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Citation	Insecta matsumurana. New series : journal of the Faculty of Agriculture Hokkaido University, series entomology, 62, 123-151
Issue Date	2005-12
Doc URL	http://hdl.handle.net/2115/10526
Type	bulletin (article)
File Information	62_p123-151.pdf

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INSECTA MATSUMURANA

NEW SERIES 62: 123–151 DECEMBER 2005

MATERIAL OF DIPTEROCARP-ASSOCIATED GALL-INHABITING COCCOIDS COLLECTED IN NEGERI SEMBILAN, MALAYA (HOMOPTERA: COCCOIDEA)

By SADAO TAKAGI, TETSURO HOSAKA, and TOSHINORI OKUDA

Abstract

TAKAGI, S., HOSAKA, T., and OKUDA, T., 2005. Material of dipterocarp-associated gall-inhabiting coccoids collected in Negeri Sembilan, Malaya (Homoptera: Coccoidea). *Ins. matsum. n. s.* 62: 123–151, 18 figs.

Four species of dipterocarp-associated gall-inhabiting coccoids were collected in Negeri Sembilan, Malaya, Malaysia, in 2003 and 2004 in surveys conducted under a project on biodiversity in tropical forests, and taxonomic accounts of them are given in this paper. One of them, *Gallacoccus longisetosus*, sp. nov., is described on the basis of two female and three male instars. This species is probably rightly referred to *Gallacoccus*, and yet peculiar among the known species of the genus in having spinous but remarkably elongated setae dorsally on the first-instar female. The other species are also referred to *Gallacoccus*, but they are not formally named owing to the insufficient material; instead, they are designated by tags coined by combining abbreviations of the collection year, locality, and host plant. One of them is closely similar to *G. longisetosus* in many adult male characters, whereas the other two resemble *Gallacoccos heckrothi* in the male nymphs or the adult female. Some features and their characters are discussed with regard to their significance in function and phylogeny: dermal pits in the first-instar female, legs in the first instar male, penial sheath pores and other sensilla, and papillae and claws in the adult male. The discussions remain preliminary, but suggest intricate relationships between function and phylogeny.

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Introduction

In recent years, Hosaka, one of the authors, has been engaged in a project on biodiversity in tropical forests, and has carried on researches into the insect fauna associated with dipterocarp fruits mainly in the Pasoh Forest Reserve, Negeri Sembilan, Malaya, Malaysia. In South-East Asian tropical rain forests, dipterocarps (and certain other trees) do not flower every year and, thus, their fruit production is irregularly punctuated by sterile years and concentrated in general flowering years, when dipterocarps in the same forests flower in succession (for a recent literature, see: Inoue and Hamid, eds., 1997). The question arises how the fruit-associated fauna on dipterocarps can be maintained when fruit production is punctuated. A possible answer may be the presence of a diet alternative to fruits during the sterile years.

Jenkins and Mabberley (1994) related how 'phytophagous larvae' consumed the 'nutrient rich core' of the full-grown gall inhabited by the coccoid *Mangalorea hopeae*. Komai (1999) recorded *Andrioplecta* sp. ('species a'), Tortricidae, Lepidoptera, from dipterocarp galls induced by beesoniid coccoids ('beenisonid coccids': apparently *Gallacoccus spinigalla* and/or *G. heckrothi*), and mentioned three other species of *Andrioplecta* as feeders on 'seeds' of dipterocarps. The larva of 'species a' was recorded not as a gall-consumer but as a predator on the gall-inhabiting coccoids. However, in general, the possibility that galls are involved in the diet of some fruit-feeding insects may not be rejected.

Dipterocarp galls, therefore, were included in the surveys. As a result, a lot of galls were collected mainly on the forest canopy 40–50m high and from more than seven species of dipterocarps including *Dipterocarpus sublamellatus*, *Shorea acuminata*, *S. leprosula*, *S. macroptera*, *S. maxwelliana*, *S. ovalis*, and *S. parvifolia*. They are diverse in size and structure; some of them are small, whereas others seem sufficiently large for the expected alternative diet. On dissection, most of the galls, small and large, appeared to have been induced by dipterous or hymenopterous insects. The smaller part of the material harboured coccoids belonging to four species, of which taxonomic accounts are given in the present paper.

Anthony (1974) recorded from Singapore a variety of galls induced by mites, midges, wasps, moths, thrips, psyllids, coccoids, aphids, and others on plants belonging to 26 families, especially the Dipterocarpaceae, Clusiaceae [Guttiferae], Myrtaceae, Lauraceae, and Euphorbiaceae. As regards the family Dipterocarpaceae, she obtained from *Shorea curtisii* two species of coccoids, *Gallacoccus anthonyae* and *G. secundus*, which inhabited galls of the 'inflorescence type' and 'fruit type' (as termed in this paper) respectively, and also midges and wasps, which were collected by rearing galls in cages, and observed galls of various types induced by midges and wasps. (She recorded another gallicolous coccoid from *S. curtisii*, later named *Beesonia shoreae*, but this coccoid provoked a merely fusiform hypertrophy on the twig.) Thus, the gall-inducing fauna on dipterocarps in the Pasoh forest does not seem much different from the fauna on *S. curtisii* in Singapore in the greater part being composed of insects other than coccoids, mainly midges and wasps.

On the other hand, on the basis of extensive examinations of herbarium specimens, Anthony (1980) and Jenkins (1992) expected that there should be an unknown number of gall-inhabiting coccoid species on dipterocarps. In view of their expectation, the coccoid material obtained in the present surveys may be far from satisfactory. Three of the four

coccoid species found in the material came from natural stands, on which, however, their galls collected were quite few. The other species occurred on saplings in the nursery set in the forest; a good number of galls were obtained but, on dissection, not a few of them were empty or contained poor coccoid material bearing evidence of predation by a dipteron. All this may suggest a general low density of coccoid galls in natural forests under a great pressure from natural enemies (predators and parasites in addition to gall-consuming insects).

All the known gall-inducing coccoids occurring on dipterocarps are deemed to belong to a phylogenetically significant group, the family Beesoniidae (Takagi and Hodgson, 2005), and the four species obtained in the present surveys are also referred to the family. The species collected in the nursery is well represented by two female and three male instars and referable to *Gallacoccus*. Another species is represented only by male instars, but it is referred to *Gallacoccus* because of its very close resemblance to the first species in the male instars. A third species is represented by the adult female and the first- and second-instar males, and the last by the adult female alone. These two species are also referred to *Gallacoccus*, but only provisionally because of the insufficient material. They resemble *Gallacoccus heckrothi* in the male nymphs or the adult female, but *G. heckrothi* itself was referred to the genus tentatively. The species from the nursery is described as a new species. The other three species are not formally named in order to avoid possible confusion in future studies. In the present paper, they are designated by tags coined by combining abbreviations of the collection year, locality and host plant. It is expected that these species will be formally named on obtaining further instars.

Coccoid taxonomy has largely been based on characters of the adult female, which is persistent in the life cycle and, therefore, easily accessible for study. In beesoniids, however, the adult females are much simplified in the external body structure in accordance with the gallicolous mode of life. In *Danumococcus parashoreae* the adult female is even so specialized that it gives little toward unravelling the taxonomic position of the species (Takagi and Hodgson, 2005). In this family, especially in *Gallacoccus* and related forms, the first-instar female and the adult male are comparatively rich in characters, and the combination of these instars may afford a good basis for recognizing a species and discussing its taxonomic position.

Generally speaking, studies in coccoid taxonomy are lacking in functional analysis of features and characters. The gallicolous mode of life may cause much modification on the insect body, especially provoking convergence and parallelism. In the section following the descriptions, some features and their characters in the first instar female and male and the adult male are adopted for exploratory discussions with regard to their significance in function and phylogeny.

The main part of the collection, including the holotype of the new species, is deposited in Entomology Unit, Forest Plantation Division, Forest Research Institute of Malaysia, Kepong, Kuala Lumpur.

Acknowledgements

The surveys were carried out with the co-operation of Dr Laurence G. Kirton, Forest Research Institute of Malaysia. Mr Tsutomu Irie and Dr Furumi Komai, Ôsaka University of Arts, partook in the surveys especially in collecting on the forest canopy. Dr Kaoru Niiyama, Forestry and Forest Products Research Institute, Japan, afforded the

opportunity to search in his plot in the Pasoh forest and also to have access to his data in identifying the host plants. Mr Sen Nishimura, Forest Research Institute of Malaysia, collected gall material on saplings of *Shorea parvifolia* in the Pasoh forest nursery. Hosaka expresses his thanks to Prof. Naoya Osawa, Kyôto University, for approving his joining in the project. The SEM photographs used in this paper were taken at the Electron Microscope Laboratory, Graduate School of Agriculture, Hokkaidô University (Mr T. Ito in charge).

The surveys were carried out on the joint project between the Forest Research Institute of Malaysia and the National Institute for Environmental Studies, Japan: Grant No. E-4, Global Environment Research Program, Ministry of Education, Japan.

Descriptions of the coccoids

Gallacoccus longisetosus Takagi, sp. nov.

Material examined. Collected on two-year-old saplings of *Shorea parvifolia* in the Pasoh forest nursery, 2004. Gall (Fig. 1) of the inflorescence type (a modified form of inflorescence), very small; fully formed ones attaining 18mm long and 8.5mm wide at maximum, compressed, roughly ovate in outline, composed of scales overlapping in distichous disposition and numbering about 10 on each side. Twenty-four galls were dissected for coccoids, including infant ones composed of much fewer scales. Coccoid specimens were obtained mainly from larger galls, whereas most of the infant ones harboured no insects. The mounted specimens include a number of first-instar females, 17 adult females, some first- and second-instar males, and two adult males. Most of the nymphs were obtained from a single gall, 12.5mm long and 7mm wide, whereas the others from five smaller galls, 7–10mm long and 4–5.5mm wide. The adult females were found under the second or third, and sometimes fourth, scale counted from the base; a single adult female or rarely two occurred on one gall. Pupae were also mounted, and three of them contained adult males, of which the bodies were nearly formed.

A considerable number of the first-instar female specimens are abnormally shrunk and badly damaged, with the ventral derm extensively broken and the legs and antennae partly or largely lost. The adult females were generally too aged, and the mounted specimens are not in good condition; some specimens are mere fragments of bodies.

Dipterous larvae and puparia were found under scales on a total of 12 galls. They probably belong to a cecidomyiid species, which was apparently an invader in the gall. The damaged or fragmentary specimens of the coccoid as well as the empty galls suggest that the dipteron was predaceous on the coccoid and that the predation was considerably severe.

Holotype. First-instar female, deposited in Entomology Unit, Forest Research Institute of Malaysia, Kepong, Kuala Lumpur, Malaysia.

First-instar female (Figs 6–8). Body elliptical, with no segmental notches on margin; segmentation distinct on ventral surface, obscure dorsally. Dorsal surface covered with a number of small, membranous, tubercular swellings; with setae all spinous but remarkably elongated, 17 along margin, 6 in a submedian longitudinal row, and 7 in an intermediate longitudinal row on each side; with many small, sclerotized, funnel-shaped pits each bearing a clear round spot on bottom, irregularly strewn on head and prothorax, arranged in transverse rows on rest of body probably on intersegmental furrows, the anteriormost row or two tending to be double: with 6 minute ducts forming

an intermediate longitudinal row on each side. Ventral surface with dermal swellings and elongate spinous setae on head and prothorax within margin; with a pair of strong caudal setae and 3 pairs of spinous setae around anus; with some dermal pits on meso- and metathorax and abdomen within margin; with 7 small ducts within margin on each side, each associated with a small sclerotized process. Derm with spicules especially clearly seen on ventral surface of meso- and metathorax and abdomen. Anterior and posterior spiracles each with a '5-locular' disc pore [see under *Remarks*]. Antennae 3-segmented; basal 2 segments well developed, wider than long, each with 1 seta; apical segment longer than wide, about as long as basal 2 segments combined, domed apically, with 3 long fleshy setae and 3 long slender setae, two of the slender setae especially long and the longest one with a minute knob apically. Legs moderately developed; tarsi each with 2 setae on ventral surface, hind tarsus with one of these setae, situated about middle, much longer than the other, about as long as the segment; tarsal digitules elongate, about as long as the segment; claws gently curved, with a trace of plantar denticle subapically.

Adult female (Fig. 9). Globular; mounted specimens roughly circular, attaining about 3mm in diameter at maximum. Derm sclerotized at full growth, with series of much sclerotized patches along supposed intersegmental furrows on ventral surface between mouth-parts and vulva. Body setae all small, sparsely scattered mainly on ventral surface; shorter setae scattered around anus. Quinquelocular disc pores uniform in size, appearing to be somewhat sunken; many pores concentrated around vulva, others sparsely scattered in a broad submarginal region laterally to legs and spiracles; a roughly crescent group of 5–13 pores associated with each spiracle. Anus small, surrounded by a broad sclerotized rim. Mouth-parts with a pair of well-developed aliform expansions. Antennae (in a specimen with the antennae in a relatively good state) 3-segmented; first segment incomplete, represented by a crescent sclerotized piece detached from second segment, with 2 setae; second segment complete, with 1 seta; third segment short, with 3 fleshy setae, 2 slender setae, and 1 small seta. Legs robust; claws crooked, with no trace of plantar denticle.

First-instar male (Fig. 10). Body elliptical, membranous, but segmentation rather distinct; with segmental rows of spicules on meso- and metathorax and abdomen on both surfaces. Small tubercular dermal swellings occurring within margin on both surfaces of thorax, obscure, often not easily discernible. Dorsal setae long and slender, occurring in submedian, intermediate, and marginal rows, those in submedian and intermediate rows somewhat variable in occurrence on abdomen. Spiracles each with a 5-locular disc pore. Antennae 3-segmented; first segment with 2 setae; second segment short, with 1 seta; apical segment a little longer than wide, domed apically, with 3 fleshy setae, 2 long slender setae, and 2 much shorter setae. Legs robust, appearing somewhat shortened; femora thickened; tibiae and tarsi also thickened, tarsi short, as long as tibiae, with digitules longer than the segment; claws gently curved, with a small plantar denticle subapically.

Second-instar male (Fig. 11). Body elongate obovate, membranous; spicules occurring in broad segmental bands on metathorax and abdomen on dorsal surface, and on meso- and metathorax and abdomen on ventral surface. Dorsal setae not particularly elongated. Quinquelocular disc pores uniform in size, appearing somewhat sunken; a few pores on dorsal surface submedially on fused head, pro- and mesothorax on each side: 1 or sometimes absent on head, 1–4 on prothorax, 1 or 2, sometimes absent, on mesothorax; 1 pore associated with each spiracle. Antennae 3-segmented; first segment

represented by a complete or interrupted slender sclerotized ring, detached from second segment, with 2 setae; second segment short, with 1 seta; third segment as long as or shorter than wide, roughly conical or stump-like, with 3 fleshy setae, 2 long slender setae, and 2 much shorter setae. Legs short and robust; tarsi as long as tibiae, with digitules longer than the segment; claws broad basally, narrowing in a curve towards apex, with or without a minute plantar denticle subapically.

Adult male (Figs 12 and 13). Macropterous. Head much narrower than thorax, which is robust, being 2.5 times as broad as the head; abdomen (excluding genital segment) as long as thorax, gradually narrowing posteriorly. Head, trunk, and legs beset with a number of tubercular papillae, of which the bases are round or elliptical. Head with papillae mainly in a longitudinal dorsomedian area from median crest to postoccipital ridge and in front of ventral eyes. Dorsal surface of thorax with papillae forming 4 groups on each side: on shoulder, between post-tergite and frame of mesothoracic ridges, on scutum, and on metatergum. Ventral surface of thorax with papillae in a group arising between fore coxae and extending posterolaterally, in a transverse group in front of frame of mesothoracic ridges, on mesepisternum, between mid coxae, and between hind coxae. Abdomen with papillae forming transverse rows on first to seventh segments on dorsal surface and on the second to seventh ventrally; eighth segment with one or a few papillae midventrally and also marginally. Legs with no papillae on coxae, 2 or 3 on mid and hind trochanters, 2–4 subapically on posterior surface of fore femur (no papillae on anterior surface), and some on mid and hind femora (mostly on anterior surface, others subapically on posterior surface) and also on all tibiae and tarsi. Abdomen with a broad sclerotized band bearing spicules across sixth to eighth segments each, and with a patch of spicules dorsally on the third to fifth each. No disc pores present except for glandular pouches on eighth abdominal segment. Head in dorsoventral view round, with median crest somewhat produced; dorsal arm of midcranial ridge absent; postoccipital ridge represented by a transverse sclerosis medially produced posteriorly in a small triangle, with lateral ends curved posteriorly; preocular ridge weak, whereas postocular ridge strongly developed. Eyes moderate in size, dorsal eyes as large as the ventral in size of cornea. Antennae as long as fore tibia, tarsus, and claw combined, 5-segmented; basal segment transverse in dorsoventral view, the second short, the third constricted basally, the fourth about half as long as the third, all these segments with hairy setae; fifth segment about as long as the third, with 5 gently curved fleshy setae and 3 slender yet stiff setae ending in a small apical knob. Pronotal ridge well represented; post-tergite represented by a sclerotized patch. Prescutum longer than wide; scutellum transversely rectangular, well sclerotized except for a small, transversely elliptical area situated medially. Postnotal apophysis represented by a small ring. Mesosternum with marginal ridge well developed, and with furca well represented. Halteres absent. Legs rather slender except for fore femora, which are swollen dorsally, and also for fore tibia and tarsus, which are nearly fused and rather thick; trochanters with basal portion much shorter than the distal; tibiae and tarsi subequal in length; claws on fore legs shortened (as compared with those on mid and hind legs), broad basally, abruptly narrowed to form a robust crooked apex, with no trace of plantar denticle; claws on mid and hind legs gradually attenuated to form a slightly curved, sharp apex, with a trace of plantar denticle subapically; tarsal digitules absent or replaced by hairy setae not distinguishable from neighbouring setae. Each glandular pouch on eighth abdominal segment bearing two setae, which extend to the apex of the genital capsule. Genital capsule in dorsoventral

view robust, broadly rounded, with many transverse rows of spicules on ventral surface, and then produced into a conical process, of which the apical margin is rounded and beset on the ventral surface with about 14 minute round structures arranged in an arch.

Remarks. The concept of the genus *Gallacoccus* is still to be revised on the basis of a broader range of species (Takagi, 2001). The present new species is referable to the genus, having many characters in common with the other known species of *Gallacoccus*. It is readily distinguishable from them in having remarkably elongated spinous setae, instead of conical setae, on the dorsal surface of the body in the first-instar female — a character newly found in *Gallacoccus* but known in *Beesonia*. The first-instar female is also remarkable in having a number of funnel-shaped sclerotized pits on the body. These pits correspond to 'sclerotized conical pits' described by Beardsley (1971) as occurring on the 'First instar larvae' (in reality, the first-instar female) of *Gallacoccus anthonyae*, each having a clear round spot on the bottom ('a minute circular opening at inner apex'). *Gallacoccus secundus* and *Gallacoccus spinigalla* also have dermal pits, but each of these pits has a clear slit (not a round spot) on the bottom [for further discussion, see under Notes on some features].

The shared possession of the dermal pits of the spot type may suggest that *G. longisetosus* is closely related to *G. anthonyae*. They also agree in their galls belonging to the inflorescence type. At the same time, the remarkably elongated dorsal setae are peculiar among the known species of *Gallacoccus*. Detailed comparisons between this species and *G. anthonyae* on female and male instars are necessary for clarifying their relationship.

The adult male of *G. longisetosus* is provided with tubercular papillae, and similar papillae occur on the adult male of *Gallacoccus heckrothi*, which was referred to the genus tentatively, and also on the adult male of *Echinogalla pustulata*, which seems only remotely related to the *Gallacoccus* species [for further discussion, see under Notes on some features]. In this instar, *G. longisetosus* is provided with three apically knobbed setae on each apical antennal segment, thus coming between *G. secundus* and *G. spinigalla* (with four such setae) and *G. heckrothi* (with two).

In the description of the first-instar female above, it is stated parenthetically that the disc pores associated with the spiracles are quinquelocular. In scanning electron microscopy, however, these disc pores show no locules, and it seems that five deltoid plates are applied on the expected locules (Fig. 6). In oil-immersion microscopy, five clear spots are seen beneath the deltoid plates, probably representing the locules.

Gallacoccus 03Ps-Smp

Material examined. Collected on *Shorea macroptera* in the Pasoh forest, 3 Sept. 2003. Gall (Fig. 2) of the inflorescence type (a modified form of inflorescence). A single gall, 43mm long, 20mm wide, and 13mm thick, was dissected for inhabiting coccoids. Mounted coccoid specimens include fragmentary exuvial casts of the first-instar male belonging to three individuals, three second-instar males all in poor condition, and 11 adult males, some of them being fairly good in condition; some pupae were also mounted. Their mother, however, was not found in spite of a careful search. No first-instar females were obtained, either. A head capsule of a coleopterous larva was found under a scale together with coccoid specimens; possibly this larva was predaceous on the coccoid.

Other galls (Fig. 3), probably induced by *Gallacoccus* 03Ps-Smp, were also

collected from *Shorea macroptera*, but they were used for testing the supposed consumption by tortricids.

First-instar male. So far as represented by the available fragmentary exuvial casts, the first-instar male is very similar to that of *Gallacoccus longisetosus* in having robust, shortened legs and in the state of the antennae. However, no such elongate setae as found in *G. longisetosus* have been observed on the exuvial casts.

Second-instar male (Fig. 14). This stage is very similar to that of *Gallacoccus longisetosus*, but differs from the latter in having more 5-locular disc pores and 2-segmented antennae. Quinquelocular disc pores occurring submedially on dorsal surface of head and thorax, and occasionally also on base of abdomen, 8–12 on each side: 1–4 on head near front margin, 3–5 on prothorax, 2 or 3 on mesothorax, 1 on metathorax, and 1 occasionally on base of abdomen; also occurring marginally on ventral surface of abdomen, 6 on each side; each anterior spiracle with 3 or 4 disc pores, of which one is isolated and situated mesad of the others; each posterior spiracle with 2 or 3 disc pores, at times one of them isolated and situated mesad. Antennae 2-segmented; basal segment represented by a slender ring, with 1 seta (thus corresponding to the second segment in *G. longisetosus*); apical segment roughly conical, a little shorter than wide. Legs appearing more reductive than in *G. longisetosus*, with tibiae especially diminished.

Adult male (Figs 15 and16). Very similar to the adult male of *Gallacoccus longisetosus*, differing from the latter mainly in the following characters: legs lacking papillae except for fore tarsi with 2–4 papillae and mid and hind tarsi sometimes with 1 or a few papillae; fore tibia and tarsus only partly fused (or sometimes appearing completely articulated); abdomen with more papillae; setae arising from glandular pouches much shorter; genital capsule with a pair of processes laterally to apex, which are beset with some minute clear spots arranged in a longitudinal row on the ventral surface.

Remarks. The close similarity of this species to *Gallacoccus longisetosus* in the examined male instars and especially the adult male strongly suggests that these species are closely related and also that *G.* 03Ps-Smp is referable to *Gallacoccus*. However, this species is quite peculiar in having a pair of processes laterally to the apex of the genital capsule. The relationship between *G.* 03Ps-Smp and *G. longisetosus* is to be revised by comparing female instars, too. The relationship of this species as well as of *G. longisetosus* to *Gallacoccus anthonyae* is also to be clarified on the basis of male and female instars [see *Remarks* under *Gallacoccus longisetosus*].

Gallacoccus 03Ps-dsp

Material examined. Collected on an undetermined dipterocarp in the Pasoh forest, 6 Sept. 2003. Gall of the fruit type (similar to an apterous fruit in external appearance), globular, ending with a small mucro (Fig. 4). A single gall, about 15mm long and 12mm wide, was dissected for coccoids; the interior space was about 8mm in diameter and harboured one adult female, a number of deposited eggs, some 60 first-instar males, and over 40 second-instar males. The body of the adult female was full of hyphae, with the contents decomposed into an amorphous mass, which was sticky in KOH solution. It was, therefore, not easy to clear the body, and the mounted specimen is not good in condition.

Adult female. Body setae slender except for some spinous ones, which seem to occur marginally and mainly on the head and just caudad of the anus; setae occurring

around vulva longish. Quinquelocular disc pores in 2 sizes, concentrated around vulva. Anus surrounded by a sclerotized rim. Mouth-parts with a pair of well-developed aliform expansions. Antennae 3-segmented; basal segment represented by an interrupted ring, detached from second segment. Tibiae as long as tarsi; claws curved, with a small plantar denticle subapically. (In the specimens, the spiracles and spiracular disc pores were not observable.)

First-instar male (Fig. 17). Body elongate obovate, with setae generally longish and a few setae on posterior end rather spinous; with transverse rows of spicules on metathorax and abdomen dorsally and on thorax and abdomen ventrally. Each spiracle with a 7-locular disc pore. Antennae 3-segmented; basal segment well developed, with 1 seta; second segment short but well represented, with 1 seta; apical segment about 1.5 times as long as wide, with 4 fleshy setae, 2 long slender setae, and 2 short setae. Legs moderate in thickness; tarsi about 1.5 times as long as tibiae; fore and mid tarsi without digitules, hind tarsi with 1 digitule, which is as long as the segment; claws much elongated, about two-thirds as long as tarsi, slender, gradually narrowing apicad to form a sharp apex, only gently curved, with a plantar denticle subapically.

Second-instar male (Fig. 18). Body elongate obovate, with setae small except 4 long and rather spinous marginal ones on each side towards posterior end; with transverse bands of spicules on abdomen dorsally and on thorax and abdomen ventrally. Quinquelocular disc pores few; 1 on prothorax and 1 or a few on each of meso- and metathorax on dorsal surface submedially on each side, a single pore on one or a few abdominal segments on ventral surface just within margin, some of these dorsal and ventral disc pores often lacking; usually 1–3 disc pores near each anterior spiracle and 3 –5 near each posterior spiracle. Small ducts present; on dorsal surface, strewn on head and thorax and arranged in submedian, intermediate, and submarignal longitudinal rows on abdomen; on ventral surface, mostly arranged in submedian and submarginal longitudinal rows, the latter being double on abdomen. Antennae 3-segmented; basal segment represented by a ring detached from second segment, with 2 small setae; second segment with 1 seta; apical segment a little longer than wide, with 6 fleshy setae and a few small setae. Tibiae and tarsi subequal in length; fore and mid tarsi without digitules (or digitules replaced by setae not distinguishable from neighbouring setae); hind tarsi with a single digitule nearly as long as the segment; claws narrowing to form a sharp apex, slightly curved, with a trace of plantar denticle subapically; a pair of ungual digitules extending beyond apex of claw.

Remarks. The first- and second-instar males are similar to those of *Gallacoccus heckrothi*, but differ, above all, in having a single long digitule on each hind tarsus and a pair of digitules on each claw (whereas *G. heckrothi* possesses no digitules on all the legs). The adult female, on the other hand, is remarkably different from that of *G. heckrothi* in having no geminate spinous setae. The examined specimen of this instar is, however, poor in condition, and no detailed comparison was possible. No specimens of the first-instar female and adult male were available, either. This species, therefore, is referred to *Gallacoccus* only provisionally.

Gallacoccus 03St-Sls

Material examined. Collected on *Shorea leprosula* at Serting, Negeri Sembilan, Malaya, Malaysia, 10 Sept. 2003. Gall (Fig. 5) fusiform, elongated to form a sharp apex. A single gall, 30mm long, 9.5mm wide, and 7.5mm thick and bearing a pair of small

thin scales (probably representing sepals) basally, was dissected. It harboured one adult female in the interior space, which was 7.5mm long and 3.5mm wide, and of which the walls were covered with a thin layer of wax. The female had eggs within the body, but there were found no eggs and no nymphs in the interior space.

Adult female. Setae occurring around anus thickened and spinous, 8 of them geminate, 2 others triple. In having the geminate setae the adult female is similar to that of *Gallacoccus heckrothi*; it is also similar to the latter in the 5-locular disc pores not uniform in size, and does not substantially differ in the antennae, mouth-parts, legs, and anus.

Remarks. The examined specimen differs from the adult female of *G. heckrothi* in having triple spinous setae (in addition to geminate setae) near the anus. It is not knowable whether the occurrence of the triple setae is a stable specific character or not. Because the nymphs, especially the first-instar female, and the adult male are unknown, it is not certain that *Gallacoccus* 03St-Sls is really close to *G. heckrothi* and also that it is rightly referred to *Gallacoccus*.

Notes on some features

Above all else, the adaptive cascade obviously emphasizes the role of functional analysis as a guiding principle for the unraveling of phylogeny, and this is a criterion that has been all but lost in the context of much cladistic analysis.

— James P. Brock, 2000

In the following lines, some features and their characters are discussed with regard to their significance in function and phylogeny. No doubt the known beesoniids are fragments from a large group and do not suffice for proceeding beyond preliminary discussions largely based on speculations. It is expected that much will be clearer as the number of examined species increases.

Dermal pits in the first-instar female

Beardsley (1971) mentioned the occurrence of 'sclerotized conical or oval pits apparently bearing minute gland orifices at their inner apices' on 'First instar larvae' of *Gallacoccus*, thus probably supposing them to be wax-secreting organs. These dermal pits are known to occur in the first-instar females of four *Gallacoccus* species: *G. anthonyae*, *G. longisetosus*, *G. secundus* and *G. spinigalla*. In the former two species, each of the pits is provided on the bottom with a round clear spot, which indeed looks like a wax-secreting orifice. However, in the latter two species, each pit is provided with a clear slit, which does not appear to be a secreting orifice. Scanning electron microscopy on dermal pits of *G. longisetosus* (Fig. 7) gave no helpful information. Assuming that the dermal pits are wax-secreting organs, their abundant occurrence arouses the question why the first-instar females of the four species need so much wax especially in marked contrast to those of the other beesoniids, which lack such pits.

The occurrence of dermal pits is not associated with galls of a particular type. Moreover, such pits do not occur in *G. heckrothi*, which is tentatively referred to *Gallacoccus*, as well as in the other beesoniid genera. The possibility that this feature has some phylogenetic significance, therefore, is not excluded, but the unknown function makes any further discussion meaningless.

Legs in the first-instar male

Remarkable sexual dimorphism has been known in the first instar of *Gallacoccus* and, though less eminent, also in the first instar of *Echinogalla*. This dimorphism may reflect sexually different manners in dispersal (in *Gallacoccus* and *Echinogalla*, the females disperse in the first instar whereas the males in the adult), but it was also attributed to another assumed factor — aggressive behaviour in the first-instar male against invaders in the gall (Takagi, 2001). In *Gallacoccus secundus* the first-instar male has unusually thickened legs (supposed to be 'strangling legs'), and in *G. spinigalla*, *G. heckrothi*, and *Echinogalla pustulata* the first-instar males are provided with unusually elongated, nearly straight, sharp claws ('piercing claws'). Their counterparts have been found in the material from the Pasoh forest: the first-instar males of *Gallacoccus longisetosus* and *G.* 03Ps-Smp possess thickened legs (which, however, appear somewhat shortened as compared with the legs in *G. secundus*), and the first-instar male of *G.* 03Ps-dsp is provided with elongated sharp claws.

In all these species the male nymphs remain within the maternal galls. *Gallacoccus secundus* induces a gall of the fruit type with a single interior space, whereas *G. longisetosus* and *G.* 03Ps-Smp occur under overlapping scales on their galls of the inflorescence type. The thickened legs, therefore, are not associated with galls of a particular type. The elongated claws, too, are found in *Gallacoccus*, and similar claws occur in *Echinogalla*, which seems not closely related to *Gallacoccus*. Apparently the development of thickened legs is not dependent on the gall type and the development of elongated claws is not restricted phylogenetically, thus adding weight to the defence hypothesis, which is to be confirmed by observations on living material.

The assumed defence by the first-instar male requires a considerable pressure from natural enemies for the development of aggressive behaviour and morphology. The dipterous larvae and puparia found in some galls of *Gallacoccus longisetosus* and the coleopterous head capsule in the gall of *G.* 03Ps-Smp, as well as gall-consuming insects [see Introduction], suggest the presence of diverse natural enemies.

Penial sheath pores and other sensilla

The genital capsule in *Gallacoccus longisetosus* is provided with minute but distinct pore-like structures on the apex, and the capsule in *Gallacoccus* 03Ps-Smp has minute clear spots, less distinctly shaped, on the processes arising laterally to the apex. Hodgson and Henderson (2004) refer to 'penial sheath pores' occurring in Coccidae, and assume that these 'pores' are campaniform sensilla.

The apical region of the genital capsule must have a chemoreceptive function, whether this function is associated with any distinctly visible structures or not; otherwise, copulation would not be carried out. The penial sheath pores and spots in the two *Gallacoccus* species appear not exactly the same in structure but, occurring on the ventral surface on which the aedeagus arises, they may reasonably be supposed to function as chemoreceptors in copulation. It remains unknown whether they are campaniform sensilla or not, no specimens having been spared for scanning electron microscopy.

Other sensilla also occur in beesoniids, though they are not always easily observable. The antennae are basically three-segmented in the nymphs and adult female, and the second segment in some forms bears a small tubercular process, which should be a sensillum (for example, Fig. 18C); the segment in other forms may also have such a sensillum, which, however, is not clearly visible or sometimes not discernible at all.

This may be due to the condition of slide-mounted specimens, but sometimes there may actually be no sensillum. Minute sensilla may universally be present on the terminal segment of adult male antennae, and also of well-developed antennae in other instars, but they may often be too minute to depict in figures of usual magnification. In general, various sensilla have not been adopted as taxonomic features.

Papillae

The adult males of four beesoniid genera are provided with a number of small teat-like processes or 'papillae' on the head and trunk and, in several species, even on the antennae or legs or on both. The development of this peculiar feature was attributed to the assumed occurrence of unusual behaviour — intersexual phoresy, which is to be confirmed by observations on living material (Takagi, 2001). Two types of papillae have been recognized: the papillae are elongate in *Danumococcus parashoreae*, *Mangalorea hopeae*, *Gallacoccus secundus*, and *G. spinigalla*, whereas tubercular in *Gallacoccus heckrothi*, *Echinogalla pustulata*, and the two newly found species, *G. longisetosus* and *G.* 03Ps-Smp. The occurrence of the tubercular type in the newly found species is noteworthy, because these species are probably rightly referred to *Gallacoccus* in contrast to *G. heckrothi*, which was placed in *Gallacoccus* only tentatively. *E. pustulata* is also an isolated form. It is apparent now that both the types occur across beesoniid genera. The occurrence of papillae, restricted to beesoniids so far, may have some phylogenetic background, but the significance of the papilla types should primarily be functional rather than phylogenetic.

Takagi (2001) suggested that *Gallacoccus heckrothi* was removable from *Gallacoccus* on account of the combination of some characters, among which the occurrence of tubercular papillae was included. The present study shows that this character has no generic value, apart from the question about the generic position of *G. heckrothi.*

Claws in the adult male

The adult males of *Gallacoccus longisetosus* and *G.* 03Ps-Smp show a remarkable differentiation of the claws in shape between the fore legs and the mid and hind legs: the claws on the mid and hind legs are similar in shape, nearly straight, and sharply pointed apically, whereas the claws on the fore legs are shortened, broad basally, and abruptly narrowed to form a robust crooked apical part.

In previous studies, no particular attention was paid to the differentiation of the claws between the fore legs and the mid and hind legs, and not all published descriptions are adequate in this regard. Adult male specimens at hand have been re-examined: *Mangalorea hopeae*, *Echinogalla pustulata*, and *Danumococcus parashoreae* show no obvious differentiation, the claws on all the legs being similar and more or less sharply pointed apically; *Gallacoccus secundus*, *G. spinigalla*, and *G. heckrothi* exhibit a weak differentiation, and the claws on the fore legs are somewhat thicker and less sharply pointed apically than those on the mid and hind legs. (The original description of the *G. heckrothi* adult male is especially incomplete and ambiguous, failing to point out this differentiation, but the accompanying figure shows the real pattern of differentiation.)

The significance of the differentiation is unknown. In *Danumococcus parashoreae* the male escapes from the maternal gall in the first instar and makes a cocoon on the lower surface of the host leaf. In *Mangalorea hopeae* the male pupates among long

external appendages of the maternal gall. In these species all the claws in the adult males are similar in size and shape. In the other species the males grow within the maternal galls until they are winged and escape, and, except for *Echinogalla pustulata*, the claws of fore legs are more or less thickened. Especially, the adult males of *Gallacoccus longisetosus* and *G.* 03Ps-Smp are provided with very robust claws on the fore legs. They also agree in emerging under overlapping scales on the galls of the inflorescence type.

A likely possibility, therefore, is that the development of differentiation in the adult male claws depends on the conditions under which the adult males escape. Emergence within the maternal galls may be a prerequisite, and the types of galls may create the conditions. On the other hand, galls induced by coccoid species of the same genus do not necessarily belong to the same type, and galls of the same type may be induced by coccoids belonging to different genera. On this account, the shared possession of the apparently derivative robust claws on the fore legs may not necessarily indicate a close phylogenetic relationship (apart from the possible close relationship between *Gallacoccus longisetosus* and *Gallacoccus* 03Ps-Smp).

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Danumococcus Takagi and Hodgson, 2005; *D. parashoreae* Takagi and Hodgson, 2005.

Echinogalla Takagi, 2001; *E. pustulata* Takagi, 2001.

Gallacoccus Beardsley, 1971; *G. anthonyae* Beardsley, 1971; *G. heckrothi* Takagi, 2001; *G. secundus* Beardsely, 1971; *G. spinigalla* Takagi, 2001.

Mangalorea Takagi, 1992 (in Raman and Takagi, 1992); *M. hopeae* Takagi, 1992 (in Raman and Takagi, 1992).

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The quotation from Brock is on page 532 of The Evolution of Adaptive Systems (Academic Press, 2000).

Fig. 1. Galls induced by *Gallacoccus longisetosus*. Scale in millimetres.

Fig. 2. Gall induced by *Gallacoccus* 03Ps-Smp. Scale in millimetres.

Fig. 3. Other galls formed on *Shorea macroptera*. Scale in millimetres.

Fig. 4. Gall induced by *Gallacoccus* 03Ps-dsp. Scale in millimetres.

Fig. 5. Gall induced by *Gallacoccus* 03St-Sls. Scale in millimetres.

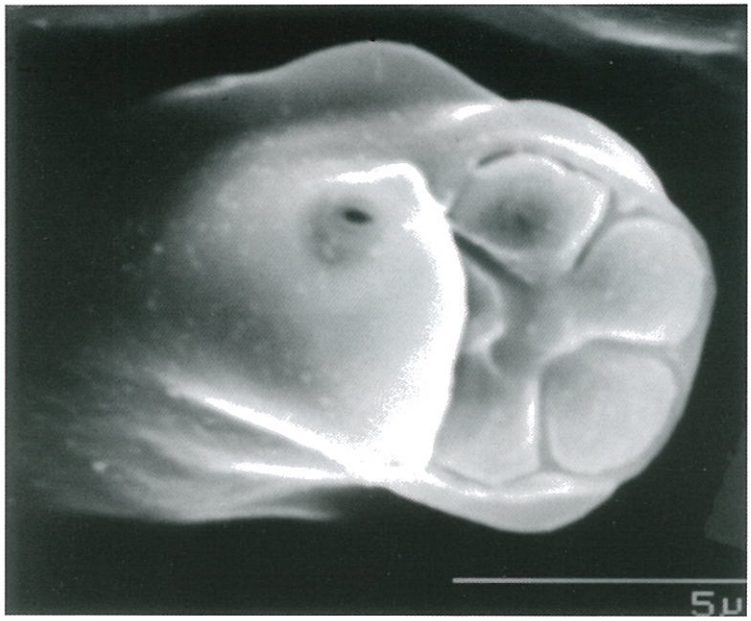


Fig. 6. *Gallacoccus longisetosus*, first-instar female: spiracular disc pore.

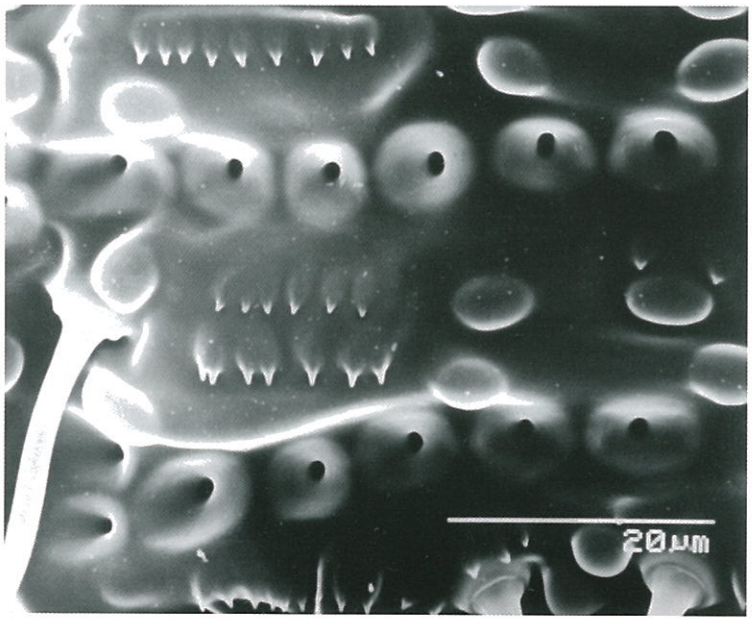
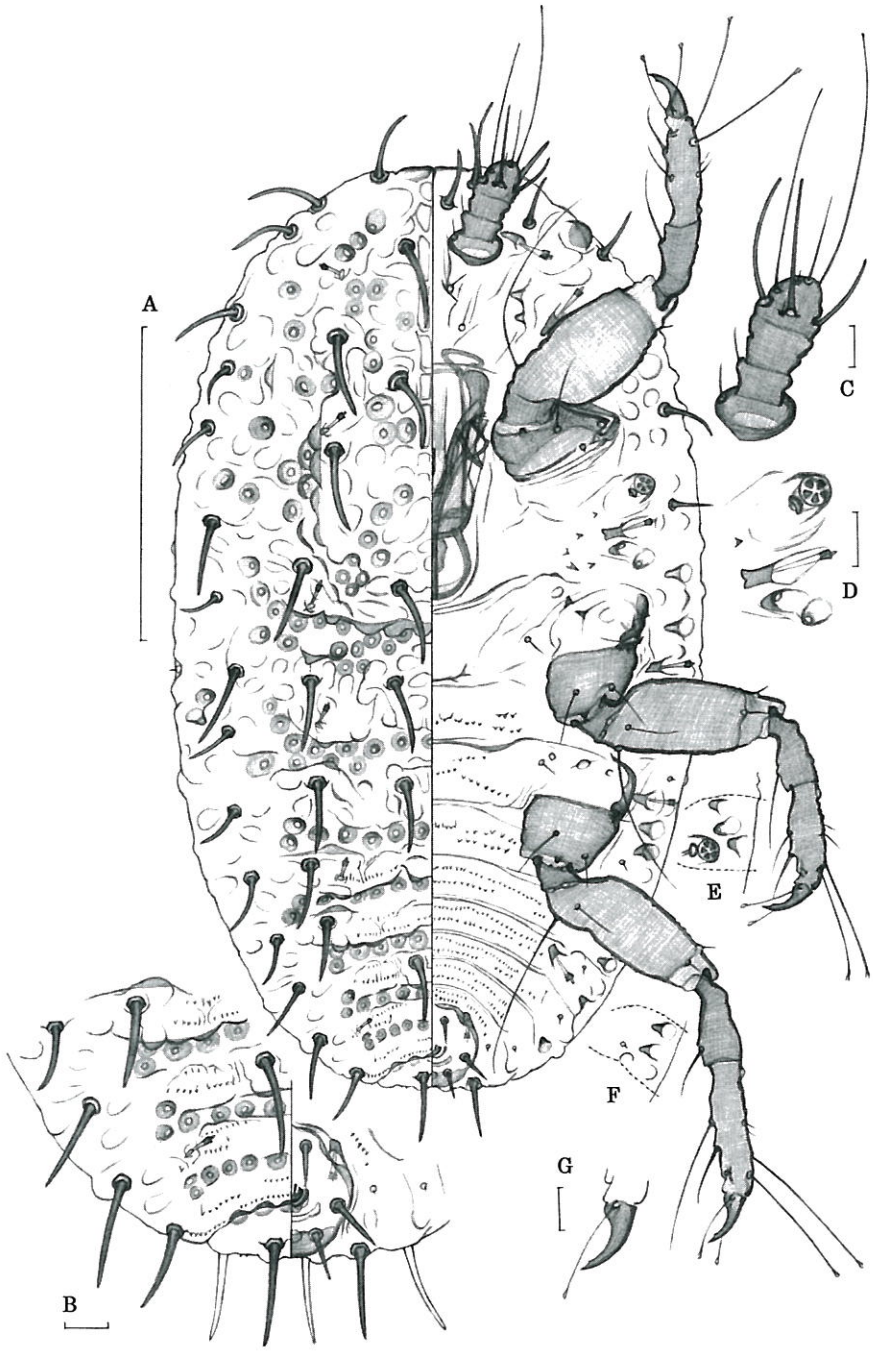


Fig. 7. *Gallacoccus longisetosus*, first-instar female: dermal pits.



Fgi. 8. *Gallacoccus longisetosus*, first-instar female. B, abdomen, apical region; C, antenna; D, anterior spiracle with gland spine and dermal pits occurring nearby; E, posterior spiracle and dermal pits, hidden under mid femur in A; F, dermal pits hidden by hind femur in A; G, claw on hind leg. Scale bars: A, 100μm (E and F magnified at the same rate as A) ; B–D and G, 10μm.

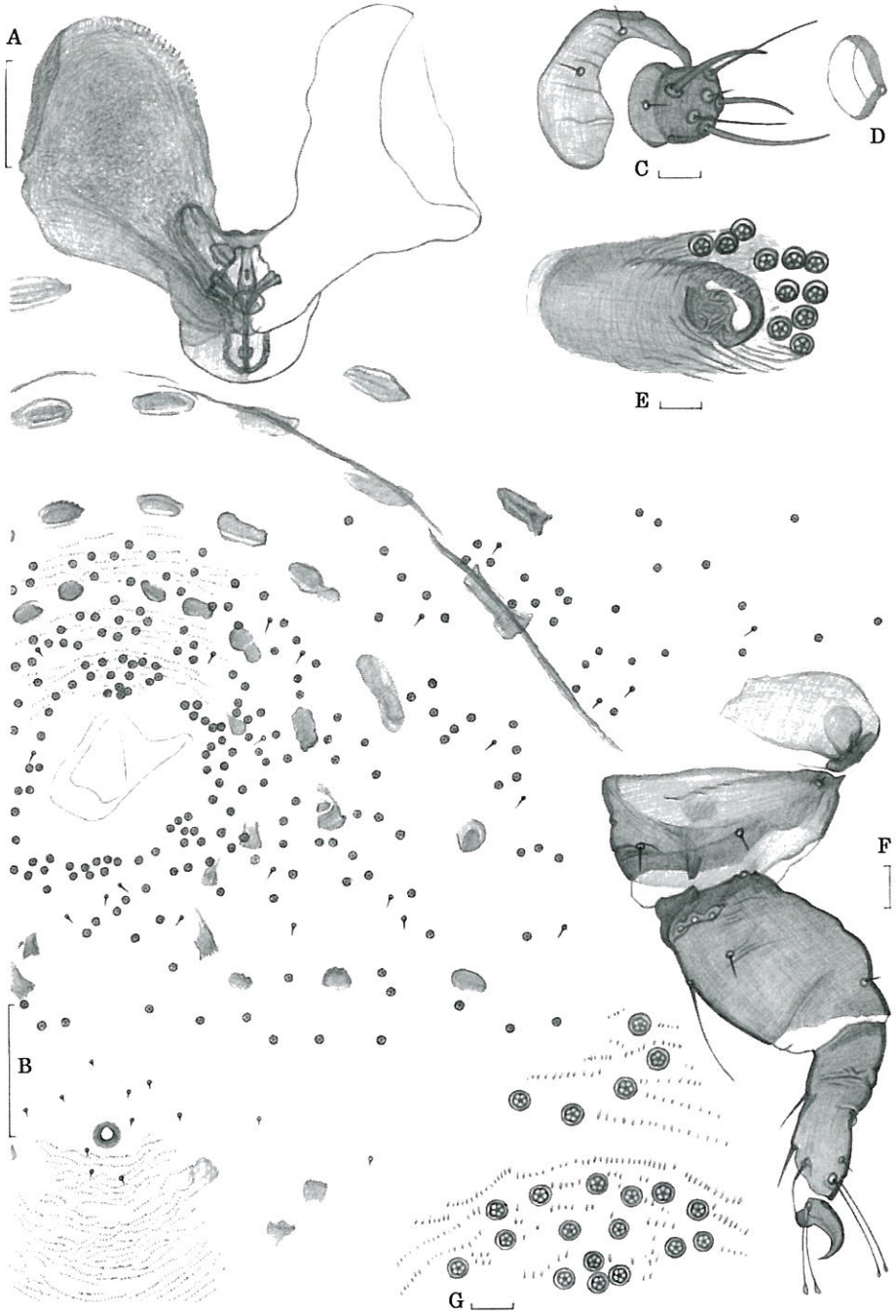


Fig. 9. *Gallacoccus longisetosus*, adult female. A, aliform expansions of mouth-parts; B, dermal features around vulva and anus; C, antenna; D, second antennal segment, dorsal surface; E, anterior spiracle; F, hind leg; G, disc pores near vulva. Scale bars: A and B, 100μm; C and E–G, 10μm (D magnified at the same rate as C).

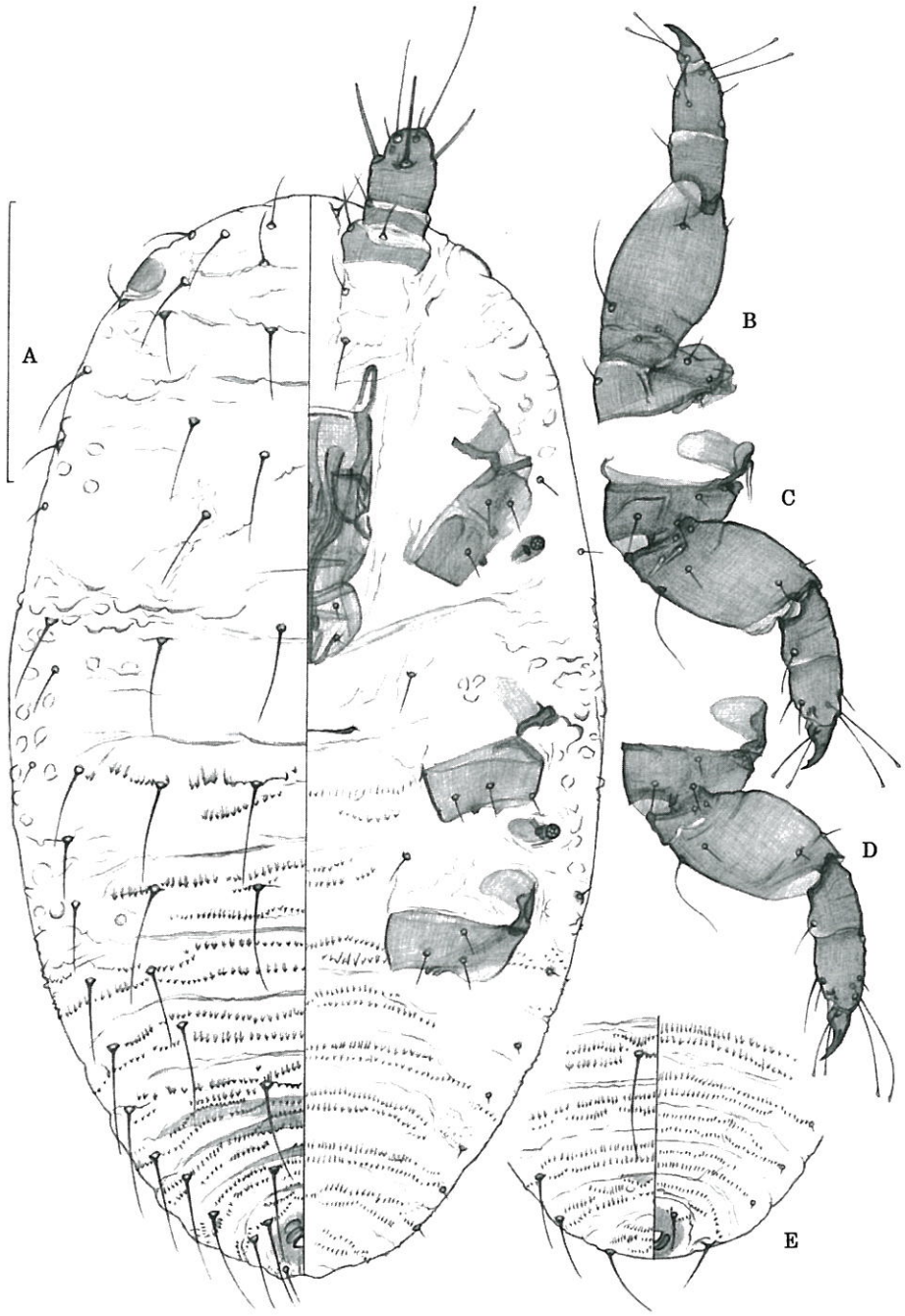


Fig. 10. *Gallacoccus longisetosus*, first-instar male. B–D, fore, mid, and hind legs; E, apical region of abdomen with anus on ventral surface (A, B–D, and E drawn from different specimens). Scale bar: A, 100μm (B–E magnified at the same rate as A).

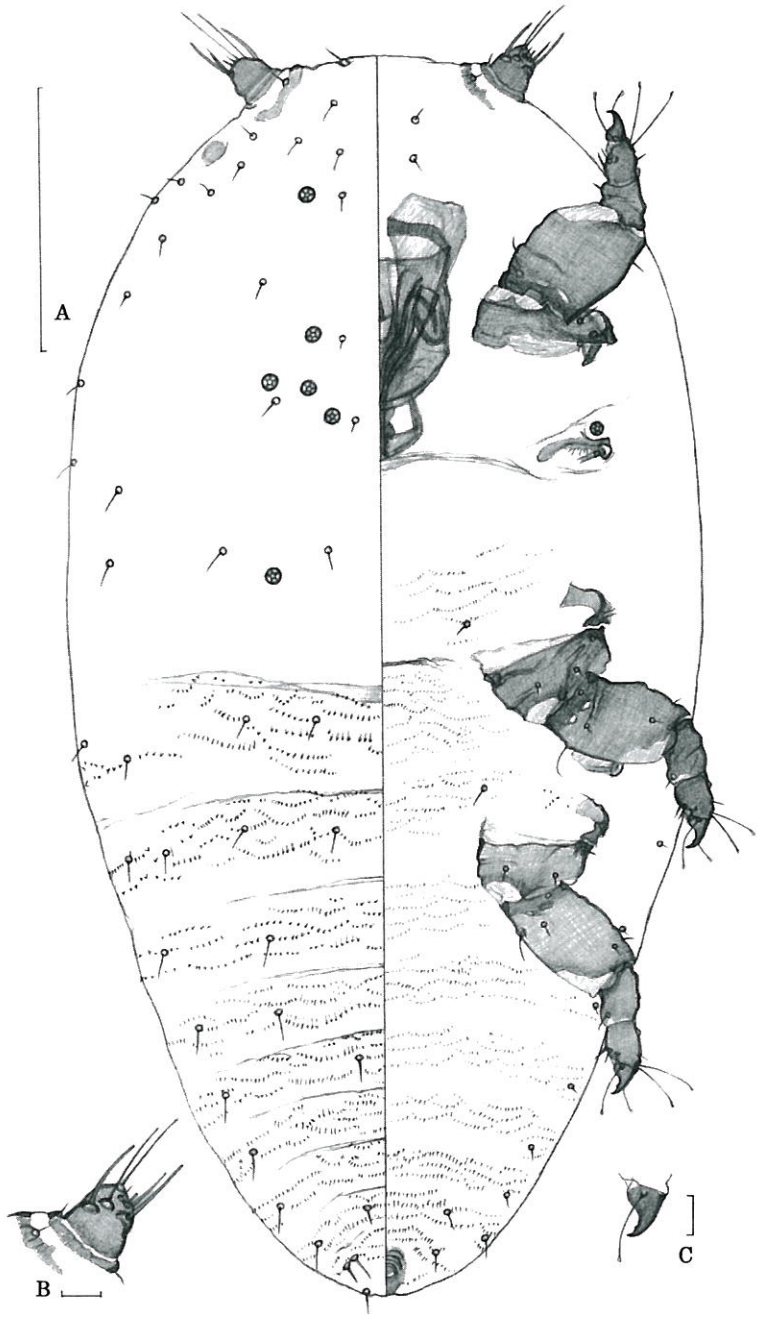


Fig. 11. *Gallacoccus longisetosus*, second-instar male. B, antenna; C, claw on hind leg. Scale bars: A, 100μm; B and C, 10μm.

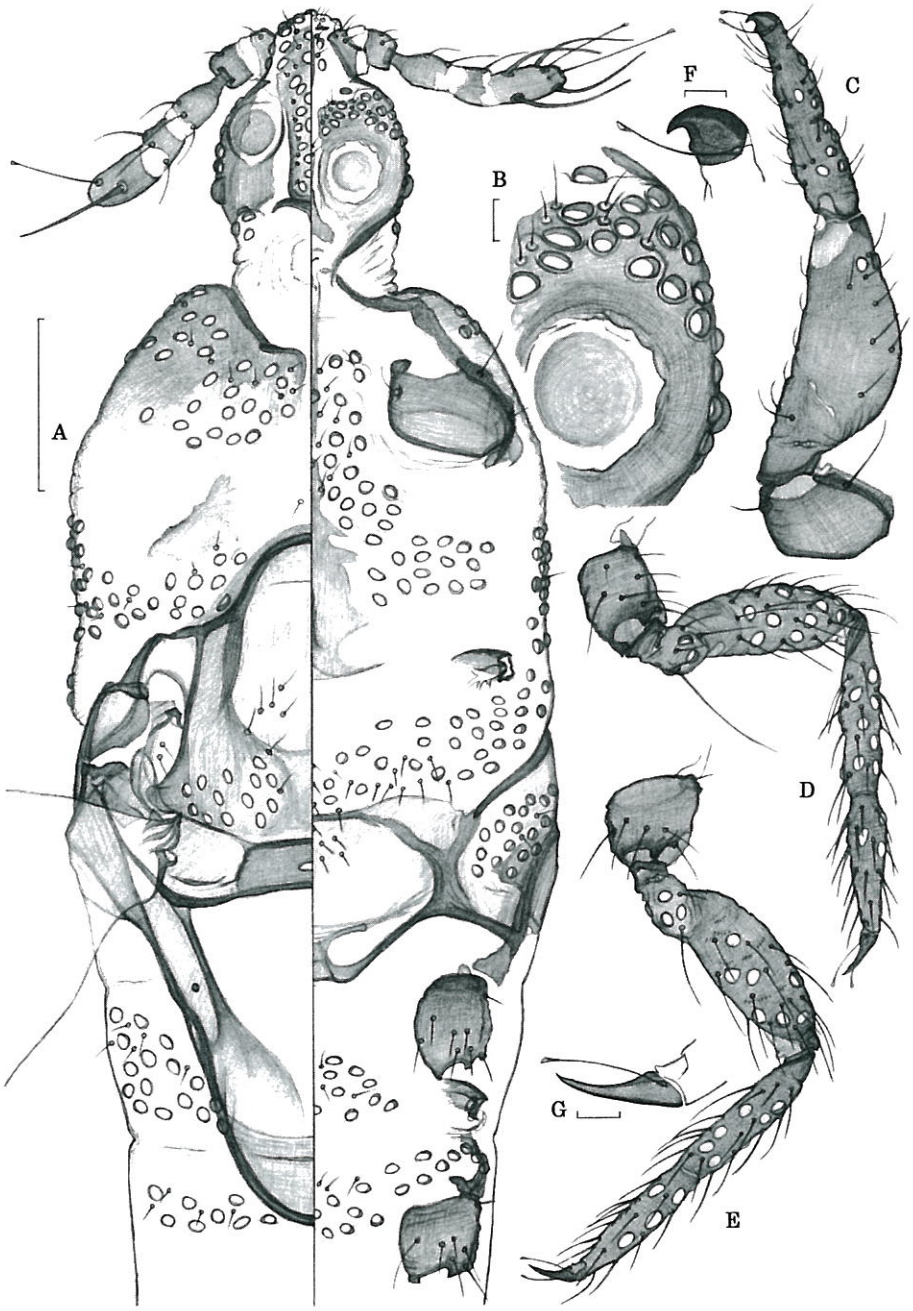


Fig. 12. *Gallacoccus longisetosus*, adult male. A, head and thorax; B, papillae in front of ventral eye; C–E, fore, mid, and hind legs; F, claw on fore leg; G, claw on hind leg (C–G drawn from the other specimen). Scale bars: A, 100μm (C–E magnified at the same rate as A); B, F, and G, 10μm.

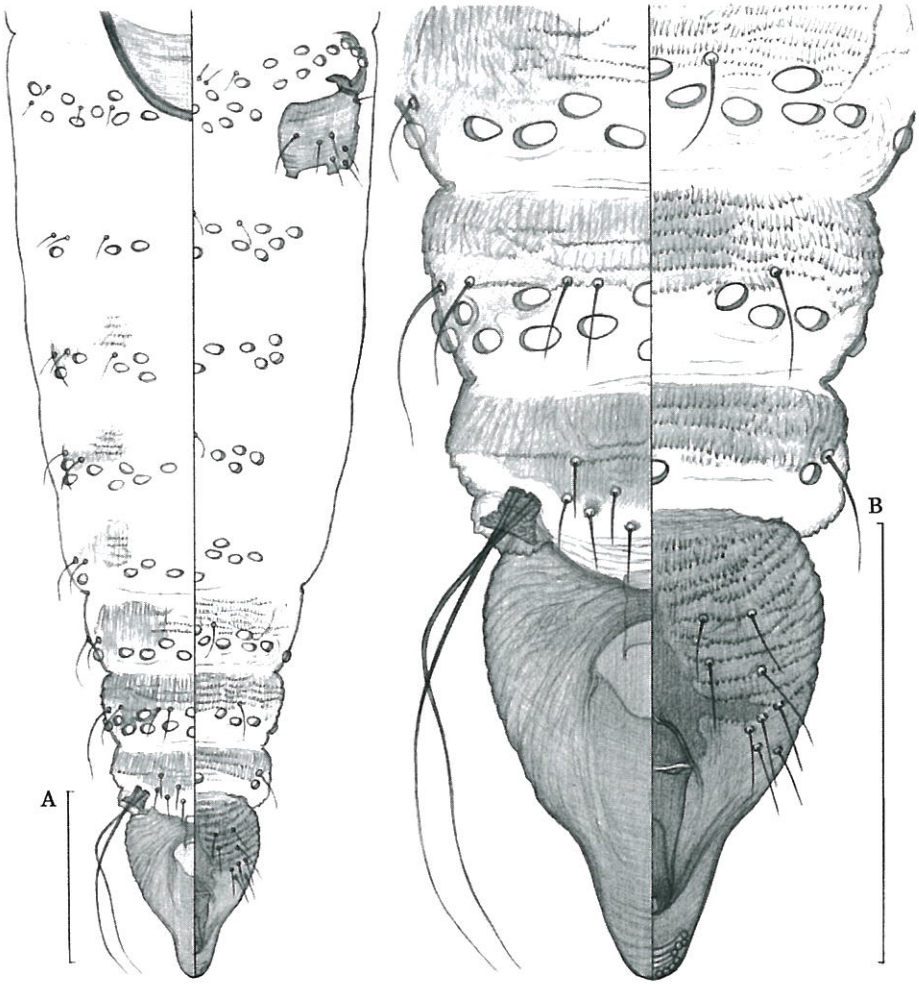


Fig. 13. *Gallacoccus longisetosus*, adult male. A, abdomen; B, posterior segments of abdomen. Scale bars: A and B, 100μm.

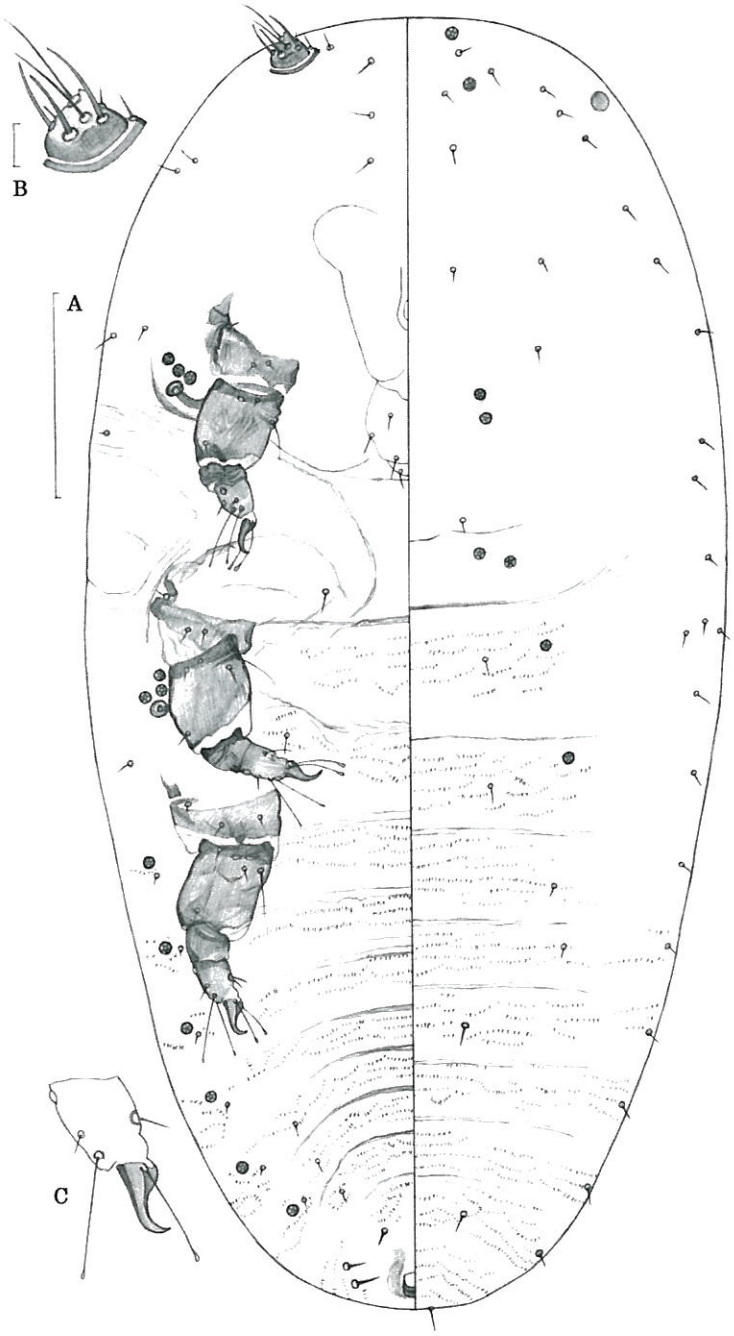


Fig. 14. *Gallacoccus* 03Ps-Smp, second-instar male. B, antenna; C, claw on hind leg. Scale bars: A, 100μm; B, 10μm (C magnified at the same rate as B).

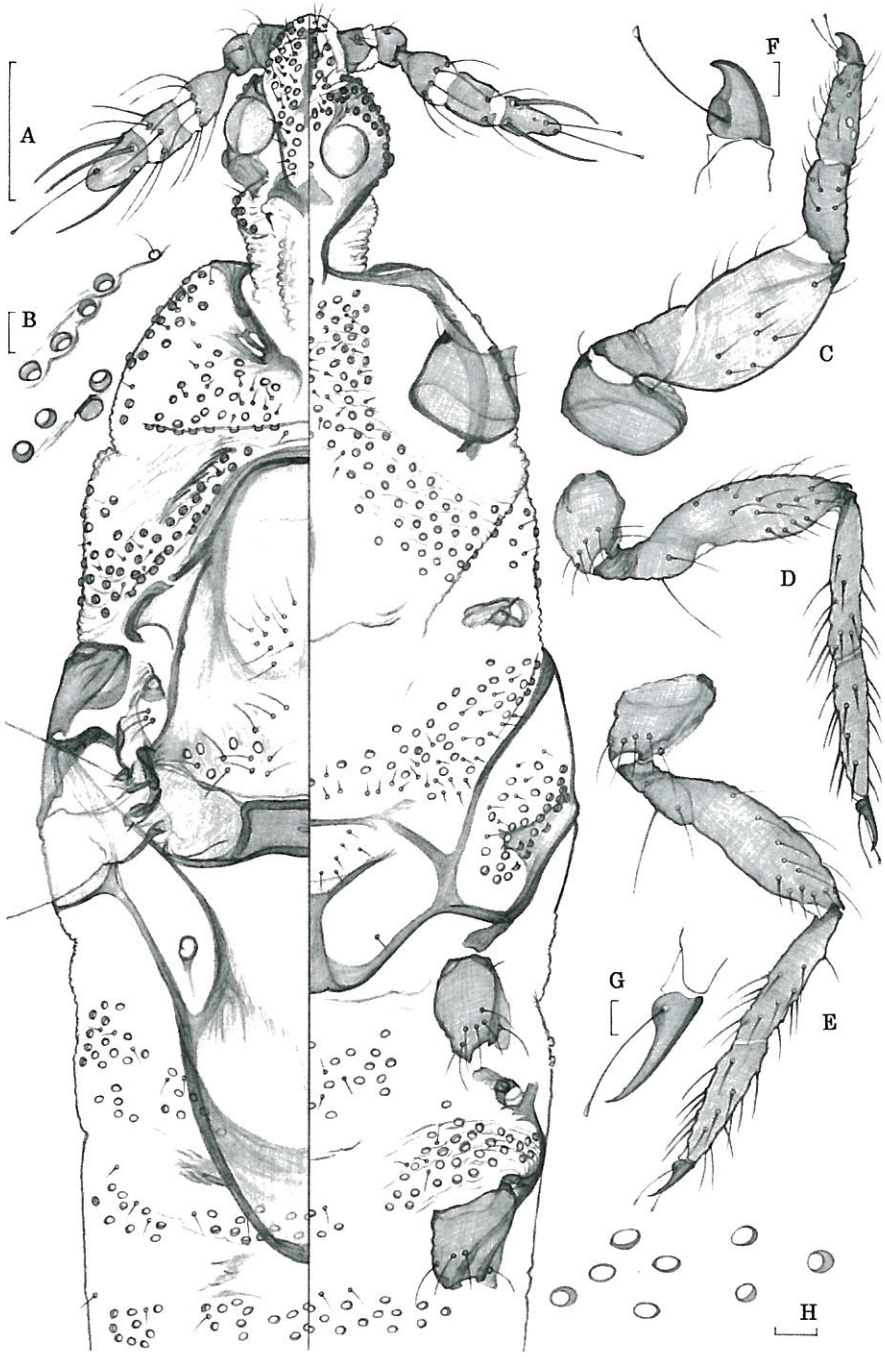


Fig. 15. *Gallacoccus* 03Ps-Smp, adult male. A, head and thorax; B, papillae occurring laterally to prescutum; C–E, fore, mid, and hind legs; F, claw on fore leg; G, claw on hind leg (C–G drawn from another specimen); H, papillae on base of abdomen, on ventral surface. Scale bars: A, 100μm (C–E magnified at the same rate as A); B and F–H, 10μm.

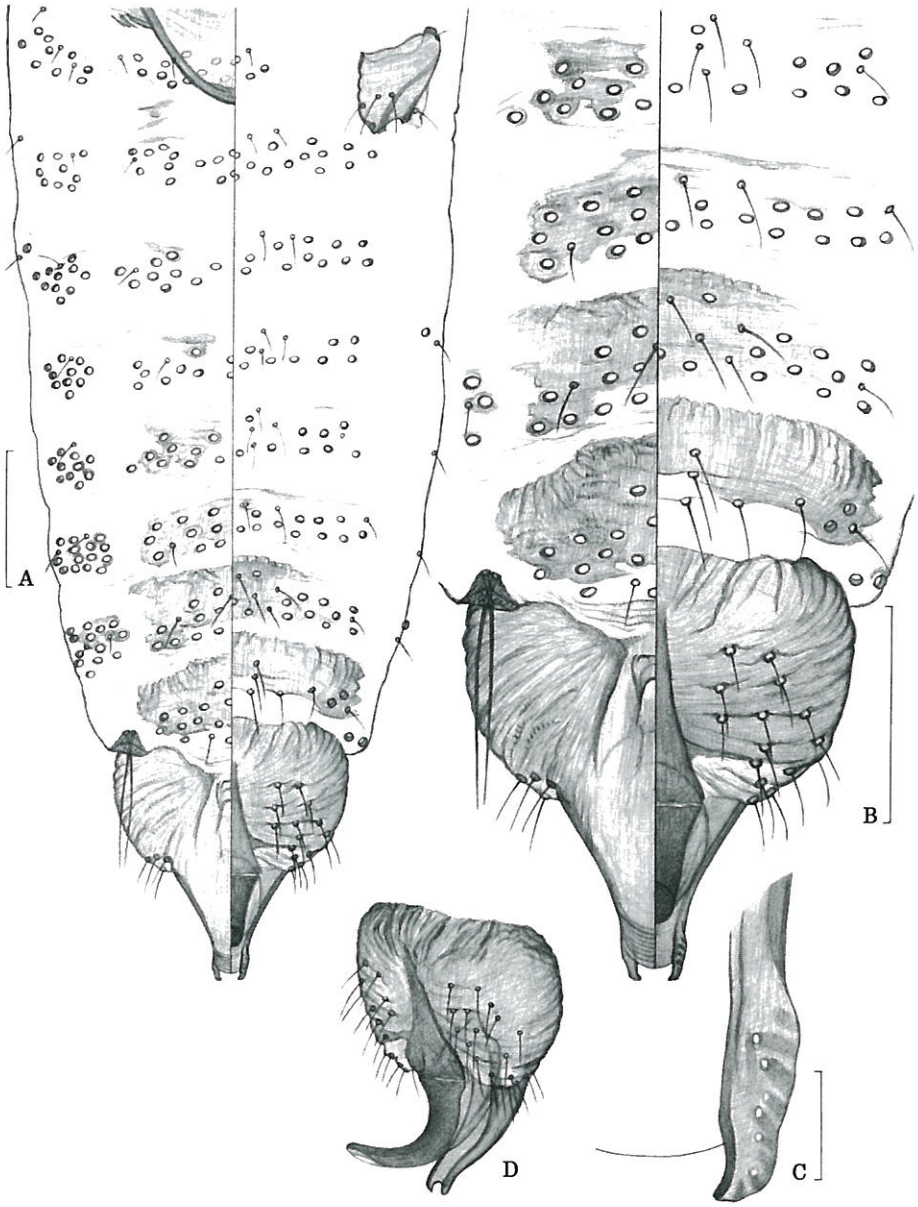


Fig. 16. *Gallacoccus* 03Ps-Smp, adult male. A, abdomen; B, posterior segments of abdomen; C, lateral process of genital capsule; D, genital capsule in an oblique ventral view. Scale bars: A and B, 100μm (D magnified at the same rate as A); C, 10μm.

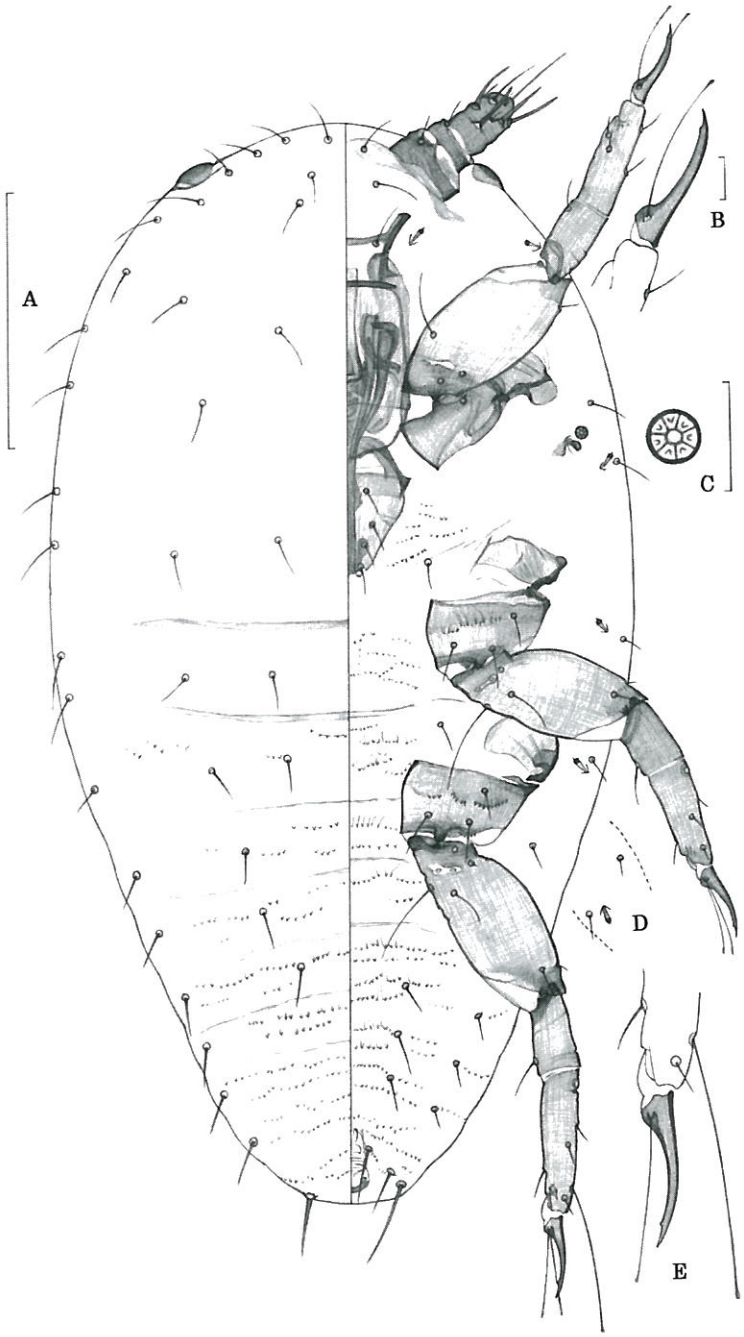


Fig. 17. *Gallacoccus* 03Ps-dsp, first-instar male. B, claw on fore leg; C, spiracular disc pore; D, part of ventral surface hidden by hind femur in A; E, claw on hind leg. Scale bars: A, 100μm (D magnified at the same rate as A); B and C, 10μm (E magnified at the same rate as B).

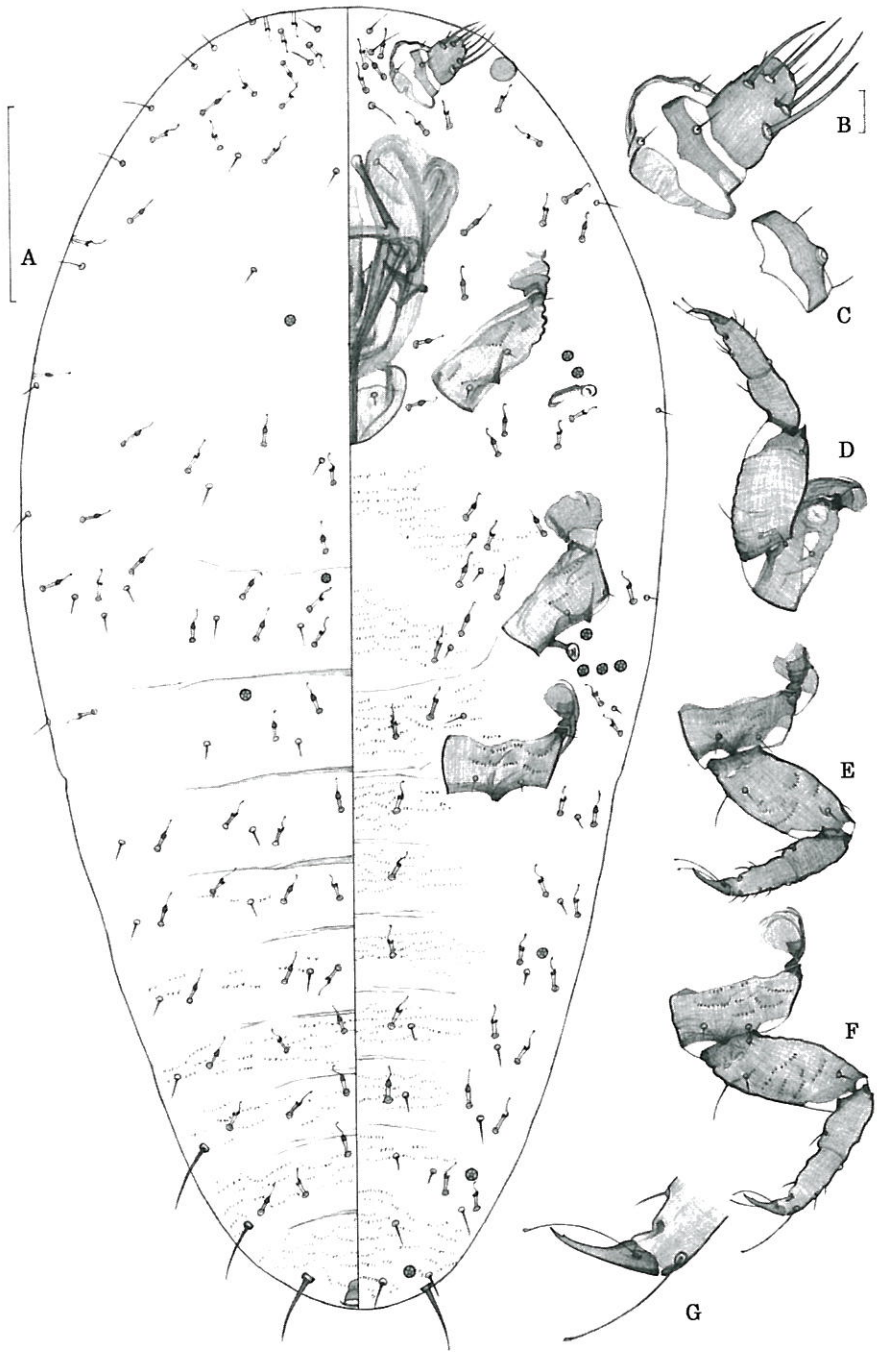


Fig. 18. *Gallacoccus* 03Ps-dsp, second-instar male. B, antenna; C, second antennal segment, dorsal surface; D–F, fore, mid, and hind legs; G, claw on hind leg (D–G drawn from another specimen). Scale bars: A, 100μm (D–F magnified at the same rate as A); B, 10μm (C and G magnified at the same rate as B).