brunei, Batu Apoi Forest Reserve, near KBFSC, 4° 33' N, 115°09' E, ex *M. trachyphylla* & *Macaranga* sp., 7, 9–11, 26–28 Aug. 1995, coll. P.J. Gullan, PJG-B15: 5(2 adult females & 16 first-instar nymphs), PJG-B22: 8(7 adult females, including 1 on slide with *C. macarangae*, & 6 first-instar nymphs), PJG-B23: 6(4 adult females & 28 first-instar nymphs) (coll. P.S. Cranston), PJG-B26: 1(1), PJG-B28: 2(1 adult female & 1 nymphal female), PJG-B51: 1(1), PJG-B52: 2(2), PJG-B56: 6(3 adult females, 2 nymphal females & 8 first-instar nymphs); East Kalimantan, Bukit Bangkirai, 1° 1.497' S, 118° 51.949' E, <100 m, ex *M. pearsonii*, 13 Feb. 2005, coll. S.-P. Quek, SPQ.727, DNA voucher 1(1); East Kalimantan, Samarinda, Tenggarong to Kota Bangun Road, <100 m, ex *M. pearsonii*, 11 June 2001, coll. S.-P. Quek, SPQ.321, DNA voucher 1(1); East Kalimantan, Wanariset to Bukit Bangkirai Road, 00° 59.29' S, 116° 55.47' E to 1° 0.72' S, 116° 52.04' E, <100 m, ex *M. hosei*, *M. hypoleuca* & *M. pearsonii*, 13 Feb. 2005, coll. S.-P. Quek, SPQ.722, SPQ.723 SPQ.724a & SPQ.725, DNA vouchers 4(4); North Kalimantan, Long Ampung, Sungai Anai trail, 1° 42.96' N, 114° 57.30' E &

1° 42.97' N, 114° 57.23' E, 700 m, ex *M. glandibracteolata* & *M. beccariana*, 9 Feb. 2005, coll. S.-P. Quek, SPQ.696, & SPQ.698a DNA vouchers 2(2); North Kalimantan, Long Ampung, Sungai Selungei trail, 1° 42.27' N, 114° 58.90' E, 700 m, ex *M. glandibracteolata*, 10 Feb. 2005, coll. S.-P. Quek, SPQ.714, DNA voucher 1(1); West Kalimantan, Siduk to Nanga Tayap, 1° 21.72' S, 110° 12.10' E & 1° 21.67' S, 110° 12.30' E, <100? m, ex *M. indistincta/velutina*, *M. aethæadenia* & *M. hosei*, 22 June 2001, coll. S.-P. Quek, SPQ.408a, SPQ.412a & SPQ.415, DNA vouchers 3(3); Sabah, Poring, ~6° N, 116° E, ex *M. pearsonii* & *M. indistincta*, 30.x.1992 & 25.xi.1992, coll. B. Fiala, #251a, 252a & 253a, 8(8); Sabah, Poring, ex *M. pearsonii*, Apr. 2001, coll. B. Fiala, #120 (TK0036) & #128 (TK0038), DNA vouchers 3(3); Sabah, Poring, ex *M. glandibracteolata*, *M. indistincta* & *M. pearsonii*, 17 Apr. 2001, coll. B. Fiala, #39 (TK0021), #40 (TK0023), #48 (TK0043), #106b (TK0031), #110 (TK0035), DNA vouchers 5(5); Sabah, Poring, ex *M. pearsonii* & *M. winkleri*, 18 Apr. 2001, coll. B. Fiala, #159 (TK0042) & #158 (TK0044), DNA vouchers 2(2); Sabah, Poring, ex *M. pearsonii*, 24 Apr. 2002, coll. B. Fiala, #120 (TK0099), DNA voucher 1(1); Sabah, Poring Hot Springs, Kipungit waterfall, ex *M. beccariana*, Dec 1994, coll. H.-P. Heckroth, #598, 1(2 adult females on slide with 5 adults of *C. penangensis*); Sabah, Poring Hot Springs, ex *M. indistincta*, no date, coll. H.-P. Heckroth, #581 & 589, 2(3, including 1 on slide with 1 adult female of *C. near circularis*) (FRIM); Sabah, Ranau, Kota Kinabalu, roadside, ex *M. beccariana*, 27 Mar. 2002, coll. B. Fiala, #124 (TK0098), DNA voucher 1(1); Sabah, road from Ranau to Sandakan, ex *M. pearsonii*, Jan. 1995, coll. H.-P. Heckroth, #631, 3(3); Sabah, road from Ranau to Sandakan, ex *M. pearsonii*, no date, coll. H.-P. Heckroth, #529, 1(4) (FRIM); Sabah, 10 km south of Ranau, ex *M. pearsonii*, 1995 or no date, coll. H.-P. Heckroth, #525, 526, 527, 614, 635 & 1203, 6(23, including 2 on slide with 1 adult female of *C. secretus*) (FRIM); Sabah, 10 km south of Ranau, ex *M. winkleri*, no date, coll. H.-P. Heckroth, #646, 1(5) (FRIM); Sabah, 60.5 km south of Ranau, ex *M. hypoleuca*, 1995, coll. H.-P. Heckroth, #629, 1(1 on slide with 1 adult female of *C. secretus*) (FRIM); Sabah, Tawau, Air Panas, ex *M. motleyana*, 15 Mar. 2002, coll. B. Fiala, #55b (TK0110), DNA voucher 1(1); Sabah, Tawau Hills, ex *M. glandibracteolata*, *M. indistincta* & *M. pearsonii*, 5–7 Apr. 2001, coll. B. Fiala, #76 (TK0025), #78b (TK0029), #77 (TK0026), #90 (TK0027), #95 (TK0033), DNA vouchers 5(5); Sabah, Tawau, ex *M. indistincta* & *M. umbrosa* [latter now correctly identified as *M. lamellata*], 12 & 20 Mar. 2002, coll. B. Fiala, #13 (TK0109) & #78b (TK0104), DNA vouchers 2(2); Sabah, Tawau, Bukit Bombalai, ex *M. glandibracteolata*, 13 Mar. 2002, coll. B. Fiala, #32 (TK0105), DNA voucher 1(1); Sabah, Tawau, ex *M. pearsonii*, 30 Aug. 2003, coll. B. Fiala, #64, 4(4); Sabah, Tawau Hills, ex *M. triloba* [now correctly named *M. bancana*], coll. H.-P. Heckroth, #477, 1(3) (FRIM); Sarawak, 2 km Lambir, ex *M. hosei*, Dec. 1992, coll. H.-P. Heckroth, #47 & #85, 3(3); Sarawak, Kubah [national park near Kuching], ex *M. aethæadenia*, Dec. 1994, coll. H.-P. Heckroth, #377, 1(3); Sarawak, Lambir, 150 m, ex *M. beccariana* & *M. hosei*, 3 Sept. 2001, coll. K. Murase, KM.s03, KM.s06, KM.s21 & KM.s24, DNA vouchers 4(4) (FDS); Sarawak, Lambir, 150 m, ex *M. beccariana* & *M. hullettii*, 2–4 Aug. 2003, coll. T. Itioka, TI.s45, TI.s54 & TI.s58, DNA vouchers 3(3) (FDS); Sarawak, 2 km Lambir NP, ex *M. beccariana*, Dec. 1992, coll. H.-P. Heckroth, #30 & #73, 7(7); Sarawak, 2 km Lambir NP, ex *M. hosei*, Dec. 1992, coll. H.-P. Heckroth, #47, 1(1 on slide with 1 adult female of *C. heckrothi*) (FRIM); Sarawak, 3 km Lambir NP, ex *M. beccariana*, Dec. 1992, coll. H.-P. Heckroth, #44, 1(1); Sarawak, 3 km Lambir NP, ex *M. beccariana*, Feb. 1993, coll. H.-P. Heckroth, #45, 1(3) (FRIM); Sarawak, 8 km Lambir NP, ex *M. lamellata*, Dec. 1992, coll. H.-P. Heckroth, #106, #107 & #113, 4(4); Sarawak, Serian, "Serian" waterfall [perhaps Ranchan Waterfall], ex *M. hypoleuca*, Dec. 1994, coll. H.-P. Heckroth, #404, 1(7); South Kalimantan, Meratus Mts, Kapayang village to Loksado, 381 m & 500 m, 2° 48.86' S, 115° 30.70' E & 2° 48.98' S, 115° 31.13' E, ex *M. bancana* & *M. motleyana*, 18 June 2001, coll. S.-P. Quek, SPQ.346b & SPQ.340, DNA vouchers 2(2); South Kalimantan, Meratus Mts, Loksado to Kandangan, 170–211 m, 2° 47.48' S, 115° 25.94' E to 2° 48.21' S, 110° 25.52' E, ex *M. motleyana*, 18 June 2001, coll. S.-P. Quek, SPQ.356a, SPQ.358a & SPQ.362, DNA vouchers 3(3). **PENINSULAR MALAYSIA:** Gombak, lower logging road, ex *M. hosei*, Feb. 1993, coll. H.-P. Heckroth, #214, 3(3); Gombak, lower logging road, ex *M. hosei*, Mar. 1993, coll. H.-P. Heckroth, #270, 6(9) (5 slides in ANIC & 1 slide with 4 adult females in FRIM); Johor, just after Mersing towards Johor Bahru, lowland, ex *M. griffithiana*, 16 Sept. 1999, coll. S.-P. Quek, SPQ.068a, 2(2); Johor, Labis Air Panas, ex *M. hosei*, coll. H.-P. Heckroth, #1069, 1(3 on slide with 1 adult female of *C. secretus*) (FRIM); 6 km Rawang, ex *M. griffithiana*, Feb. 1993, coll. H.-P. Heckroth, #206, 6(4 adult females + 2 probably third-instar females).

Note. This species was recognised as a variety as well as a separate morphospecies and referred to as "*C. tumuliferus* var. *C. 84*" and "morphospecies *C. 214*" by Heckroth *et al.* (1998). Specimens of this new species form Clade 3, referred to as "near *tumuliferus*", in Quek *et al.* (2017, fig. 3). This clade has several very closely related subgroups, which we consider to be geographic variants, which mostly do not appear to exhibit consistent

morphological differences (see below under Comments); thus measurements for the description below were based on adult females from across Borneo, despite some variation in live appearance among females (note that live appearance is unknown for most specimens of this species).

Etymology. Early in our study we confused specimens of this species with those of *C. tumuliferus*, with which it shares many morphological similarities, including the raised areas on the dorsum; hence, we have named this new species "pseudotumuliferus" from the Latin "pseudo-" meaning "false".

Adult female. Unmounted material. In life, adult females varied from bright, shining pink to red (Fig. 2E) to brownish-yellow, depending on collection locality and perhaps age. Available adult females preserved in ethanol were bright pinkish red in colour. Body broadly oval to almost circular, having a fairly definite arrangement of dorsal humps (Fig. 11A–C) with the marginal row of humps most obvious and the central area of dorsum varying from having humps to almost flat; mature females covered dorsally with a brittle, whitish, glassy secretion, easily broken, moulded into elevations corresponding to those of the body, with secretion in the central part of dorsum variable among specimens from different collections (Fig. 11A–C).

Slide-mounted adult female (n=19, all from Borneo and including holotype and 8 paratypes; Fig. 12). Body oval to circular, 1.7–3.6 (holotype 2.45) mm long, 1.2–3.2 (holotype 2.06) mm wide.

Dorsum. Derm (dd) completely membranous, weakly areolated, with clear area of each areolation usually 4–7 μm in widest dimension; with a series of humps (oval, elongate to irregularly circular raised areas of cuticle) present in a submarginal row of 23–25 (11 or more rarely 12 on each side, plus always 1 medially on head), 3 or 4 on each side submedially, and sometimes 3 or 4 slightly raised areas medially but poorly defined. Dorsal setae (dset) very short, each 2.5–3.0 μm long with rounded apex, scattered on dorsum; humps difficult to discern on younger slide-mounted specimens. Simple pores (sp) each 2.5 μm wide, scattered evenly on dorsum. Preopercular pores (pop) each 2.5–6.3 (mostly 3.0–5.0) μm wide, often scarce and easily confused with simple pores, present in a small group of 3–18 anterior to anal plates. Dorsal microducts (dmic) in areolations each about 2.0 μm wide, appearing bilocular under high magnification. Anal plates (anplt) each broadly triangular with anterolateral margin usually slightly convex and slightly longer than posterolateral margin, length of each plate 1.2–1.8 times width, inner lobes fairly well developed and with a tessellated texture but often difficult to see, each plate 148–183 μm long, 90–140 μm wide, anterolateral margin 135–170 μm long, posterolateral margin 98–133 μm long; each plate with 12–20 dorsal setae (except for specimens from the Meratus Mountains and some from Gombak; see Comments section for variation), each seta 10–23 μm long. Anal ring (ar) bearing 10 setae, each 85–125 μm long.

Margin. Eyespots present slightly removed from dorsal margin, each 17.5–22.5 μm in maximum dimension, often difficult to detect. Marginal setae (mset) variable in length and robustness among specimens, sharply spinose to flagellate, usually present in 2 or 3 rows, rarely (Meratus Mountains specimens only) in an irregular single row on part of margin, each seta 12–65 μm long, with 25–63 setae between anterior and posterior stigmatic areas on each side of body. Stigmatic setae (stgset) shorter than marginal setae, usually numbering 3 per cleft, occasionally fewer (but often lost from DNA vouchers), spinose with rounded apices, all setae subequal in length or median seta slightly longer, each 3.0–18.0 (mostly 7.5–12.5) μm long.

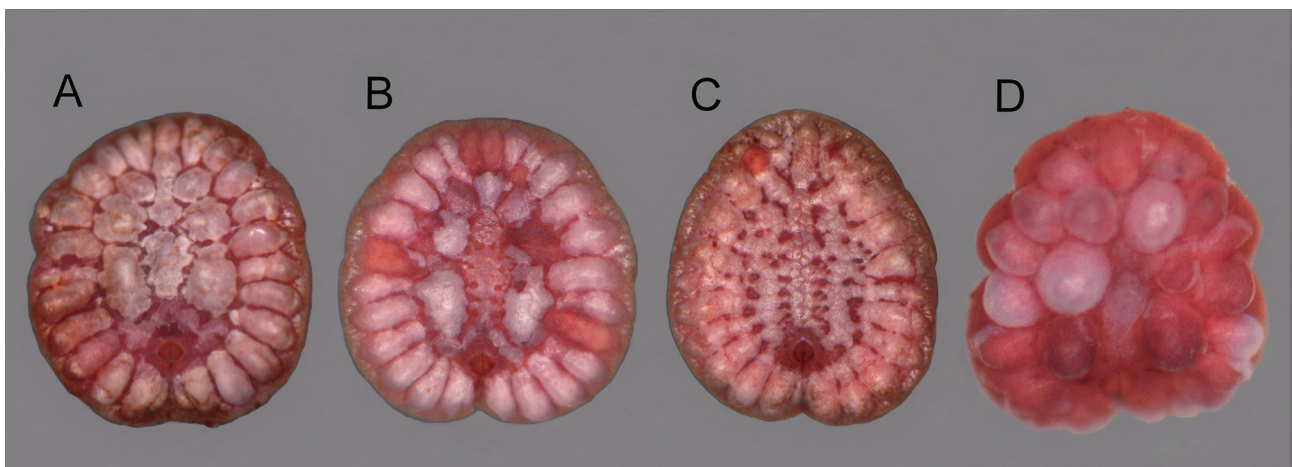


FIGURE 11. Photographs of the dorsum of adult females preserved in ethanol: A–C, *C. pseudotumuliferus* Gullan & Kondo sp. n., showing variation in the numbers and shapes of dorsal elevations or humps; D, *C. tumuliferus* Morrison.

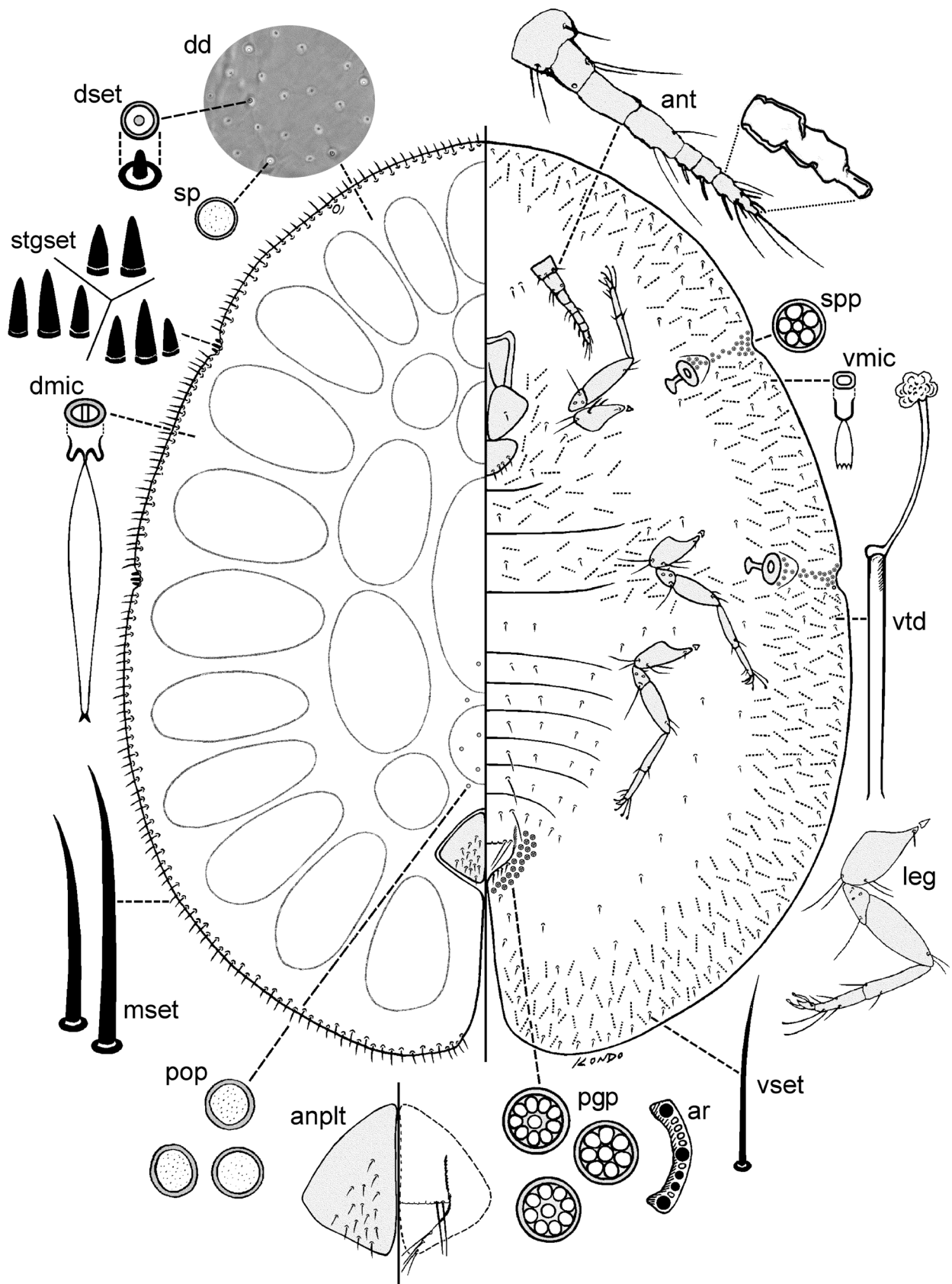


FIGURE 12. Adult female of *Coccus pseudotumuliferus* Gullan & Kondo sp. n. Abbreviations as in Fig. 3.

Venter: Derm membranous. Ventral setae (vset) slender, longest submedially on posterior abdominal segments, each 15–80 µm long, elsewhere shorter, 10–30 (mostly ≤20) µm long. Interantennal setae numbering 2 pairs, each seta 12–15 µm long. Ventral tubular ducts (vtd) present in a broad submarginal band; each duct with outer ductule 17–20 µm long, inner ductule 15–20 µm long, and duct opening about 2 µm wide. Ventral microducts (vmic) each 2.0–2.5 µm wide, scattered fairly evenly on venter. Pregenital disc-pores (pgp) each with 7–11 loculi, each pore 5–7 µm wide. Antennae (ant) 7 segmented, each 215–265 µm long; apical antennal segment 37.5–52.5 µm long, with apical prolongation 6–15 µm long and usually ≥10 µm on at least 1 antenna (rarely absent); fleshy setae present on last 3 segments. Mouthparts normal; clypeolabral shield 200–258 µm long, 170–228 µm wide; labium 90–115 µm long, 120–150 µm wide. Legs with hind trochanter + femur 148–175 µm long; hind tibia + tarsus 140–188 µm long; all tarsal digitules each 35–45 µm long; claw digitules each 22–30 µm long, claws each 20–27 µm long. Spiracles normal: anterior peritremes each 55–78 µm wide; posterior peritremes each 65–83 µm wide. Spiracular pores (spp) each 4–5 µm wide, almost all with 5 loculi.

Comments. Heckroth *et al.* (1998) pointed out that *C. tumuliferus* and *C. tumuliferus* var. *C. 84* were morphologically very similar and presumably closely related, and although they thought that these two *Coccus* species shared the same ant partner, the associations now are known to be more complex (Quek *et al.* 2017). Heckroth *et al.* (1998) recorded *C. pseudotumuliferus* (as var. *C. 84*) only on Borneo, in both secondary and primary forest, from 14 species of *Macaranga* but most abundant on *M. beccariana*. Also, as stated in Quek *et al.* (2017, table S7), morphospecies *C. 214* of Heckroth *et al.* (1998) resembles *C. pseudotumuliferus*. PJG examined three Heckroth specimens (collection #214 from *M. hosei* at Gombak, Peninsular Malaysia) of this morphospecies and considered them to be identical to adult females from Heckroth collection #270 (also from *M. hosei* at Gombak), as well as sufficiently similar to Bornean collections of *C. pseudotumuliferus* to be treated as a geographic form of this species, at least until further information is available. On Borneo, Heckroth *et al.* (1998) recorded morphospecies *C. 214* exclusively from primary forest, but on Peninsular Malaysia, where there is little primary forest left, the few collections were from secondary forest. The only Heckroth specimens from Borneo slide-mounted and identified by him as *C. 214* are apparently *C. near circularis* (#522, 573, 640, 1140 & 1410) and probably *C. penangensis* (#550), all from Poring Hot Springs (difficult to identify as many specimens are poorly cleared). We assume that Heckroth first recognised his morphospecies *C. 214* based on females from Gombak that have this 214 collection number, but later decided that the morphospecies also occurred on Borneo. Probably on Borneo it may have been confused with *C. near circularis* and *C. penangensis* because Heckroth's doctoral thesis states that *C. 214* is very similar to *C. penangensis* and cannot be distinguished without slide preparation. As discussed above in the note following the list of specimens examined, there is a small amount of genetic variation among specimens of *C. pseudotumuliferus* from different areas of Borneo as well as some variation in live appearance (although live appearance is poorly recorded). Morphological variation across the geographic range of this species is discussed in the third paragraph below. Our type series is restricted to specimens from the Crocker Range in Sabah largely because of variation across the range of specimens that we consider to be this species (see Note after the listing of type specimens above).

Adult females of *C. pseudotumuliferus* from Borneo can be distinguished from all other species of *Coccus* known from *Macaranga* by having the combination of (i) very short dorsal setae that can appear to be absent; (ii) 11, rarely 12, dorsal submarginal raised areas (humps) on each side of body plus 1 medially on head (most obvious on non-slide-mounted specimens); (iii) usually 12–20 setae per anal plate; and (iv) one or both apical antennal segments with a prolongation typically ≥10 µm long. Adult females of *C. pseudotumuliferus* are most similar to the adult females of *C. caviramicolus*, *C. secretus* and *C. tumuliferus*, which also have extremely short dorsal setae, but adult females of *C. pseudotumuliferus* differ from those of *C. caviramicolus* in having marginal setae mostly tapering to a point (fimbriate in *C. caviramicolus*); from *C. secretus* in having dorsal setae rounded at the apices (tapering to a point in *C. secretus*) and the dorsal setae of the anal plates much shorter (15–45 µm long in *C. secretus* as compared with 10–23 µm long in *C. pseudotumuliferus*); and from *C. tumuliferus* in the number of submarginal raised areas (8 on each side plus 1 medially on head in *C. tumuliferus* as compared with 11, rarely 12, in *C. pseudotumuliferus*), the shape of these raised areas (usually oval to elongate in *C. pseudotumuliferus* but more circular in *C. tumuliferus*), and the number of stigmatic setae (often only 1 per cleft in *C. tumuliferus* as compared with mostly 3 in *C. pseudotumuliferus*).

There is a lot of variation in the length and robustness of the marginal setae, which range from short (15–25 mm long) rather robust setae to longer (50–80 µm) slender and usually flagellate setae, even among females

collected from different plants in a single locality. However the molecular data (Quek *et al.* 2017) strongly suggest that this variation in the marginal setae is not indicative of cryptic species because specimens that are identical in the nuclear genes sequenced can have different marginal setae. However, five specimens from the Meratus Mountains in the Indonesian province of South Kalimantan, that form a poorly supported subclade in the data of Quek *et al.* (2017), have fewer setae on the anal plates (7–10 per plate compared with the usual 12–20) and their marginal setae tend to be in a single row, especially on the head and thorax. A number of adult females from Peninsular Malaysia (see list in 'Material examined' above) represent the only record of this species from outside of Borneo. However, they differ from Bornean collections of *C. pseudotumuliferus* in having their marginal setae mostly in a single row. Furthermore, specimens from near Mersing in the Johor area (SPQ.068a) and from near Rawang (Heckroth #206) have marginal setae mostly with fimbriate apices, whereas specimens from Gombak (Heckroth #214 and #270) have mostly flagellate marginal setae (occasionally each up to 60 µm long) with just a few fimbriations on some setae. Additionally, the anal plate setae on specimens from Gombak number only 7–13 and these females also have an indistinct pattern of dorsal raised areas. Unfortunately there are no DNA data available for any of these Peninsular Malaysian specimens to suggest whether the morphological differences reflect genetic distinctness from the Bornean populations of *C. pseudotumuliferus*.

Coccus pseudotumuliferus may occur on rare occasions inside the hollow stems of non-*Macaranga* host plants (see Heckroth *et al.* (1998) for morphospecies *C.* 214), but PJG and TK have not seen these coccid specimens to verify their identity.

***Coccus secretus* Morrison**

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(Figs 2F, 13)

Coccus secretus Morrison, 1921: 662.

Type material examined. Holotype: adult female, **PENINSULAR MALAYSIA:** Penang Island, in hollow stems of *Macaranga triloba* [now correctly named *M. bancana*], date not given, coll. I.H. Burkill, ex coll. E.E. Green, 1(2, holotype, clearly marked, and 1 paratype adult female) (USNM). **Paratypes: PENINSULAR MALAYSIA:** same slide as holotype, 1(3) (USNM; a second slide with immature female not seen); **SINGAPORE:** in hollow stems of *Macaranga*, date not given, coll. I.H. Burkill, 3(4) (USNM). Morrison (1921) noted slight morphological differences between the females from these two collections, in the length of the dorsal anal plate setae and the length of the middle spiracular seta, but considered these differences insignificant in terms of even varietal segregation.

Examined non-type material from original collection. SINGAPORE: Selandar [= Selangor] forest, in hollow stem of *Macaranga triloba* [now correctly named *M. bancana*], date not given, coll. I.H. Burkill, 5-b, 1(6) (BMNH); same data as previous slide except '1318' (instead of 5-b), 1(3) (BMNH). **PENINSULAR MALAYSIA:** Penang Island, in hollow stems of *M. triloba* [now correctly named *M. bancana*], coll. I.H. Burkill, 2693, 6(11) (BMNH). These eight BMNH slides have the same data as the type collection listed above and the last two collections have the same Burkill collection numbers (1318 and 2693) as provided by Morrison (1921). However, none of the specimens are types, as explained in the Materials and methods.

Other material examined. BORNEO: Brunei, Batu Apoi Forest Reserve, 4° 33' N, 115° 09' E, *Macaranga* sp., *M. beccariana*, *M. tanarius* [a doubtful identification, since this species is a non-mymecophyte] & *M. trachyphylla*, 2–27 Aug. 1995, coll. P.J. Gullan, PJG-B2: 1(1), PJG-B7: 1(1), PJG-B8: 9(9), PJG-B11: 7(7), PJG-B46: 4(3 adult females & 1 third-instar female), PJG-B47: 5(5) & PJG-B50: 1(1); East Kalimantan, ~60 km NW of Balikpapan, 0° 06' S, 117° 10' E, 60–200 m, ex *M. pearsonii*, 15 & 16 Nov. 1992, coll. B. Fiala, #152 & #159a, 4(3 adult females & 1 second-instar female); East Kalimantan, Bukit Bangkirai, 1° 1.497' S, 118° 51.949' E, <100 m, ex *M. velutina*, 13 Feb. 2005, coll. S.-P. Quek, SPQ.728, DNA voucher 1(1); East Kalimantan, Samarinda to Kota Bangun, 0° 15.735' S, 116° 39.667' E & 0° 17.866' S, 116° 41.446' E, <100 m, ex *M. motleyana* & *M. pearsonii*, 11 June 2001, coll. S.-P. Quek, SPQ.324 & SPQ.325, DNA vouchers 2(2); North Kalimantan, Long Ampung, Sungai Anai trail, 1° 42.973' N, 114° 57.344' E, 700 m, ex *M. ?indistincta*, 9 Feb. 2005, coll. S.-P. Quek, SPQ.695a&b, DNA vouchers 2(2); Sabah, Crocker Range, Keningaum to Ulu Kimanis trail, ~5.28° N, ~116.05° E, 250 m, ex *M. bancana*, 19 Oct. 1999, coll. S.-P. Quek, SPQ.142 & SPQ.146, DNA vouchers 2(2); Sabah, Crocker Range,

Tambunan to Kota Kinabalu Road, Rafflesia Reserve, 1200 m, ex *M. hypoleuca*, 15 Oct. 1999, coll. S.-P. Quek, SPQ.100a, DNA voucher 1(1); Sabah, Crocker Range, forest behind Tambunan, 600 m, ex *M. hypoleuca* & *M. motleyana*, 18 Oct. 1999, coll. S.-P. Quek, SPQ.116 & SPQ.120, DNA vouchers 2(2); Sabah, Luasong, ex *M. indistincta* & *M. winkleri*, 4 Sept. 2003, coll. B. Fiala, #95 & 96, 3(3); Sabah, Poring, logging road, ex *M. pearsonii*, 10 Mar. 2002, coll. B. Fiala, #2 (TK0102), DNA voucher 1(1); Sabah, Poring, 140 km NE of Kota Kinabalu, ~6° N, ~116° E, 500 m, ex *M. beccariana* & *M. indistincta*, 28 Oct. 1992 & 3 Nov. 1992, coll. B. Fiala, #8 & #34, 3(3); Sabah, Poring, 140 km NE of Kota Kinabalu, ~6° N, ~116° E, 500 m, ex *M. pearsonii*, 1 Nov. 1992, coll. B. Fiala, #28a, 4(4) (2 ANIC, 2 FRIM); Sabah, road to Sandakan, ex *M. hypoleuca*, 16 Feb. 1992, coll. B. Fiala, #12a, 3(3); Sabah, Tawau Hills, ex *M. glandibracteolata*, 5 Apr. 2001, coll. B. Fiala, #78a (TK0028), DNA voucher 1(1); Sabah, 10 km south of Ranau, ex *M. pearsonii*, no date, coll. H.-P. Heckroth, #1203, 1(1 with 2 adult females of *C. pseudotumuliferus*) (FRIM); Sabah, 60.5 km south of Ranau, ex *M. hypoleuca*, 1995, coll. H.-P. Heckroth, #629, 1(1 on slide with 1 adult female of *C. pseudotumuliferus*) (FRIM); Sarawak, Lambir, ex *Macaranga* sp. & *M. kingii* [the latter now named *M. umbrosa*], 24 Feb. 1992, coll. B. Fiala, #38a & #39a, 2(2); Sarawak, Lambir, ex *M. bancana*, *M. hullettii* & *M. trachyphylla*, 2003 or 2–4 Aug. 2003, coll. T. Itioka, TI.s32, TI.s38 & TI.s62, DNA vouchers 3(3) (FDS); Sarawak, 2 km Lambir, ex *M. trachyphylla* & *M. hosei*, Dec 1992, coll. H.-P. Heckroth, #72 & #85, 6(6); Sarawak, 3 km Lambir, ex *M. trachyphylla*, Dec 1992, coll. H.-P. Heckroth, #92, 4(4); South Kalimantan, Meratus Mts, Kapayang village, 966 m, ex *M. bancana*, 17 June 2001, coll. S.-P. Quek, SPQ.334, DNA voucher 1(1). **PENINSULAR MALAYSIA:** Johor, Mawai camp, ~1.871° N, ~103.954° E, <100 m, ex *M. hypoleuca* & *M. pruinosa*, 5 Sept. 1999, coll. S.-P. Quek, SPQ.023a & SPQ.024, DNA vouchers 2(2); Johor, Sedili, 14 km from Route 3, <100 m, ex *M. pruinosa*, 5 Dec. 1999, coll. S.-P. Quek, SPQ.180a, DNA voucher 1(1); Pahang, near Kuantan, Pancing Falls, <100 m, ex *M. bancana*, 15 Sept. 1999, coll. S.-P. Quek, SPQ.059, DNA voucher 1(1); Pasoh, ex *M. hosei* & *M. hypoleuca*, Mar. 1992 & 11 Mar. 1992, coll. B. Fiala, #125a, #132a, 168a, 193a & 195a, 13(11 adult female & 2 third-instar females); Fraser's Hill, ex *M. hosei*, Mar. 1993, coll. H.-P. Heckroth, #280, 5(5) (2 ANIC, 3 FRIM); Genting, 950 m, ex *M. hullettii*, Mar. 1993, coll. H.-P. Heckroth, #212, #213 & 220, 14(14); Gombak, lower logging road, ex *M. hosei*, Feb. 1992, coll. H.-P. Heckroth, #230, 4(4); Gombak, ex *M. hosei*, Feb. 1993, coll. H.-P. Heckroth, #214, #234 & #235, 9(7 adult females & 2 third-instar females); Gombak, lower logging road, ex *M. triloba* [now *M. bancana*] & *M. hosei*, Mar. 1993, coll. H.-P. Heckroth, #209, #268 & #270, 7(7); Johor, Labis Air Panas, ex *M. hosei*, coll. H.-P. Heckroth, #1069, 1(1 on slide with 3 adult females of *C. pseudotumuliferus*) (FRIM); Sekinjang, ex *M. pruinosa*, Feb. 1993, coll. H.-P. Heckroth, #239, 5(3 adult females & 2 third-instar females including one with pharate adult). **SINGAPORE:** Bukit Timah Forest Reserve, inside stem of *Macaranga*, 1 Mar. 1994, coll. J.H. Martin, JHM6388, 6(23 adult females, 1 nymphal female & 6 first-instar nymphs) (BMNH); Bukit Timah, 1° 21' N, 103° 47' E, 100 m, inside stem of *Macaranga*, 8 Apr. 1989, coll. P.S. Ward, PSW10253, 4(4). **SUMATRA:** Gunung Leuser area, ~3° 50' N, 97° 40' E, ex *M. hypoleuca*, 31 Oct. 1993, coll. U. Maschwitz, sent by B. Fiala, #12a, 1(1); Ketambe, ~3° 50' N, ~97° 40' E, ex *M. hypoleuca*, 30 Oct. 1992, coll. U. Maschwitz, sent by B. Fiala, #1359, 2(2).

Material examined from non-*Macaranga* host plants: **PENINSULAR MALAYSIA:** Selangor, Ulu Gombak, in *Lepisanthus tetraphylla* (Sapindaceae) in association with *Crematogaster* ants, 28 Mar. 1994, coll. G. Riedel, #94-125.2, 2(2); Selangor, Ulu Gombak, in *Pometia pinnata* (Sapindaceae) in association with *Crematogaster* ants, 19 Apr. 1994, coll. G. Riedel, #94-150.2, 5(5); Selangor, Ulu Gombak, ~300 m, ex hollow stem of *Ryparosa fasciculata* (Achariaceae) in association with ants of *Cladomyrma ?petalae*, 20 Sept. 1993, coll. A. Moog, #93/161, 2(2); Selangor, Ulu Gombak, ex hollow stem of *Strychnos vanprukii* (Loganiaceae) in association with *C. ?petalae*, 7 Mar. 1993, coll. A. Moog, #93/111, 1(1); Selangor, Ulu Gombak, ~300 m, ex hollow stem of *S. vanprukii* in association with *Cladomyrma* sp., 12 Jan. 1995, coll. A. Moog, #95/4, 1(1); Perak, road 59, 25 km to Tanah Rata, ex hollow stem of *Saraca thaipingensis* (Fabaceae) in association with *C. ?petalae*, 13 Mar. 1993, coll. A. Moog, #93/116, 1(1).

Adult female. Unmounted material. “Slightly longer than wide, flat, the center usually slightly elevated, with faint radiating ridges around the margin, dirty pale brown, appearing as if covered with a thin film of dust; ..” (Morrison 1921: 662). Morrison’s description probably was based on dried specimens and thus differs in body colour from live specimens photographed from two regions in Borneo. Live adult females varied from pale yellowish-white to pale pink or dark pink (Fig. 2F), depending on age, with the dorsal wax appearing granular due to being composed of small irregularly shaped pieces, and the marginal stigmatic areas were often distinct due to accumulation of white wax.

Slide-mounted adult female (n=34, including 7 paratypes; Fig. 13). Body oval, often broadest posteriorly, 1.2–3.4 mm long, 1.0–2.7 mm wide.

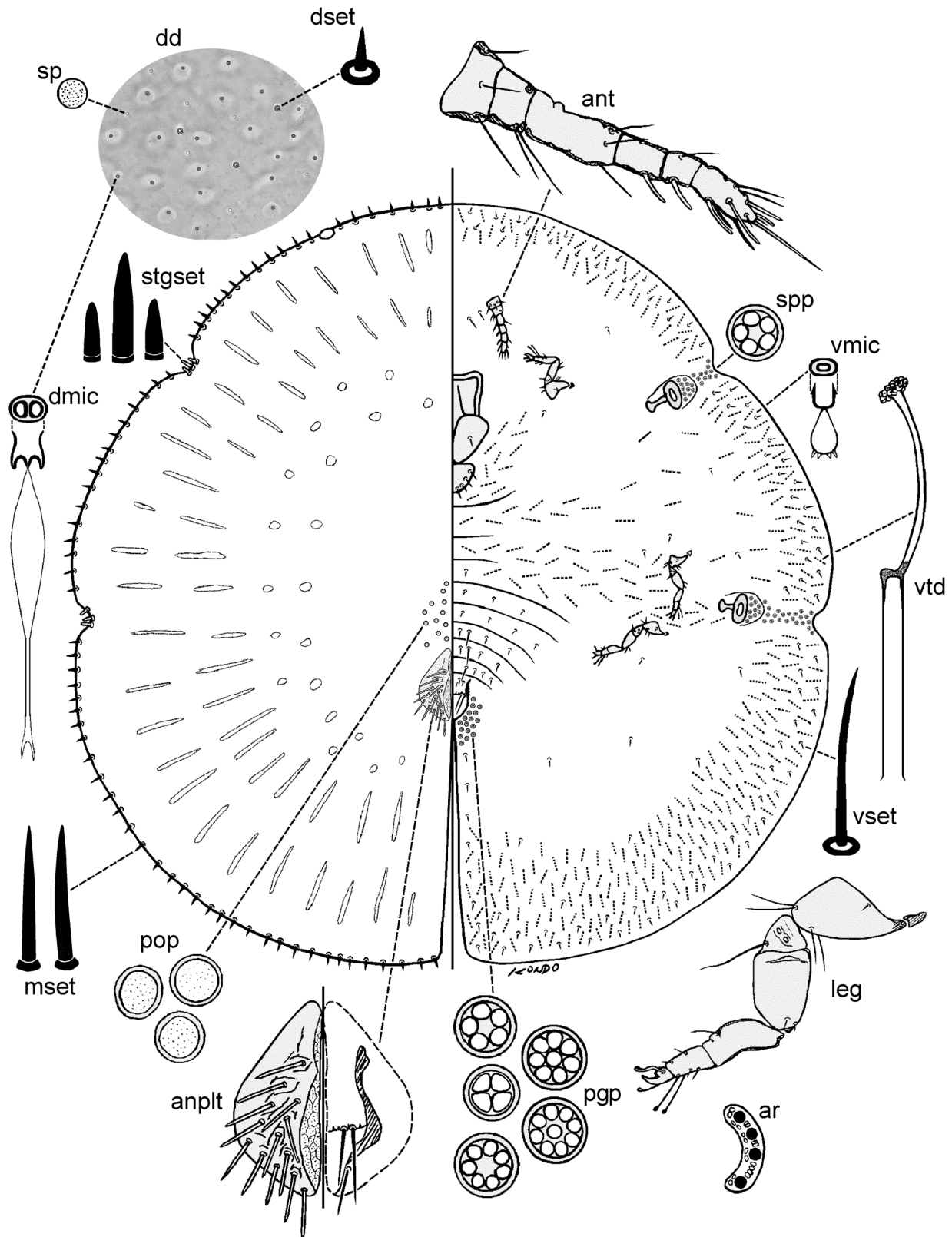


FIGURE 13. Adult female of *Coccus secretus* Morrison. Abbreviations as in Fig. 3.

Dorsum. Derm (dd) membranous and areolated, with very distinct, lightly sclerotised submarginal lines radiating inwards at right angles to margin. Dorsal setae (dset) very short, as long as or slightly longer than width of setal base, each 2.5–10.0 (4–5 μm on paratypes) μm long, tapering to a point, scattered on dorsum. Simple pores (sp) each 1.5–2.0 μm wide, scattered evenly on dorsum. Preopercular pores (pop) circular to oval in shape, very variable in size and number (sometimes absent), if present each 2.5–7.5 μm wide, scarce to numerous, in a group of 2–34 anterior to anal plates. Dorsal microducts (dmic) in areolations each about 2–3 μm wide, appearing bilocular under high magnification. Anal plates (anplt) each almost subcircular with anterolateral margin slightly longer than posterolateral margin and lateral margin rounded, 1.9–2.7 (mostly 2.1–2.4) times longer than wide, often with apex slightly truncate or indented, inner lobes normal, membranous with a tessellated texture, each plate 140–203 μm long, 65–85 μm wide, anterolateral margin 98–150 μm long, posterolateral margin 75–118 (usually 85–100) μm long; each plate with 6–16 dorsal setae, each seta stout and typically ≥ 2 μm wide for most of length and 15–45 (mostly 20–30) μm long with pointed, rounded or expanded apex; setae usually present on posterior two-thirds of each plate. Anal ring (ar) bearing 8 setae [Morrison (1921: 663) says 6 setae, but the thinner pair are difficult to see], each 70–95 μm long.

Margin. Eyespots present slightly removed from dorsal margin, each 12–25 μm in maximum dimension, often not detected or hard to detect. Marginal setae (mset) sharply spinose, present in 1 row, each 12.5–35.0 (mostly 15–30) μm long, with 10–21 setae between anterior and posterior stigmatic areas on each side of body. Stigmatic setae (stgset) well developed, almost always numbering 3 (very rarely 2) per cleft, sharply spinose, median setae longest, each 20–48 (mostly 25–35) μm long, lateral setae each 10–33 (mostly 15–25) μm long.

Venter. Derm membranous. Ventral setae (vset) slender, longest submedially on posterior abdominal segments, each 17–70 μm long, elsewhere shorter, each 10–18 μm long. Interantennal setae usually numbering 2 pairs, each of a different length, with each seta of each pair either 15–25 μm or 27–50 μm long, more rarely 3 or 4 pairs with each seta 10–35 μm long. Ventral tubular ducts (vtd) present in a broad submarginal band; each duct with outer ductule 12–15 μm long, inner ductule 17–20 μm long, and duct opening about 2 μm wide. Ventral microducts (vmic) each 2–3 μm wide, scattered fairly evenly on venter. Pregenital disc-pores (pgp) each with 4–8 (mostly 7) loculi, each pore 5–8 μm wide. Antennae (ant) usually 6 (rarely 5) segmented, each 108–158 μm long; apical segment 20–33 μm long; fleshy setae present on last 3 segments when 6 segmented, and on last 2 segments when 5 segmented. Clypeolabral shield 180–250 μm long, 163–213 μm wide; labium 80–113 μm long, 100–132 μm wide. Legs very small, with hind trochanter + femur 38–68 μm long; hind tibia + tarsus 43–80 μm long; all tarsal digitules each 15–25 μm long; claw digitules each 13–18 μm long, claws each 10–15 μm long. Spiracles normal: anterior peritremes each 50–88 μm wide; posterior peritremes each 55–90 μm wide. Spiracular pores (spp) each 4–6 μm wide, with 2–7 (mostly 5) loculi.

Comments. Adult females of *C. secretus* can be distinguished from all other species of *Coccus* known from *Macaranga* by having the combination of (1) short antennae (each <160 μm long and usually with 6 segments); (2) very small legs (e.g., hind trochanter + femur <80 μm long); (3) short dorsal setae (≤ 10 μm long) tapering to a point; (4) a single row of sharply spinose marginal setae, each mostly 15–30 μm long; and (5) robust anal plate setae, each typically ≥ 2 μm wide for most of its length and mostly 20–30 μm long. Adult females of *C. secretus* are most similar to the adult females of the *C. tumuliferus* group (*C. caviramicolus*, *C. pseudotumuliferus* and *C. tumuliferus*) in having very short dorsal setae but they differ from those females in that their dorsal setae each taper to a point (apex rounded in the other species), their marginal setae are never in 2 rows and never flagellate or fimbriate (sometimes in 2 or even 3 rows and often fimbriate or flagellate in the other species) and their anal plate setae mostly are longer (typically 20–30 μm long) and distinctively broad for their full length (tapering to a point and usually ≤ 20 μm long in the other species). Specimens of *C. secretus* from non-*Macaranga* host plants were indistinguishable morphologically from females from *Macaranga*, although four of the five non-*Macaranga* females measured had a slightly larger length to width ratio for their anal plates (2.5–2.7) compared with *Macaranga* females (ratio never greater than 2.4).

The analysis of Quek *et al.* (2017) using two nuclear genes found *C. secretus* to be separated from the other *Coccus* species on *Macaranga* by the placement of *C. hesperidum*. This topology also was recovered in one of the two mitochondrial data sets of Ueda *et al.* (2010). We have not been able to see and verify the identity of the specimen called *C. hesperidum* that was used in the papers of Ueda *et al.* (2008, 2010) and Quek *et al.* (2017), but its proximity to the *Macaranga* coccids in the nuclear DNA tree of Quek *et al.* (2017) is consistent with the observation that *C. penangensis* is close to *C. hesperidum* based on analysis of two ribosomal genes, one nuclear

gene and *COI* (Lin *et al.* 2013). It seems that *C. secretus* is not closely related to the other specialist *Coccus* partners of the myrmecophytic *Macaranga* species. Further analyses including additional genes and a diversity of *Coccus* species are required to determine the relationships of *C. secretus* to other *Coccus* species.

Coccus secretus is a widespread species occurring in both primary and secondary forests of Borneo, Peninsular Malaysia, Singapore and Sumatra (Heckroth *et al.* 1998; list of Material examined above). It also has been collected a number of times from inside the hollow stems of non-*Macaranga* host plants (see list above) even though such plants have been surveyed much less frequently than *Macaranga*. Heckroth *et al.* (1998) recorded *C. secretus* inside the hollow stems of both myrmecophytes and non-myrmecophytes in association with both the obligatory plant-ant genus *Cladomyrma* and non-specific *Crematogaster* species. Quek *et al.* (2017) found that *C. secretus* in most cases made up a small proportion of the coccid partners of the specialist *Crematogaster* ants and myrmecophytic *Macaranga* species. Thus, it is possible that *C. secretus* is a more facultative or opportunistic partner than the other *Coccus* species found in the system.

***Coccus tumuliferus* Morrison**

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(Figs 11D, 14)

Coccus tumuliferus Morrison, 1921: 655.

Coccus tumulifer Lindinger, 1932f: 197. Unjustified emendation; discovered by Williams & Ben-Dov, 2009: 46.

Type material examined. Holotype: adult female, **SINGAPORE:** on *Macaranga hypotema* [sic, see below], E.E. Green letter dated 8.vi.1916, coll. I.H. Burkill, 1(2, holotype clearly marked and 1 paratype adult female) (USNM). **Paratypes:** same data as holotype but two slides specify "in hollow stems of *M. hypotema*", 4(4 adult females, including 1 on slide with holotype, + 2 slides with a number of first-instar nymphs) (USNM; the 1 slide with 3 paratype females not seen). Morrison's original description refers to five adult females and several mounted "larvae", and this accords with the slides listed above, all of which have Morrison type labels on both the slides and their envelopes. However there is another USNM slide of this species which appears to have been prepared and labelled by Green from original Burkill material as its label starts: "Ctenochiton / tumuliferum / Green, ms. / Part of type / material." (details listed immediately below), but these specimens are not mentioned by Morrison in the original description of this species.

Examined non-type material from original collection. SINGAPORE: in hollow stems of *Macaranga hypotema* [sic], coll. I.H. Burkill, 1(2 adult females + 1 third-instar female) (USNM; slide labelled by Green and discussed above); in hollow stems of *Macaranga hypoleuca*, attended by ants, coll. I.H. Burkill, 2(2) (BMNH). The BMNH also has another 10 slides, with a total of 29 adult females and nymphs, of this Singapore collection from Burkill; PJG examined these slides in 1994 and made notes but did not take measurements. All of these BMNH slides have similar data to the type collection listed above, but they are not type specimens, as explained in the Materials and methods.

Note. The USNM type slides give the host plant as *M. hypotema* and Morrison (1921) listed the host as *M. hypolema*, but there is no such species. The BMNH slides give the host as *M. hypoleuca*, which is a member of the *Pachystemon* section of *Macaranga* (Davies *et al.* 2001).

Other material examined. BORNEO: Sarawak, Santubong, ex *M. hypoleuca*, Dec. 1994, coll. H.-P. Heckroth, 445, 447, 450, 451 & 453, 5(14 + 1 adult female of *C. macarangae*) (2 slides ANIC, 3 slides FRIM). **PENINSULAR MALAYSIA:** Fraser's Hill, ex *M. hypoleuca*, Mar. 1993, coll. H.-P. Heckroth, #284, 3(3); Gombak, lower logging road, ex *M. hosei*, Feb. 1992, coll. H.-P. Heckroth, #230, 2(2; 1 female taken from the mandibles of an ant); Johor, Kota Tinggi to falls, lowland, ex *M. hypoleuca*, 5 Sept. 1999, coll. S.-P. Quek, SPQ.018, DNA voucher 1(1); Johor, Mawai camp, Ginger Hill, ~1.871 N, ~103.954 E, <100 m, ex *M. hypoleuca*, 7 Sept. 1999, coll. S.-P. Quek, SPQ.027, SQP.030 & SPQ.032, DNA vouchers 3(2 adult females + 1 immature female); Johor, Sedili, 14 km from Route 3, <100 m, ex *M. hypoleuca*, 5 Dec. 1999, coll. S.-P. Quek, SPQ.182, DNA voucher 1(1); Pahang, near Kuantan on road to Pancing Falls, <100 m, ex *M. hypoleuca*, 15 Sept. 1999, coll. S.-P. Quek, SPQ.054, DNA voucher 1(1); Pahang, Kuantan to Johor Road, 299 km to Johor, lowland, ex *M. pruinosa*, 16 Sept. 1999, coll. S.-P. Quek, SPQ.062, SPQ.063a & SPQ.064, DNA vouchers 3(3); Pahang, Kuantan to Johor Road, 299 km to Johor, <100 m, ex *M. hypoleuca*, 16 Sept. 1999, coll. S.-P. Quek, SPQ.066 & SPQ.067,

DNA vouchers 2(2); Terengganu, Bauk Hill, <100 m, ex *M. hypoleuca*, 12 Sept 1999, S.-P. Quek, SPQ.038, DNA voucher 1(1). **SINGAPORE:** Old Upper Thompson Road, ~1.381 N, ~103.813 E, <100 m, ex *M. hypoleuca*, 4 Oct. 1999, coll. S.-P. Quek, SPQ.090, DNA voucher 1(1).

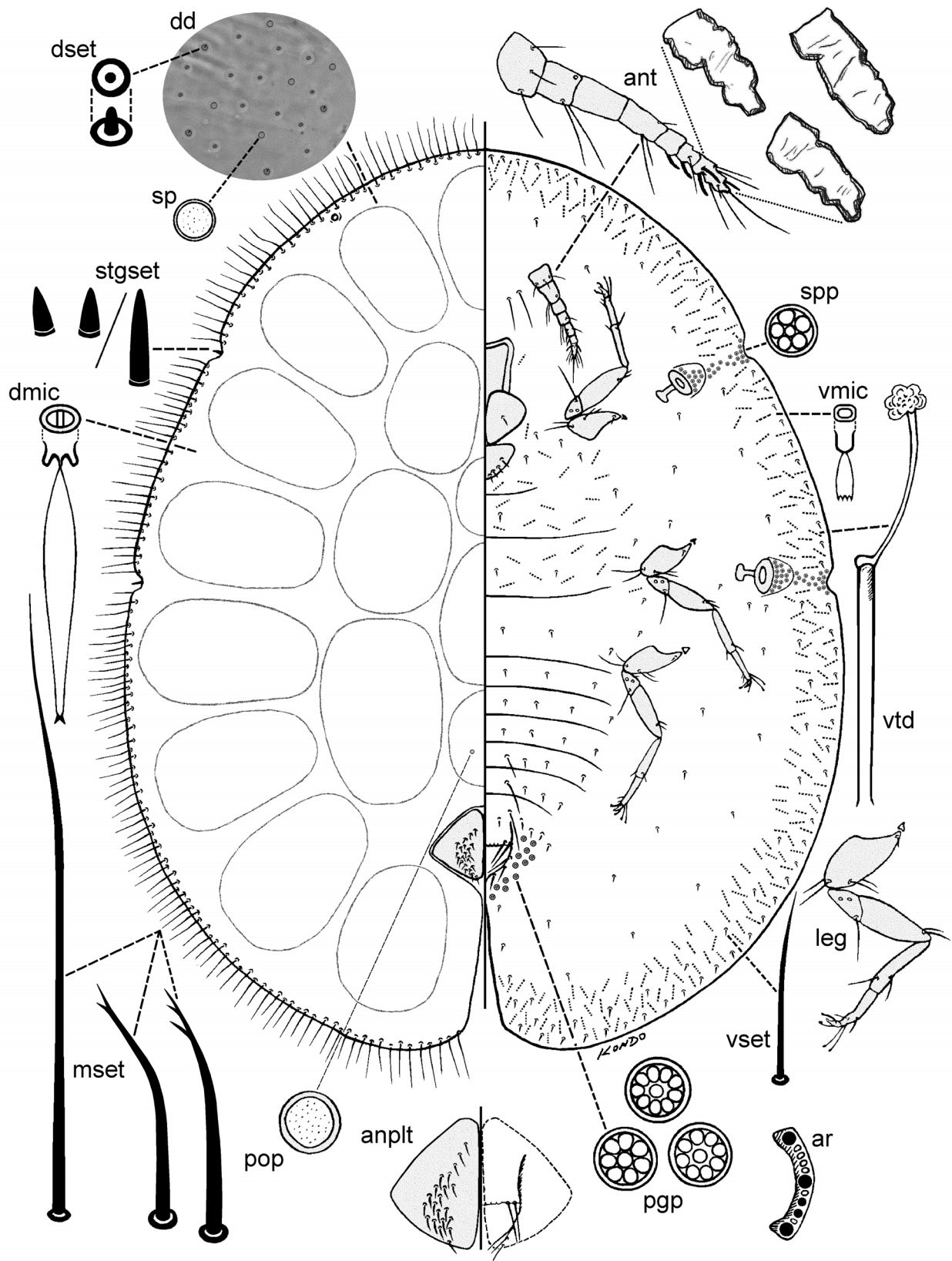


FIGURE 14. Adult female of *Coccus tumuliferus* Morrison. Abbreviations as in Fig. 3.

Adult female. Unmounted material. “.. rarely broad oval, but usually broadened behind and triangular with angles rounded; plane of dorsal surface flat, but in dried specimens covered with relatively large knobs having a fairly definite arrangement of a median longitudinal single row and on each side of this two other rows, the outer one forming a continuous row around the body at the margin; dorsally covered with a thin, brittle, whitish but more or less translucent, glassy secretion, very easily broken and usually more or less wanting, molded into elevations and depressions corresponding to those of the body, this covering normally wanting over the flattened extreme margin of the body; body color dull brown, of secretory covering, as stated, translucent whitish; .. (Morrison 1921: 655). For the present revision, the available adult females preserved in ethanol were pinkish red in colour (Fig. 11D). Although Morrison recorded the body of dry adult females as dull brown, but this is unlikely to reflect the colour in life.

Slide-mounted adult female (n=16, including holotype and paratypes; specimens from Santubong in Sarawak excluded; Fig. 14). Body oval to broadly oval, 1.5–2.8 mm long, 1.2–2.4 mm wide, widest in posterior half.

Dorsum. Derm (dd) completely membranous, areolated; with a series of humps (oval to circular raised areas of cuticle) present in a submarginal row of 17 (typically 8 on each side plus 1 medially on head), 3 on each side submedially, and usually 3 medially but these often poorly defined. Dorsal setae (dset) very short, each 2–3 μm long with rounded apex, scattered on dorsum. Simple pores (sp) each 2.5–3.0 μm wide, scattered evenly on dorsum. Preopercular pores (pop) each 3.8–5.0 μm wide, scarce, present in a small group of 1–5 anterior to anal plates. Dorsal microducts (dmic) in areolations each 2.0–2.5 μm wide, appearing bilocular under high magnification. Anal plates (anpl) each triangular with anterolateral margin longer than posterolateral margin, inner lobes fairly developed, with a tessellated texture, each plate 150–198 μm long, 100–125 μm wide, anterolateral margin 140–163 μm long, posterolateral margin 90–128 μm long; each plate with 14–22 dorsal setae, slender spinose, each 8–23 μm long. Anal ring (ar) probably always bearing 10 setae [Morrison (1921: 657) says 8 setae, but the thinner setae are difficult to see], each 100–155 μm long.

Margin. Eyespots present slightly removed from dorsal margin, each 20–28 μm in maximum dimension. Marginal setae (mset) of 2 broad types usually not found together on a specimen (but female SPQ.030 with both types): (1) long (20–110 μm) and flagellate, present in 1 or 2 rows (rarely up to 3 rows on part of margin) (as illustrated in Fig. 14); (2) short (12–28 μm long) and with apices mostly fimbriate (or at least divided), usually present in a single row, rarely in 2 rows on parts of margin; with about 7–30 marginal setae between anterior and posterior stigmatic areas on each side of body. Stigmatic setae (stgset) of variable length and development, numbering 1–3 but usually 1 (rarely absent) per cleft, median seta 3–25 μm long, lateral ones if present each 3.0–7.5 μm long, spinose and tapering to a rounded point, rarely 3 very short setae ($\leq 5 \mu\text{m}$) present.

Venter. Derm membranous. Ventral setae (vset) slender, longest submedially on posterior abdominal segments, each 20–88 μm long, elsewhere shorter, 7.5–40 μm long. Interantennal setae in 2 pairs, each seta 50–70 μm long. Ventral tubular ducts (vtd) present in a broad submarginal band; each duct with outer ductule about 15 μm long, inner ductule about 17.5 μm long, and duct opening about 2.5 μm wide. Ventral microducts (vmic) each about 2 μm wide, scattered fairly evenly on venter. Pregenital disc-pores (pgp) each with 7–9 loculi, each pore 5–7 μm wide. Antennae (ant) usually 7, rarely 6, segmented [Morrison (1921) recorded 8 segments but this appears to be erroneous], each antenna 210–270 μm long; apical antennal segment 30–43 mm long, with apical prolongation 2–8 μm long on at least 1 antenna (often absent on 1 or both antennae of pair); fleshy setae present on last 3 segments when 7 segmented, and on last 2 segments when 6 segmented. Mouthparts normal; clypeolabral shield 210–270 μm long, 170–235 μm wide; labium 80–100 μm long, 120–150 μm wide. Legs with hind trochanter + femur 155–195 μm long; hind tibia + tarsus 155–200 μm long; all tarsal digitules each 28–40 μm long; claw digitules each 25–30 μm long, claws each about 30 μm long. Spiracles normal: anterior peritremes each 45–58 μm wide; posterior peritremes each 50–65 μm wide. Spiracular pores (spp) each 4–5 μm wide, mostly with 5 loculi, rarely 4.

Comments. Adult females of *C. tumuliferus* can be distinguished from all other species of *Coccus* known from *Macaranga* by having the combination of (i) very short dorsal setae that can appear to be absent; (ii) almost always 8 dorsal submarginal raised areas on each side of body plus 1 medially on head (most obvious on live or ethanol-preserved specimens); and (iii) usually 14–22 dorsal setae per anal plate, each slender spinose and mostly $\leq 20 \mu\text{m}$ long. Adult females of *C. tumuliferus* are most similar to the adult females of *C. caviramicolus*, *C. pseudotumuliferus* and *C. secretus*, which all also have extremely short dorsal setae, but they differ from females of *C. caviramicolus* in having marginal setae either flagellate or with few fimbriations (strongly fimbriate in *C. caviramicolus*) and anal plates with a ratio for the length of the anterolateral margin to posterolateral margin of

1.12 to 1.38 (ratio mostly 1.41 to 2.06 in *C. caviramicolus*); from *C. secretus* in having dorsal setae rounded at the apices (tapering to a point in *C. secretus*) and the dorsal setae of the anal plates are usually much shorter (each 8–23 µm long in *C. tumuliferus* compared with 15–45 µm long in *C. secretus*); and from *C. pseudotumuliferus* in the number of submarginal raised areas (typically 8 on each side plus 1 medially on head in *C. tumuliferus* compared with usually 11 on each side plus 1 medially on head in *C. pseudotumuliferus*), the shape of these raised areas (usually circular in *C. tumuliferus* but oval to elongate in *C. pseudotumuliferus*), and the number of stigmatic setae (0–3 but usually 1 per cleft in *C. tumuliferus* compared with usually 3 per cleft in *C. pseudotumuliferus*).

Heckroth *et al.* (1998) recognised *C. tumuliferus* from both Borneo and Peninsular Malaysia and recorded it as most common on *M. hypoleuca*, which is a common and widespread tree in both regions (Davies 2001). We had available for study 16 slide preparations, each containing from one to six adult females, made by Heckroth and identified by him as *C. tumuliferus* from Borneo. Five slides (#445, 447, 450, 451 and 453, ex *M. hypoleuca*, Santubong [probably on the lower slopes of Mt Santubong], Sarawak) have adult females of *C. tumuliferus*, but the other 11 slides (#495, 525, 526, 527, 581, 589, 598, 629, 631, 635 and 614, ex either *M. bancana*, *M. hypoleuca*, *M. indistincta*, *M. beccariana* or *M. pearsonii*, from three areas in Sabah) contain specimens of *C. pseudotumuliferus*. Other than the specimens from Santubong, all other records for *C. tumuliferus* are from Singapore and Peninsular Malaysia and, given that it is unlikely that Heckroth's specimens of *C. tumuliferus* are mislabelled, the explanation for this distribution is probably geographic. Santubong is in the region of Sarawak closest to Singapore and West Malaysia and may have been isolated from the rest of Sarawak by past geological and environmental conditions. The Kuching area (including Mt Santubong) of western Sarawak is south of the Lupar Valley and a geological fault called the Lupar Line. This fault marks the southwestern boundary of the rock formation called the Rajang Group in Sarawak (Moss 1998; Wang *et al.* 2016). The Lupar Valley contains a large river, the Batang Lupar, surrounded by extensive swamp forests, which may have created a barrier to the dispersal of some taxa. A barrier effect of the Lupar Valley has been hypothesised for a species of Malaysian frog for which populations from Peninsular Malaysia and western Sarawak were more genetically similar than populations in western Sarawak were to those in northeastern Sarawak (Zainudin *et al.* 2010).

The adult females of *C. tumuliferus* from Santubong have 7–9 dorsal submarginal humps on each side of the body and of the typical shape for *C. tumuliferus*; 12–16 dorsal anal plate setae on the six females for which they are visible clearly; flagellate marginal setae up to 90 µm long (but usually <60 µm) in 1 or 2 rows; 1–4 stigmatic setae per cleft with each seta usually 10–25 (rarely up to 36) µm long; and an apical antennal prolongation 5–8 µm long (rarely 10 µm long on one antenna of a pair); thus these females barely differ in key morphological features from females collected from Singapore and Peninsular Malaysia. Further collecting and molecular assessment of *C. tumuliferus* from the Kuching region (i.e., south of the Lupar Line) would be valuable. Furthermore, *C. tumuliferus* may occur in the northwestern part of West Kalimantan but no collections have been made in that region.

Discussion

In this study we recognise 10 species of *Coccus* associated with *Crematogaster* ants (almost all from the *Crematogaster borneensis*-group) living inside the hollow stems of *Macaranga* plants in Southeast Asia. Three of these *Coccus* species are described as new to science in this paper, although additional undescribed species may exist (see third paragraph below). The adult females of two species, *C. lambirensis* and *C. secretus*, show several morphological distinctions from the other *Macaranga* coccids and it is possible that both of these species are more generalist in their associations than the other *Coccus* species. The morphology and ecological associations of *C. lambirensis* and *C. secretus* are discussed further in the respective Comments section for each species, as well as in the last paragraph below for *C. secretus*.

Heckroth *et al.* (1998) recognised two morphological groups among the *Macaranga* coccids. These were the *C. tumuliferus* group comprising *C. tumuliferus*, a variety of that species and two morphospecies (C. 214 and C. 296), and the *C. penangensis* group containing *C. penangensis*, *C. macarangae*, *C. macarangicolus* and one morphospecies (C. 41 = an immature of *C. penangensis*; refer to the section on 'Species recognition' prior to the key to species). *Coccus secretus*, *C. caviramicolus* and several rare entities were not grouped. The *C. penangensis* group of Heckroth *et al.* (1998) was not recovered in the molecular study of Quek *et al.* (2017); however, the *C. tumuliferus* group of Heckroth *et al.* was recovered as a well-supported clade by Quek *et al.* (2017), except that it

also included *C. caviramicolus* that Heckroth *et al.* had not grouped. The adult females of the three species, *C. caviramicolus*, *C. pseudotumuliferus* and *C. tumuliferus*, which form that clade, share the morphological feature of very short dorsal setae (≤ 3 μm long) that are broad and apically rounded. These setae are difficult to detect and need to be viewed with x100 objective under oil. Adult females of *C. secretus* also have short dorsal setae but they are slightly longer (4–5 μm) and taper to a point. Females of *C. secretus* also have other morphological features (such as very rounded anal plates, unusual anal plate setae and very small legs relative to body size) that set this species apart from the *C. tumuliferus* group and the other *Coccus* species. In addition, available data from nuclear genes (Quek *et al.* 2017) suggest that *C. secretus* is not closely related to the other species of *Coccus* from *Macaranga* (see Comments for *C. secretus*). Further molecular data are required to determine the relationships of the *Macaranga* coccids to other species of the genus *Coccus*.

During his Ph.D. studies, Hans-Peter Heckroth recognised a number of morphospecies. Three of these have been discussed above (i.e., morphospecies C. 41 discussed under 'Species recognition', and *Coccus tumuliferus* var. C. 84 and morphospecies C. 214 under our new species *C. pseudotumuliferus*). The morphospecies referred to as C. 296 by Heckroth *et al.* (1998) appears to be a distinct new species that belongs to the *C. tumuliferus* group as stated by Heckroth *et al.* (1998, p. 433) and suggested by Quek *et al.* (2017, table S7). Heckroth *et al.* (1998) reported that it occurred at several sites only in West Malaysia and mainly on *M. hypoleuca*. We only have seen specimens from a single collection made in March 1993 by H.-P. Heckroth (#267) from the hollow stem of a plant of *M. hypoleuca* on the upper logging road at Gombak in Peninsular Malaysia. Some females were parasitised by *Coccophagus acanthosceles* Waterston (Hymenoptera: Aphelinidae), identified by A. Polaszek in 1993, with two of the coccids from Heckroth's collection sent by Polaszek to PJG for identification. Three additional adult females and two female nymphs of C. 296 from Heckroth's #267 were slide-mounted by PJG in 1994 (previously sent to PJG by HPH). No additional specimens suitably preserved for intact DNA exist and no DNA data are available; thus its relationship to *C. tumuliferus* and *C. pseudotumuliferus* is unclear and it would be judicious to collect fresh material prior to description of this morphospecies as a new species.

The antiquity and phylogeography of members of the *Macaranga-Crematogaster-Coccus* system have been the subject of several studies, but all based on data from just one or a few genes. The age of the sections containing the myrmecophytic species of *Macaranga* is not certain, but Fiala *et al.* (2016) found that the group composed of *M. constricta*, *M. motleyana* and *M. griffithiana* diverged from its sister group within section *Pachystemon* between 5 to 10 Ma (based on *ITS* sequences, see this paper for an updated phylogeny of *Macaranga* based on the dated phylogenetic estimation of van Welzen *et al.* (2014)). Van Welzen *et al.* did not include most of the obligate myrmecophytic species, which they said were recently speciated. Quek *et al.* (2004) estimated the clade of *Crematogaster* ants associated with *Macaranga* to be at least 12 million years old (mid Miocene) based on *COI* divergence rates that were congruent with other independent evidence, but a later more comprehensive study, using *COI* and *COII* genes (Quek *et al.* 2007), revised the estimate for the earliest diversification of these ants to between 15.9 and 22.6 Ma (early to mid-Miocene). In contrast, the age of the clade of *Coccus* species associated with these *Crematogaster* ants is much less clear. Ueda *et al.* (2008), using *COI* data from the coccids collected with the ant samples analysed by Quek *et al.* (2007), estimated the minimum age for the coccids to be half that of the ants, about 9–7 Ma. A subsequent study on the phylogeography of these coccids, again using only mitochondrial sequences (Ueda *et al.* 2010), suggested that the coccids repeatedly migrated between Peninsular Malaysia and Borneo. However, as explained in the Introduction (above) and in Quek *et al.* (2017), the mitochondrial-based phylogenetic estimate for the *Coccus* samples suffered from inadvertent inclusion of pseudogenes and thus the phylogeographic and age interpretation for the coccids is suspect. The analyses of Quek *et al.* (2017), based on two nuclear genes, recovered coccid clades congruent with morphological data, but this study did not attempt to re-evaluate the age and biogeographic history of the coccids. It is likely that the specialist *Macaranga*-associated *Coccus* species (= the "Main Clade" in figure 3 of Quek *et al.* (2017)), that is excluding *C. secretus*, have a similar or younger crown-group age to their plant and ant hosts. *Coccus secretus* may not be part of the same clade as the other *Macaranga* coccids, as discussed under the Comments for that species. Also, *C. secretus* is more generalist in its associations with ants and host plants, whereas the *Coccus* species of the Main Clade appear to be more obligately associated with *Macaranga* myrmecophytes. Only further sampling of *Coccus* species and populations and the use of additional genetic data will resolve questions concerning the relationships of the species, the timing of their origin, and their coevolution with *Macaranga* plants and *Crematogaster* ants.

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