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**FOUR GALL-INDUCING ERIOCOCCIDS, WITH NOTES ON
DIPTEROCARP-ASSOCIATED GALL-INHABITING COCCOIDS
(HOMOPTERA: COCCOIDEA: ERIOCOCCIDAE AND BEESONIIDAE)**

By SADAŌ TAKAGI

Abstract

TAKAGI, S., 2001. Four gall-inducing eriococcids, with notes on dipterocarp-associated gall-inhabiting coccoids (Homoptera: Coccoidea: Eriococcidae and Beesoniidae). *Ins. matsum. n. s.* 58: 51–113, 34 figs.

Four gall-inducing eriococcids are described: *Gallacoccus secundus* Beardsley, 1971, occurring on *Shorea curtisii* in Singapore, *G. spinigalla* and *G. heckrothi*, spp. nov., occurring on an unidentified plant (assumed to be a *Shorea* species) in Malaya, and *Echinogalla pustulata*, gen. et sp. nov., occurring on *Shorea falcifera* and *S. glauca* in Malaya. They induce globular galls each inhabited by a single female. *G. spinigalla* and *E. pustulata* induce galls of the same echinate type in spite of their remote relationship. The males complete their metamorphosis in the maternal galls. The female crawlers and the adult males appear synchronically from the maternal galls as in *Mangalorea hopeae* (Beesoniidae). This phenomenon, when combined with the absence of long caudal setae in the crawlers and the presence of papillae on the bodies of the adult males, suggests that the female crawlers are phoretic on the adult males. In the 4 eriococcid species and especially in the *Gallacoccus* species sexual dimorphism is remarkable in the 1st instar. Some features and characters of the female crawlers may be useful in the supposed intersexual phoresy. The 1st instar males have unusually robust legs or unusually elongate claws, and seem to be produced continuously in the maternal galls. The possibility is posed that they are thus armed and constantly present against invading natural enemies. Facts are assembled in support of the view that there should be a great number of unknown coccoid species inducing galls on dipterocarps in tropical Asia. The significance of atavism in the evolution of organisms is mentioned.

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1. INTRODUCTION

1.1. Scope

The plant family Dipterocarpaceae consists of nearly 600 species classified in some 17 genera. The greater part of the species belong to the subfamily Dipterocarpoideae, which comprises 12 genera occurring in tropical Asia and 1 genus (represented by 1 species) in the Seychelles. Other species are known from tropical Africa and Madagascar. Recently 2 species have been discovered in tropical South America (Guiana Highlands and Colombia) and referred to the family. ‘The distribution of the Dipterocarpaceae suggests a greater age for the family than is documented by the known fossil record’ and ‘calls for an origin before the pieces of Gondwanaland had drifted very far apart’ (Cronquist, 1981).

In tropical Asia the family is distributed in a broad region from India and Sri Lanka to New Guinea, and is especially rich in the number of species in western Malesia (west of the Makassar Strait, including the Malay Peninsula, Borneo, and Sumatra), where trees of the family are abundant in the lowland and low montane forests. ‘Where they do grow, they are extraordinarily plentiful. Half the trees whose crowns can be seen from an aeroplane—the *emergents*, as they are called—are dipterocarps’ (Veevers-Carter, 1984). This type of rain forest is called ‘the dipterocarp forest’, though it is composed not only of diverse species of dipterocarps but also of much more numerous species of other plant families. Dipterocarps also predominate in other parts of tropical Asia, growing in other types of forests, which are much simpler in composition than the rain forest. ‘Although dipterocarps today show their greatest diversity in Far Eastern rain forests, they did not originate in that area, but in either South America or Africa, prior to the final severance of dispersal opportunities between the two continents, probably at some time during the Late Cretaceous. The recent discovery of the most primitive dipterocarp *Pakaraimaea* in South America may point to a New World origin for the family, although of course this genus may be relict. Even the subfamily Dipterocarpoideae originated within the West, since its most primitive representatives are in rain forest outliers in the Seychelles (*Vateriopsis*) and Sri Lanka, and there are well-authenticated records of *Dipterocarpus* from the E. African Tertiary. Dipterocarpaceae were clearly extensively represented in the monsoon forests of the Sunda region during the Late Oligocene and Early Miocene, and thus were already in place across the SE Asian region at the time of widespread expansion of evergreen rain forests in the later part of the Early Miocene’ (Morley, 2000).

Coccoidea associated with and restricted to dipterocarps must bear a characteristic portion of the fauna of tropical Asia, and the evolutionary histories of some of them may be traceable back to the age of Gondwanaland. In spite of these expectations, our knowledge of the coccoid fauna associated with dipterocarps is still very meagre in contrast with the richness of the plant species. However, 5 species of coccoids belonging to 3 genera and 2 families have been known to induce galls on dipterocarps in India, Myanmar, and Singapore [as will be shown in 1.2]. Besides, there is evidence that unknown species of gall-inhabiting coccoids occur on dipterocarps in tropical Asia and tropical Africa and are numerous in Southeast Asia (Anthony, 1980; Jenkins, 1992; Jenkins and Mabblerley, 1994) [3.1]. Dipterocarp-associated gall-inhabiting coccoids (abbreviated to DGC’s in this paper) are worthy of study especially for clarifying the faunal characteristics of tropical Asia, because, as generally recognized, ‘the guild of gall-forming organisms is a specialized one, the members of which develop a close physiological and developmental relationship with host plants’ (Larew, 1990). Moreover, the gall provides space and food not only for the gall-

inducing organism but also for inquilines, parasites, predators, and gall-consumers, thus creating a new field of evolution for all of them. In fact, my observations strongly suggest that the gall-inhabiting coccoids studied in this paper have developed extraordinary behaviours [3.2, 3.3]. DGC's with the expected richness of species, therefore, may be promising also for studying the evolution of strategies developed in association with gall-inhabitation. Several coccoids induce on dipterocarps remarkably echinate galls. Jenkins (1992) discovered such galls on herbarium specimens of many dipterocarps [3.1]. I adopt the hypothesis proposed by him and restated by Jenkins and Mabberley (1994) that the echinate galls represent the pericarpial phenotype of an ancestor of the Dipterocarpaceae—unknown in the normal ontogeny of these plants. The hypothesis, therefore, supposes atavism. While atavism may not fully be admitted from the viewpoint of the current theory of evolution, it finds support in a multitude of taxonomic observations and developmental experiments. Atavism requires that gene expression should be organized in some hierarchical way to maintain potential of ancestral phenotypes, and thus suggests further capacity of the organized gene expression and carries implications for the essential features of evolution [3.4].

The primary purpose of the present study is to describe 4 species of gall-inhabiting coccoids occurring in Singapore and Malaya. Three of them are new species and one represents a new genus. Two species are associated with dipterocarps of the genus *Shorea*. The other two were collected from an unidentified plant, which, however, should also be a *Shorea* species. Thus the study contributes to the knowledge of DGC's, but is still far from clarifying the supposed rich fauna. I have, however, prepared the manuscript with a broader scope in the hope that this paper will be useful in stimulating and promoting researches on DGC's, which may be a promising group for undertaking an approach to evolutionary patterns and mechanisms of organisms on taxonomic ground.

1.2. Historical

1.2.1. Green (1926, 1928) described a remarkable coccoid of unknown affinity, *Beesonia dipterocarpi*, which induces 'large foliaceous galls' each inhabited by as many as a dozen females on *Dipterocarpus tuberculatus* in Burma (now Myanmar). Another dipterocarp-associated species of *Beesonia* was mentioned by Anthony (1974a) and Beardsley (1984), and was described by Takagi (1995) under the name *Beesonia shoreae*. It induces small but deep pits each inhabited by a single female on the twigs of the dipterocarp *Shorea curtisii* in Singapore. These *Beesonia* species exhibit larval polymorphism, of which the exact state and significance are still unknown. Two other species of *Beesonia* are known from warm-temperate eastern Asia, inducing pits on the branches of oaks (Fagaceae): *B. napiformis* (= *Xylococcus napiformis* Kuwana, 1914; = *B. quercicola* Ferris, 1950; = *B. albohirta* Hu and Li, 1986) and *B. brevipes* Takagi, 1987, both described on the basis of parthenogenetic forms. Hu et al. (1995) studied a bisexual form of *Beesonia* occurring on oaks, and referred it to *B. napiformis*. They synonymized *B. brevipes* with *B. napiformis* on the supposition that the 1st instar female of *B. brevipes* described as such by Takagi (1987) should be the 1st instar male of *B. napiformis*. In reality, however, specimens in exuviation (such as shown by Takagi, 1987: Fig. 6) clearly show that the 1st instar larva described by Takagi belongs to the female. Hu et al. reproduced in their paper Takagi's figure of the 1st instar female of *B. brevipes*, giving it the caption '*Beesonia napiformis* (Kuwana), free-living first instar male', and thus they did not show the real features of their 1st instar male. To my knowledge, the genus *Beesonia* comprises 4 distinct species: 2 dipterocarp-associated

species and 2 oak-associated species. The dipterocarp-oak combination in host association is hardly expected from the viewpoint of plant phylogeny, yet there are other examples of the combination (Takagi, 1995). The family Beesoniidae, erected by Ferris (1950) for *Beesonia*, has generally been accepted, though it has recently been enlarged to include the South American *Limacoccus* [3.1].

1.2.2. Jenkins studied the development of a densely echinate gall induced on *Hopea ponga* in southern India and also of the gall-inducing organism, an unnamed coccoid. The results are included in his thesis (1992) and summarized in Jenkins and Mabberley (1994). The coccoid is now known as *Mangalorea hopeae*, which was described by Takagi in Raman and Takagi (1992) as a member of the family Beesoniidae. In that paper Raman gives detailed observations on the development of the gall, and Takagi suggests the occurrence of intersexual phoresy in the coccoid [3.2]. The gall of *Mangalorea hopeae* is, when fully grown, shaped like a sea urchin or a breadfruit in external appearance. Each gall contains a single female, whereas a number of males occur on the outer surface of a gall, completing their development in gaps available among the dense spines.

1.2.3. Beardsley (1971) described 2 gall-inhabiting coccoids, *Gallacoccus anthonyae* and *G. secundus*, as occurring on the dipterocarp *Shorea pauciflora* in Singapore, and referred them to the family Eriococcidae. His study was based on material collected and submitted to him by Anthony, who corrected the host plant to *Shorea curtisii* (Anthony, 1974a, 1974b). In 1968–1970, Anthony carried out extensive surveys on plant galls on the summit of Bukit Timah (163m), Singapore, and discovered more than 100 galls induced by various organisms including the 2 *Gallacoccus* species [for her survey area, see 4]. She published her studies on the galls of the *Gallacoccus* species in her 1974 papers and some succeeding ones, compiled them in her thesis (1980), and summarized them in Rohfritsch and Anthony (1992). In either species, the gall is inhabited by a single female, and the male completes its metamorphosis within the maternal gall. While occurring on the same plant species (*Shorea curtisii*), these *Gallacoccus* species induce galls of quite different types (Figs. 1–3).

1.2.4. Anthony examined herbarium collections in search of galls similar to those of *Gallacoccus anthonyae* and *G. secundus* occurring on *Shorea curtisii* [1.2.3], and discovered galls on sheets of 24 *Shorea* species from Southeast Asia. The results are given in her thesis (1980) [3.1]. In connection with his studies on the echinate gall induced by *Mangalorea hopeae* on *Hopea ponga* [1.2.2], Jenkins surveyed literature, herbaria, and field localities in an attempt to extend the record of galls to other dipterocarps. The results of his surveys, given in his thesis (1992) and summarized by Jenkins and Mabberley (1994), show that 68 dipterocarp species belonging to *Shorea*, *Vatica*, *Dipterocarpus*, *Hopea*, and the African *Monotes* bear galls induced by unknown or unstudied organisms [3.1].

1.2.5. Beardsley (1984) revised gall-inducing Coccoidea, among which *Gallacoccus anthonyae*, *G. secundus*, *Beesonia dipterocarpi*, and ‘an apparently undescribed species of *Beesonia* from twig galls of *Shorea curtisii* in Singapore’ were mentioned as occurring on dipterocarps. The last species was described under the name *Beesonia shoreae* by Takagi (1995) [1.2.1].

1.2.6. Miller and Gimpel (2000) published a catalogue of the Eriococcidae. In the catalogue they recognize *Gallacoccus* as a genus of the family, and give a summary of published information on the genus and the 2 known species, *G. anthonyae* and *G. secundus*. Anthony’s correction of the host plant [1.2.3], however, is not mentioned.

1.3. Material

1.3.1. In 1990, at Kuantan, Malaya, I collected some echinate galls (Fig. 4) on dipterocarp saplings, which were identified with *Shorea falcifera* and *Shorea glauca* by Mr K. M. Kochummen. The view is adopted that the causal organisms belong to a single coccoid species, *Echinogalla pustulata*, gen. et sp. nov., in spite of the different host plant species. This coccoid may have some relationship to *Gallacoccus*, but is apparently not closely related to the latter.

1.3.2. In 1992 I stayed in Singapore for a short time and obtained from *Shorea curtisii* 2 galls of *Gallacoccus secundus*, from one of which I have mounted some specimens. At that time I got another gall, apparently of *Gallacoccus anthonyae*, from *S. curtisii*, but I found no insect in it.

1.3.3. In 1993 I received from Dr H. P. Heckroth alcohol-immersed material of coccoids, which he had collected at Gombak, Malaya, 'along the logging road near the place [Field Study Centre, University of Malaya]' from undetermined plants 'of apparently the same species that were less than 2m high' (his letter: 16.11.1993). Two species have been found in his material. They share some unusual characters of the 1st instar females with *Gallacoccus anthonyae* and *G. secundus*, and are described in this paper as members of *Gallacoccus*: *G. spinigalla* and *G. heckrothi*, spp. nov. *G. spinigalla* is closely related to *G. secundus*, from which it cannot be distinguished in the adult female, whereas *G. heckrothi* is referred to the genus rather tentatively. Fragments of galls are included in the alcohol-immersed material. Curiously enough, the gall of *G. spinigalla* is quite different from that of *G. secundus*, being echinate like the gall of *Echinogalla pustulata*, whereas the gall of *G. heckrothi* is similar to that of *G. secundus*. In the herbarium surveys made by Anthony (1980) and Jenkins (1992) [1.2.4], echinate galls similar to those of *G. spinigalla* and *E. pustulata* were found on some species of *Shorea*; in Anthony's (1980) surveys galls similar to those of *G. secundus* and *G. heckrothi* were found on many species of *Shorea* [3.1]. All this strongly supports the view that the saplings from which *G. spinigalla* and *G. heckrothi* were collected belong to a *Shorea* species. It excites special attention that these 2 species induce the galls of the quite different types on the same plant species as in the case of *G. anthonyae* and *G. secundus* occurring on *Shorea curtisii*. It is also noteworthy that *G. spinigalla* and *Echinogalla pustulata* induce similar echinate galls in spite of their different generic positions.

1.3.4. I got 2 galls on *Hopea sangal* in Bako National Park, Sarawak (Borneo Is.) [91ML-131], and mounted 1 specimen of the adult female coccoid from one of them. No insect was found in the other gall. This coccoid may belong to the *Gallacoccus-Echinogalla* group, and apparently represents another genus [3.1]. It is not described in the present paper, because the specimen is not only poor in condition but also much simplified in external structure as usual for the adult female in this group. As will be shown, the 1st instar female is especially useful for recognizing genera and species in these gall-inhabiting coccoids.

2. DESCRIPTIONS

2.1. Comments on some features and terms

2.1.1. Disc pores. The adult females of the *Gallacoccus* and *Echinogalla* species have 5-locular disc pores. The disc pores of *G. heckrothi* have been examined with a SEM. Two types of 5-locular disc pores are present: one of them is larger, with a linguiform process

visible inside the outer wall of each locule (Fig. 7), and the other appears to have no such process (Fig. 8). In the other 3 species the 5-locular disc pores, though somewhat variable in size, seem to belong exclusively to the former type so far as observed in light microscopy. These types, however, are not distinguished in the descriptions of the adult females. Quinquelocular disc pores also occur in the 2nd instar males of *G. secundus*, *G. heckrothi*, and *E. pustulata* (no specimen of this stage has been available from the material of *G. spinigalla*). The 1st instar females of the 4 species and the 1st instar males of *G. heckrothi* and *E. pustulata* have a 5- or 7-locular (Fig. 9) disc pore associated with each spiracle.

2.1.2. Tubular ducts. Several types of tubular ducts have been observed in the examined species. Microtubular ducts, minute ducts with a geminate structure at the inner end, occur in the 1st instar females of all the 4 species, and also in the 1st instar males of *Gallacoccus heckrothi* and *Echinogalla pustulata*. Ducts of another type are larger, with a cup-like structure at the inner end, from which a filamentous ductule arises, and are found in the 2nd instar males of *G. secundus*, *G. heckrothi*, and *E. pustulata* (no specimen of this stage has been available from the material of *G. spinigalla*). Similar but smaller ducts occur in the adult female of *E. pustulata*.

2.1.3. Dorsal processes in the 1st instar females. The 1st instar females of the *Gallacoccus* species are beset with a number of prominent processes on the dorsal surface. On the thoracic segments they are combined in a complicated manner. In slide-mounted specimens, however, they are depressed by the cover-glass and more or less deformed. Beardsley (1971) described the combination of these processes as 'a meshwork of small plate-like areas' in the diagnosis of the genus, and as 'a coarse cellular meshwork of irregularly shaped polygonal areas separated by narrow sclerotized bands' in the diagnosis of *G. secundus*. SEM observations have been made on the 1st instar female of *G. heckrothi* (Figs. 10–12). When viewed from above, the dorsal processes are irregularly polygonal and combined to form segmental blocks. On the prothorax they form a large transverse block, which is curved in the shape of a shallow inverted U. The mesothoracic block is a nearly round mass emarginate on the posterior margin, its anterior margin fitting the curved posterior margin of the prothoracic block. The metathoracic block is also nearly round, but smaller, its anterior margin fitting the emarginate posterior margin of the mesothoracic block. In lateral view the dorsal surface of the body is rugged in a complicated manner owing to the dorsal processes upstanding in various heights and the conical setae being also erect. All these patterns are hardly observable in depressed slide-mounted specimens. The descriptions and drawings given below, however, are exclusively based on slide-mounted specimens.

2.1.4. Dorsal pits in the 1st instar females. The 1st instar females of *Gallacoccus secundus* and *G. spinigalla* possess many small pit-like invaginations on the dorsal surface. These pits are somewhat sclerotized, each having a membranous slit on the bottom. According to Beardsley (1971), similar pits occur in *G. anthonyae*, but each of them has on the bottom 'a minute circular opening' instead of a slit. He assumed the slit or 'circular opening' to be a gland orifice, but there is no evidence for his assumption. These pits remind me of the dorsal spots of the Conchaspidae.

2.1.5. Caudal setae in the 1st instar larvae. In all the examined species the 1st instar larvae of both sexes have no trace of long caudal setae (this statement is not repeated in the descriptions of the species). Many other Coccoidea have well-developed caudal setae in the 1st instar. In the species of *Gallacoccus* and *Echinogalla* the corresponding setae may be obsolete or replaced by shortened setae not distinguishable from neighbouring ones.

This state is also the case with *Mangalorea hopeae*.

2.1.6. Aliform appendages of mouth-parts in the adult females. In the adult females of the 4 examined species the mouth-parts are expanded into a pair of enormous fan- or wing-like appendages, which are sclerotized and well stained throughout, with or without more strongly stained stripes (Figs. 20A, 21A, 22A). Similar appendages of the mouth-parts have been observed in *Mangalorea hopeae* (Raman and Takagi, 1992: Fig. II.7), and are undoubtedly present in *Gallacoccus anthonyae* (Anthony, 1974b: Pl. X, Figs. 4, 6). They may be termed 'aliform appendages of mouth-parts', though they are not mentioned in the descriptions of the species.

2.1.7. Papillae in the adult males. Macropterous adult males have been available for study in all the 4 species. For light microscopy they were prepared in the same method as that adopted for the other stages, and mounted in Canada balsam with fragments of cover-glass inserted between the slide-glass and the cover-glass. In all the 4 species the adult males are beset with a number of small processes or 'papillae' on the head, thorax and abdomen. The adult male of *Gallacoccus heckrothi* has many papillae even on the antennae and legs. The papillae are elongate and nearly ellipsoidal (in *Gallacoccus secundus* and *G. spinigalla*) or low and tubercular (in *G. heckrothi* and *Echinogalla pustulata*) (Figs. 13, 30–33). The adult male of *Mangalorea hopeae* is also beset with papillae (Raman and Takagi, 1992: Figs. II.16, II.22), which are similar to those occurring in *G. secundus* and *G. spinigalla*. These processes are not modified setae, lacking a basal socket.

2.1.8. Glandular pouches in the adult males. The adult males have a pair of glandular pouches on the 8th abdominal segment as usual in the Eriococcidae, Pseudococcidae, Coccidae and other families of the Coccoidea. Each pouch is a funnel-shaped invagination lined with glandular organs, and is provided with 2 long setae arising from the bottom. SEM observations have been made on the pouches of *Gallacoccus heckrothi* (Figs. 13–15). They are covered with wax-secreting locules on the whole surface with no interspace, and each locule is provided with a linguiform process, which occupies most of the space within the locule. The pouches are so tightly packed with locules that each of them looks as if it were an unusually large multilocular pore. The walls separating the locules are combined to form a honeycomb-like framework, though no locules are exactly hexagonal. Trifurcate patterns are outstanding on the comb instead. The interpretation is adopted that the glandular system of the pouch is composed of 3-locular disc pores appressed together. In this interpretation each 3-furcate pattern corresponds to the locule-separating septa of a 3-locular disc pore, which are projected beyond the level of the surrounding wall of the pore. In the other 3 species individual disc pores can easily be recognized at least in the periphery of a pouch, where they are not appressed together. In light microscopy the type of these disc pores cannot always be determined, but usually they appear to be 3-locular.

2.1.9. Afifi's (1968) terms are adopted for describing the adult males. For the term 'papillae', see 2.1.7. The abbreviations 'abd I–VIII' stand for the 1st to 8th abdominal segments.

2.1.10. There have been available some specimens containing a developing body of the succeeding instar, so that the sequence of male instars, from the 1st instar to the 2nd and then to the prepupa, has been confirmed. Sexual dimorphism is remarkable in the 1st instar, and the male and the female are easily recognizable even in this instar. The examined specimens of the female are crawlers and adults, and no specimens of the stage intermediate between them have been available. The coccoid species described in this paper are easily distinguishable from each other in the 1st instar female, whereas *Gallacoccus secundus*

and *G. spinigalla* are hardly separable in the adult female. Specimens of the 1st instar female, therefore, are designated for the holotypes of the new species. The genera *Gallacoccus* and *Echinogalla* are also recognized with emphasis on this stage, which is peculiarly featured probably in connection with dispersal [3.2, 3.3].

2.1.11. The holotypes, together with some other specimens, are deposited in the collection of the Entomology Division, Forest Research Institute of Malaysia, Kepong, Selangor, Malaysia.

2.2. *Gallacoccus* Beardsley, 1971

Type species: *Gallacoccus anthonyae* Beardsley, 1971.

No specimens of the type species have been examined in the present study. I got 1 gall apparently of this species at the type locality [1.3.2]. It was 1.3cm long and 0.9cm wide, and, therefore, at an early stage of formation (according to Anthony, 1974a, the gall of *G. anthonyae* can reach 6cm in length). It looked fresh when collected, but contained no insect.

Beardsley erected the genus for *Gallacoccus anthonyae* and *G. secundus*, and gave a generic diagnosis on the basis of the adult female and the 'first instar larva' (in reality, the 1st instar female). *G. spinigalla*, sp. nov., well agrees with his generic diagnosis. In the first instar male, however, it is remarkably different from *G. secundus* [for the significance of this difference, see 3.3] (the 1st instar male of *G. anthonyae* is unknown). When *G. heckrothi*, sp. nov., is also added to the genus, his generic diagnosis should be modified. I do not present here a modified description of the genus, because *G. heckrothi* is referred to the genus rather tentatively. The 4 species of the genus induce galls of different types [1.2.3, 1.3.3].

Beardsley recorded *G. anthonyae* and *G. secundus* as occurring on *Shorea pauciflora*. The host plant was later corrected to *S. curtisii* [1.2.3]. Tang and Hao (1995) applied a modified name, *Gallococcus*, to the genus (p. 436, 440, 661), while using the original spelling *Gallacoccus*, too (p. 441). The connecting vowel used in the original spelling is indeed inappropriate, but is not to be corrected under the current rule (Code, 1999: Article 32.5.1).

2.3. *Gallacoccus secundus* Beardsley, 1971

2.3.1. Material examined. Two elongate globular galls were collected at the type locality, Bukit Timah, Singapore, on a young tree of *Shorea curtisii*, 6 July, 1992. From one of them, 2.5cm long and 1.5cm wide, were mounted 1 adult female, 3 1st instar females, 29 1st instar males, 3 2nd instar males, and about 20 adult males. No insect was found in the other gall, which was 1.6cm long and 0.9cm wide and apparently immature (according to Anthony, 1974a, the gall of this species reaches 3.5cm in length and 2cm in width).

Beardsley described the adult female and the 1st instar female. The specimens I have examined of these stages practically agree with his descriptions including the sizes and numbers of features.

2.3.2. First instar female (Fig. 16). In addition to Beardsley's description ('First instar larva'), the following characters should be given. The examined specimens, apparently at the crawling stage, are elongate obovoid. Conical setae thickly walled, thus leaving a narrow hollow space inside. Anterior and posterior spiracles each with a 7-locular disc pore situated just laterally to peritreme. Microtubular ducts present, occurring sparsely as follows on each side: 6 submedians on dorsal surface, forming a longitudinal series, the posteriormost occurring on abd V; 6 on ventral surface along margin (in Fig. 16 the anteriormost is hidden

by the antenna). Anus on ventral surface near posterior end of body. Antennae: basal and 2nd segments broader than long, basal segment with 2 setae, the 2nd with 1; 3rd segment about twice as long as wide, with 8 setae on distal half, one of them being much longer than the antennal segments combined. Legs well developed, rather slender; tarsi much longer than tibiae, nearly twice as long as the latter in hind legs; tarsal digitules nearly as long as the segment; claws gently curved, with an inconspicuous denticle near apex on plantar surface; ungual digitules much longer than claws.

2.3.3. Adult female. The single specimen examined is about 4mm in diameter as mounted. It must be more aged than the holotype adult female (which is 2.4mm in diameter, according to Beardsley). Though it is rather poor in condition, it agrees with Beardsley's description fairly well.

2.3.4. First instar male (Fig. 23). The examined specimens, probably not much aged, are elongate obpyriform, tapering from the pro- or mesothoracic region towards the posterior end of the body. Derm membranous, both dorsal and ventral surfaces with transverse rows of spicules across metathorax and abdominal segments and with rudiments of such rows on mesothorax. Setae occurring on posterior abdominal segments spinous; none are conical. Eyes sclerotized; antennae and legs strongly sclerotized. Anus on ventral surface near posterior end of body. Spiracles with no disc pore. Antennae 3-segmented; basal and 2nd segments broader than long, the basal segment with 2 setae, the 2nd with 1 seta and 1 low tubercle (sensillum?); 3rd segment nearly twice as long as wide, truncate apically, with as many as 8 setae on distal half, a few of them short and stiff, the others about as long as 3rd segment. Legs strong and robust; fore legs with trochanter+femur about half as deep as long, mid and hind legs also with femur remarkably thickened; tarsi distinctly longer than tibiae, about 1.3 times as long as the latter in hind legs; tarsal digitules about as long as the segment; claws gently curved, with an inconspicuous denticle near apex on plantar surface; ungual digitules extending beyond apex of claw.

2.3.5. Second instar male (Fig. 27). Derm with transverse rows of spicules on both surfaces of abdominal segments, and also in thoracic region on ventral surface. Setae occurring on posterior abdominal segments spinous. Spiracles with no disc pores. Anus at posterior end of body. Quinquelocular disc pores present on both surfaces; on dorsal surface occurring submedially as follows: a few on head and pro- and mesothorax each, 1 on metathorax, and 1 occasionally present on abd VII; on ventral surface: 1 mesal to antenna, a few in front of anterior spiracle, others occurring submedially and submarginally on mesothorax to abd VII (abdominal segments each with 1 submedian and several submarginal disc pores; abd VII at times with the submedian pore only). Tubular ducts present on dorsal surface, 1 submedially on each of metathorax and abd I-VII. Antennae 3-segmented; basal and 2nd segments much broader than long, the basal segment with 2 setae and the 2nd with 1; 3rd segment a little longer than broad, truncate apically, with 7 or 8 setae, a few of them much shorter than the others. Legs relatively short; tarsi longer than tibiae, about 1.3 times as long as the latter in hind legs; tarsal claws little curved, with a minute denticle near apex on plantar surface.

2.3.6. Adult male (Fig. 30). Head large, about half as broad as thorax; abdomen (excluding genital capsule) a little longer than thorax, gradually narrowing posteriorly on distal half. Head, prothorax, mesothorax partly, metathorax, and abdomen (except for genital capsule) beset with a number of ellipsoidal papillae, occasionally some papillae being reduced to round tubercles. No disc pores present (except for glandular pouches of abd VIII [2.1.8]). Abd VIII with a sclerotized patch of derm dorsally on anterior margin.

Transverse rows of spicules on abdominal segments. Head in dorsoventral view roughly round in outline, with genae demarcated from anterior portion of head by slight constrictions; dorsal arm of midcranial ridge absent; preocular ridge well represented on dorsal surface around anterior margin of dorsal eye; postocular ridge also well developed; postoccipital ridge well represented, not divided laterally, the lateral arm bending posteriorly. Eyes prominent; dorsal eyes nearly 1.5 times as large as ventral eyes in diameter of cornea. Antennae as long as fore tibia, tarsus, and claw combined, 5-segmented; basal segment transversely rectangular in outline, the 2nd globular, the 3rd constricted basally, gradually broader apically, about twice as long as broad, the 4th about half as long as the 3rd, all these segments with hairy setae; 5th segment longest, nearly 2.5 times as long as broad, broadest subbasally, with 6 fleshy falcate setae, and with 4 long, stiff, and apically knobbed setae arising on apical to subapical part of the segment (in Fig. 30 is shown at the base 1 hairy seta, which is, however, usually absent). Pronotal ridge well represented, connected on ventral surface with proepisternum+cervical sclerite. Post-tergite indicated by a sclerotized patch. Prescutum much longer than scutum; scutellum transversely rectangular, well sclerotized except for a discoidal median area. Postnotal apophysis well developed. Mesosternum with marginal ridge well represented, and with furca well developed and sclerotized. Halteres absent. Legs rather slender; trochanters with basal portion much shorter than distal one; fore femora thickened, nearly half as deep as long; mid and hind femora less thickened; tibiae distinctly longer than tarsi, about 1.4 times as long as the latter in hind legs; tibiae and tarsi with setae on ventral surface more or less spinous; no tarsal digitules present; claws slightly curved, with no denticle; claws of fore legs stout, those of mid and hind legs slender; unguis extending beyond apex of claw, slightly knobbed apically. Genital capsule conical in dorsoventral view; aedeagus curved down in lateral view.

2.4. *Gallacoccus spinigalla*, sp. nov.

2.4.1. Material examined. Collected at Gombak, Selangor, Malaya, near the Field Study Centre, University of Malaya, along the logging road, on an undetermined plant, which is probably a *Shorea* species [1.3.3], March and April, 1993, H. P. Heckroth. About 40 1st instar females, 4 adult females, about 30 1st instar males, and about 20 adult males were mounted from alcohol-immersed material, which includes fragments of echinate galls. Judging from the fragments, the gall is very similar to that induced by *Echinogalla pustulata*.

2.4.2. First instar female (Fig. 17). The examined specimens are apparently at the crawling stage, yet they are more or less swollen on the ventral side, so that, when mounted, the margin of the ventral surface a little bulges out of the body outline, which is elongate obovoid. Dorsal derm slightly sclerotized. Conical setae thickly walled, thus leaving a narrow hollow space inside. On dorsal surface conical setae occurring in 3 longitudinal series on each side (though these series are sometimes rather arbitrarily discriminated): about 17 marginals around body from head to caudal end (abd VIII); 8 submedians on head, thorax, and abd I, II, and IV; about 11 intermediates on thorax and abdomen, the posteriormost of them occurring on abd III. On ventral surface 4 conical setae occurring as follows: 1 within margin on head (in Fig. 17 almost hidden by antenna), 1 laterally to anterior and posterior spiracles each, and 1 marginal on abd VIII. Dorsal processes of derm forming transverse folds across thoracic segments and abd I–III; round processes occurring across abd IV–VII, and also between dermal folds and on marginal area. Ventral surface with conical or digitiform processes of derm occurring marginally and submarginally,

especially numerous on mesothorax. Dermal pits present on meso- and metathorax and abdominal segments, occurring just posteriorly to the dermal folds or round processes, elliptical, each with a membranous slit on bottom. Microtubular ducts occurring as follows on each side: 6 submedians on dorsal surface, forming a longitudinal series, the posteriormost occurring on abd V; 6 near margin on ventral surface (in Fig. 17 the anteriormost is hidden by the antenna). Spiracles each with a 5-locular disc pore laterally to peritreme. Anus small, situated on ventral surface near posterior end of body. Antennae 3-segmented; basal and 2nd segments broader than long, the basal segment with 1 or 2 setae, the 2nd smaller than the basal, with no seta; 3rd segment about twice as long as broad, with 8 setae, one of them much longer than the others, being nearly twice as long as antennal segments combined. Legs well developed, rather slender, the mid and hind legs arising near body margin; tarsi much longer than tibiae, about 1.5 times as long as the latter in hind legs. Each tarsus with 2 setae on ventral surface; on the hind tarsus, one of the setae, arising about the middle of the segment, is much longer than the other, being as long as the segment. Tarsal digitules as long as the segment in fore and mid legs, longer than the segment in hind legs. Claws elongate, nearly as long as tibiae, a little curved, with a slight denticle near apex on plantar surface; unguis digitules distinctly longer than claws.

2.4.3. Adult female (Fig. 20). Globular, much simplified in structure. Quinquelocular disc pores somewhat variable in size, strewn broadly around anterior spiracles and also in a broad band along body margin on posterior half of body, completely surrounding vulva; also thinly scattered anteriorly to anus. Dorsal derm spiculate in some segments anterior to anus. Setae occurring around anus spinous. Anus simple, strongly sclerotized along margin of anterior half, with a sclerotized patch of derm just anteriorly. Antennae 3-segmented; basal segment incomplete, being represented by a crescent-shaped sclerite, with 2 setae (occasionally absent?); 2nd segment complete or incomplete, with no seta; 3rd segment short, apex truncate, with 5 or 6 fleshy setae subequal in length. Eye spots occurring laterally to and at some distance from antennae, sclerotized, but with an obscure outline, nearly as large as 3rd antennal segment. Legs compared with body obviously diminished in size, yet with distinct segments, stout; tibiae and tarsi subequal in length; claws stout, strongly curved, with a denticle near apex on plantar surface; tarsal digitules not particularly elongated; unguis digitules surpassing claws. A group of small humps (or a patch of reticulate derm) occurring behind each hind coxa.

2.4.4. First instar male (Fig. 24). The examined specimens are spindle-shaped, being broadest in mesothoracic region, then narrowing anteriorly and posteriorly. Derm on both surfaces transversely spiculate on thoracic and abdominal segments. Setae occurring on posterior segments of abdomen spinous. Eyes sclerotized. Spiracles with no disc pore. Anus at caudal end of body. Antennae 3-segmented; basal and 2nd segments broader than long, the basal with 1 seta; 2nd segment smaller than the basal, with no seta; 3rd segment about 1.7 times as long as broad, with 8 setae on distal half, the longest seta longer than 2nd and 3rd segments combined, slender and stiff. Legs rather stout; tarsi longer than tibiae, about 1.5 times as long as the latter in hind legs; tarsal digitules longer than the segment; claws a little shorter than tibiae, the distal half elongated into a slightly curved, narrow, sharp process, with no denticle; unguis digitules extending beyond apex of claw.

2.4.5. Adult male (Fig. 31). Head small, much narrower than thorax, which is about 2.5 times as broad as the head; abdomen (excluding genital capsule) about as long as thorax, gradually narrowing posteriorly in distal half. Head, prothorax, mesothorax partly, metathorax, and abdomen (except for genital capsule) beset with a number of ellipsoidal

papillae, occasionally some of the papillae being reduced to round tubercles. No disc pores present (except for glandular pouches of abd VIII [2.1.8]). Abd VIII with a sclerotized patch of derm dorsally on anterior margin. Transverse rows of spicules on abdominal segments. Head in dorsoventral view roughly conical except for genae, which are demarcated from the anterior portion of the head by lateral constrictions and gently lobed laterally; dorsal arm of midcranial ridge absent; preocular ridge represented by a weakly sclerotized band on anterior margin of dorsal eye; postocular ridge well represented; postoccipital ridge well represented, not divided laterally, the lateral arm bending posteriorly. Eyes moderate in size, dorsal eyes a little larger than the ventral in diameter of cornea. Antennae as long as fore tibia, tarsus, and claw combined, 5-segmented; basal segment transversely rectangular in outline, the 2nd globular, the 3rd constricted basally, gradually broader apically, about 1.7 times as long as broad, the 4th about half as long as the 3rd, all these segments with hairy setae; 5th segment longest, nearly twice as long as broad, with 6 fleshy falcate setae, and with 4 long, stiff, and apically knobbed setae arising on apical to subapical part of the segment. Pronotal ridge well represented, connected on ventral surface with proepisternum+cervical sclerite. Post-tergite indicated by a slender sclerosis. Prescutum much longer than scutum; scutellum transversely rectangular, well sclerotized except for a small discoidal median area. Postnotal apophysis well developed. Mesosternum with marginal ridge well represented, and with furca well developed and sclerotized. Halteres absent. Legs rather slender; trochanters with basal portion much shorter than the distal one; fore femora somewhat thickened; mid and hind femora less thickened; tibiae distinctly longer than tarsi, about 1.5 times as long as the latter in hind legs. Tibiae and tarsi with setae on ventral surface more or less spinous; no tarsal digitules. Claws slightly curved, with no denticle; claws of fore legs stout, those of mid and hind legs slender; unguis extending beyond apex of claw, slightly knobbed apically. Genital capsule conical in dorsoventral view; aedeagus curved down in lateral view.

2.4.6. Remarks. I have failed to find any distinct difference in the adult female between this species and *Gallacoccus secundus*. I have no doubt, however, that the two are distinct species, being easily distinguishable in the 1st instar larvae of both sexes and also in the adult male.

In the 1st instar female, *G. spinigalla* is distinguishable from *G. secundus* by the following characters: 1) no dermal pits are present on the head and prothorax; 2) the spiracular disc pores are 5-locular [7-locular in *G. secundus*]; 3) the 2nd antennal segment has no seta [has 1 seta]; 4) the seta arising at the middle ventral surface of the hind tarsus is very long [as long as the other ventral seta of the segment]; 5) the claws are apparently elongate [not particularly elongate].

In the 1st instar male, *G. spinigalla* differs from *G. secundus* 6) in the legs not much thickened [much thickened, with the femora unusually robust], 7) in the 2nd antennal segment having no seta nor tubercular process [having 1 seta and 1 tubercular process], and 8) in the claws elongated to form narrow, sharp processes [not particularly elongated].

In the adult male, *G. spinigalla* is distinguishable from *G. secundus* mainly 9) in having a much smaller head and smaller eyes.

G. spinigalla is apparently closer to *G. secundus* than to *G. anthonyae* not only in the adult female but also in the 1st instar female, running to *G. secundus* in Beardsley's (1971) keys. In the 1st instar male, *G. spinigalla* appears to be strikingly different from *G. secundus* owing to character 6). But this difference suggests different behavioral traits in the 1st instar males rather than a remote phylogenetic relationship between the species [3.3].

The gall induced by *G. spinigalla* is quite different not only from that of *G. secundus* but also from the galls of the other known species of *Gallacoccus*, being echinate like the gall of *Echinogalla pustulata* (Fig. 4). *Mangalorea hopeae* (Beesoniidae), associated with the other dipterocarp genus *Hopea*, also induces an echinate gall, which, however, differs in the details of the spines. Apparently the facies of the galls reflect neither the taxonomic relationships of the coccoids nor those of the host plants. The significance of the occurrence of these echinate galls in the remotely related coccoids will be discussed in a later section [3.4].

2.5. *Gallacoccus heckrothi*, sp. nov.

2.5.1. Material examined. Collected at Gombak, Selangor, Malaya, near the Field Study Centre, University of Malaya, along the logging road, on an undetermined plant, which is probably a *Shorea* species [1.3.3], March and April, 1993, H. P. Heckroth. A number of 1st instar larvae of both sexes, 9 adult females, 9 pupae and about 40 adult males were mounted from alcohol-immersed material. Fragments of galls are included in the material. They show no processes on the external surface. One dry gall was also available. It was elongate globular, 3.8cm long and 2.8cm wide, glabrous on the external surface, with the distal end produced to form a short tube for exit. It was apparently full-grown, and there was found within it no insect other than 1 half-destroyed body of the 1st instar male, which was buried in powdery wax covering the inner wall of the gall. In general appearance the gall is similar to that of *G. secundus*, though the latter is not smooth on the external surface, being 'covered with bumps each of which has an apical tuft of hairs' (Anthony, 1974a).

2.5.2. First instar female (Figs. 9–12, 18). The examined specimens, apparently at the crawling stage, are elongate and slender, broadest across mesothorax, then gradually narrowing posteriorly, the last segment produced posteriorly to form a pair of moderate prominences, which are called here 'anal lobes'. Dorsal derm slightly sclerotized. Conical setae thinly walled. On dorsal surface conical setae occurring in 3 longitudinal series on each side (though these series are sometimes rather arbitrarily discriminated): about 17 marginals occurring around body from head to anal lobe (abd VIII), the one on anal lobe longer than the others; 8 submedians on head, thorax and abd I, IV, and VIII, elongate, longer than neighbouring conical setae, the posteriormost of them situated mesad of the posteriormost conical seta occurring on anal lobe; about 11 intermediates, the posteriormost of them occurring on abd III. On ventral surface 3 conical setae occurring on each side as follows: 1 submedian just mesally to basal antennal segment; 1 laterally to fore coxa; 1 submedian near posterior end of body. Dorsal processes of derm mostly tubercular, occurring in a broad median region and also marginally and submarginally [for SEM observations, see 2.1.3]. Ventral surface with small conical or tubercular processes on head and thorax, and with minute conical processes medially across metathorax and abdominal segments. Microtubular ducts arranged as follows on each side: 6 submedians on dorsal surface, forming a longitudinal series, the posteriormost occurring on abd V; 6 on ventral surface along margin. Eyes rather small. Spiracles each with a 7-locular disc pore. Anus on ventral surface near posterior end of body. Antennae porrect, parallel or nearly so, 3-segmented; basal segment nearly square in outline, constricted halfway, with 1 seta; 2nd segment smaller, as long as broad, expanded apically, with 1 seta; 3rd segment 2.5 times as long as broad, constricted basally, nearly parallel on lateral margins, round apically, with 8 setae on distal half, various in length, the longest of them being as long as the 3 segments combined. Legs

arising near body margin, well developed; femora deeply excavated subapically on ventral surface; tarsi much longer than tibiae, about 1.6 times as long as the latter in hind legs. Tarsal digitules much longer than the segment, about 1.7 times as long as the segment in hind legs. Claws elongate, rather strongly curved to form a hook, with no denticle (in Fig. 18E the plantar surface is slightly swollen on the middle of its distal half, but this is not always the case); unguis digitules far exceeding claws.

2.5.3. Adult female (Figs. 7, 8, 21). Globular, much simplified in structure. Quinquelocular disc pores variable in size [for SEM observations, see 2.1.1], strewn around body on both surfaces except on head, where they are limited to the dorsal surface; broadly scattered in prothoracic region on dorsal surface and also anteriorly to anus; densely strewn between anus and vulva and laterally to vulva, none anteriorly to vulva. Derm with spicules on some segments anterior to anus. Setae occurring around anus spinous, some setae occurring anteriorly to anus often geminate. Anus simple, strongly sclerotized on margin except posteriorly, with a sclerotized patch of derm just anteriorly. Antennae 3-segmented; basal segment reduced to a complete or incomplete slender ring, with 2 setae; 2nd segment also represented by a slender ring, with 1 seta; 3rd segment stump-like in shape, with 6–8 fleshy setae, a few of them sometimes much shorter than the others. Eye spots obscure. Legs stout; tibiae and tarsi subequal in length, these segments combined shorter than femora; claws curved, with a denticle near apex on plantar surface. Tarsal and unguis digitules with apical knob much enlarged; tarsal digitules subequal to the segment in length; unguis digitules far surpassing claws.

2.5.4. First instar male (Fig. 25). Elongate, broadest in mesothorax, gradually narrowing posteriorly. Setae hairy including long ones occurring on posterior end of body. Derm with transverse rows of spicules on both surfaces of abdominal segments; some spicules medially on ventral surface of meso- and metathorax. Microtubular ducts present, occurring as follows on each side: 6 submedians on dorsal surface, forming a longitudinal series; 6 on ventral surface along margin (in Fig. 25 one of them is hidden by the mid femur). Antennae 3-segmented; basal and 2nd segments transversely rectangular in outline, each with 1 seta, the 2nd much smaller than the basal; 3rd segment about twice as long as broad, with about 6 setae on distal half. Spiracles each with a large 7-locular disc pore. Anus on ventral surface at posterior end of body. Legs rather slender; tarsi longer than tibiae, 1.5 times as long as the latter in hind legs; claws elongate, longer than tibiae, little curved, slender, and sharp, with a minute denticle on plantar surface near apex. Tarsal digitules reduced into short setae; unguis digitules obsolete.

2.5.5. Second instar male (Fig. 28). Tapering posteriorly on abdomen when young, elongate elliptical when fully grown. Quinquelocular disc pores occurring submarginally on ventral surface as follows: 1–4 in front of anterior spiracle; 0 or 1 in front of mid coxa; 1–3 in front of posterior spiracle; 1 or 2 laterally of hind coxa and also on succeeding 6 segments each. Tubular ducts occurring on both surfaces except on posteriormost abdominal segment, scattered on head and prothorax, nearly in sparse transverse rows on succeeding segments. Setae hairy including long, rather thick ones occurring on posterior end of body. Derm spiculate on dorsal surface of abdominal segments and on ventral surface of meso- and metathorax and abdominal segments. Anus situated on ventral surface near posterior end of body. Antennae 3-segmented, apparently diminished as compared with those of 1st instar male, basal segment with 2 setae, the 2nd with 1 seta, and the 3rd with about 7 setae. Legs relatively short; tibiae and tarsi subequal in length; claws nearly straight, with or without a minute denticle near apex on plantar surface. Tarsal digitules represented by

short setae; unguar digitules obsolete.

2.5.6. Adult male (Figs. 13–15, 32). Head very small, about 1/3.5 as broad as thorax; abdomen (excluding genital capsule) about as long as thorax, gradually narrowing posteriorly on distal half. Head, prothorax, mesothorax except for area enclosed by scutellum and postnotal sclerite, metathorax, abdomen, and legs beset with a number of tubercular papillae, antennae and ventral surface of genital capsule with some tubercular papillae. No disc pores present (except for glandular pouches of abd VIII [for SEM observations of the pouches, see 2.1.8]). Abd VIII sclerotized dorsally. Transverse rows of spicules on abdominal segments. Head in dorsoventral view roughly conical, with genae demarcated from anterior portion of head by lateral constrictions and lobed laterally; dorsal arm of midcranial ridge absent; pre- and postocular ridges slender; postoccipital ridge well represented, not divided laterally. Eyes moderate in size, dorsal and ventral eyes subequal in diameter of cornea. Antennae about as long as fore tibia, tarsus and claw combined, 5-segmented, the 2nd to 5th segments each with a few papillae; basal segment nearly rectangular, the 2nd rather globular; 3rd constricted basally, gradually broader apically, about 1.5 times as long as broad; 4th as long as the 3rd, these segments with hairy setae; 5th segment as long as the 4th, with 6 fleshy falcate setae and also with 2 long, stiff, and apically knobbed setae arising on apical part of segment. Pronotal ridge well represented, connected on ventral surface with proepisternum+cervical sclerite. Post-tergite represented by a sclerotized patch of derm. Prescutum nearly 1.5 times as long as scutum; scutellum transversely rectangular, well sclerotized except for a transversely elliptical median area. Postnotal apophysis well developed. Mesosternum with marginal ridge represented by a fold-like sclerotization, and with furca well developed and sclerotized. Halteres absent. Legs well developed, with a number of papillae except on claws; fore femora somewhat thickened; tibiae longer than tarsi, about 1.5 times as long as the latter in hind legs; claws with no denticle, claws of fore and mid legs narrow and sharp; no tarsal digitules; unguar digitules extending beyond apex of claw. Genital capsule in dorsoventral view globular in basal portion; produced into a conical process in distal portion; aedeagus curved down in lateral view.

2.5.7. Remarks. This species agrees with *G. secundus* and *G. spinigalla* in many characters, but differs from them mainly as follows.

In the 1st instar female, 1) the last abdominal segment is produced into a pair of lobes ('anal lobes'), 2) the conical setae are not thickly walled, 3) the submedian conical setae except the posteriormost are elongate, 4) no dermal pits are present, 5) the ventral surface is beset with many tubercular or conical processes, 6) the basal antennal segment is nearly square in outline, and the 2nd is expanded apically [both these segments are shorter than wide and the 2nd is not expanded apically in *G. secundus* and *G. spinigalla*], 7) the femora are deeply excavated subapically on the ventral surface, and 8) the claws are more strongly curved.

In the adult female, 9) the disc pores have 2 types [2.1.1], 10) the disc pores occur on the head as well as on the posterior portion of the body, and 11) some dorsal setae are geminate.

In the 1st instar male, 12) microtubular ducts are present, and 13) each spiracle is provided with a 7-locular disc pore [no disc pore].

In the adult male, 14) the papillae are tubercular [nearly ellipsoidal], 15) the antennae, legs, and genital capsule as well as the trunk are beset with papillae, 16) the 5th antennal segment is provided with 2 knobbed setae [4 knobbed setae] (in addition to 6 fleshy falcate setae), and 17) the prescutum is relatively short.

Some of these characters, when combined, may have generic value, justifying the erection of a new genus for this species. In this regard, character 2), 4), 6), 14), and 16) are noteworthy. Character 1) may also be added to the supposed generic characters, though I am not certain whether the lobes are homologous with the anal lobes of *Eriococcus* and other eriococcid genera. I have no doubt, however, that *G. heckrothi* has some relation to the other 3 species of *Gallacoccus*, even if it should be removed from the genus. Because our knowledge of this insect group is still very meagre, I tentatively refer this species to *Gallacoccus*. I expect that discoveries of related species will show that the combination of characters mentioned above is stable and worthy of generic value.

The gall induced by *G. heckrothi* is very similar to that of *G. secundus*, though these species are not particularly closely related to each other.

2.6. *Echinogalla*, gen. nov.

Type species. *Echinogalla pustulata*, sp. nov.

This genus is erected on the basis of the type species alone. It is compared here with *Gallacoccus* because there is no other genus adequate for making a comparison with it. In reality, *Echinogalla* greatly differs from *Gallacoccus* (as represented by the 3 species described in this paper) in the characters given below. It disagrees also with the original description of *G. anthonyae*, the type species of *Gallacoccus*, in most of the mentioned characters of the 1st instar and adult females.

In the 1st instar female, 1) the dorsal body setae are bluntly spinous [conical in *Gallacoccus*], and decreased in number, being absent in the intermediate area, 2) the dorsal surface of the cephalothorax and the base of abdomen is covered with a number of low pustular swellings [with eminent processes on the cephalothorax and abdominal segments], 3) 5 pairs of microtubular ducts occur submedially on the dorsal surface, and 4 pairs submarginally on the ventral surface [6 pairs on either surface], 4) the anus appears to be situated on the dorsal surface of the 7th abdominal segment [at the body end on the ventral surface], 5) the anus is provided with 2 pairs of robust conical setae [with no setae], and 6) the femora are provided with 1 seta on the ventral surface [with 2 setae]. Furthermore, no dermal pits occur on the dorsal surface, but this is also the case with *G. heckrothi*.

In the adult female, 7) small tubular ducts occur among 5-locular disc pores [no tubular ducts present], 8) the antennae are 2-segmented [3-segmented], 9) the spiracles are provided with an enlarged peritreme [with the peritreme not particularly enlarged], 10) the anus is enclosed within a rudimentary cellular ring, which usually bears a pair of spinous setae [enclosed by an incomplete simple ring], and 11) the legs are rudimentary and much deformed [complete in segmentation].

In the 1st instar male, 12) the dorsal surface of the cephalothorax is covered with pustular swellings [with no pustular swellings], 13) 5 pairs of submedian microtubular ducts occur on the dorsal surface, and 4 pairs of submarginals on the ventral surface [6 pairs on either surface in *G. heckrothi*; no ducts in *G. secundus* and *G. spinigalla*], and 14) the femora are provided with 1 seta on the ventral surface [with 2 setae].

In the adult male, 15) the genal area is enlarged, occupying a greater part of the head [not particularly enlarged], 16) the midcranial ridge is obsolete [represented by the ventral arm], 17) the postoccipital ridge is obsolete [well represented], 18) the scutellum is much reduced in size [well developed], 19) the mesosternum is ill developed, with the marginal ridge obsolete and with the furca nearly obsolete [well developed, with the marginal ridge and furca complete], 20) the head is produced apically to form a small triangle, with the

antennae arising on the sides of the triangle, 21) the antennae are 6-segmented [5-segmented], 22) the apical antennal segment is provided with 4 fleshy setae and 2 knobbed setae (in addition to other much shorter setae) [with 6 fleshy setae and 4 or 2 knobbed setae], and 23) the genital capsule is serrate on the lateral margins of its distal half. Furthermore, the tarsi are much longer than the tibiae. This character may also be of generic value, because in all the 3 examined species of *Gallacoccus* the tarsi are definitely shorter than the tibiae. Character 23) is not only useful in separating *Echingalla* from *Gallacoccus* but also quite unusual in the Coccoidea.

Echinogalla pustulata remarkably differs from the *Gallacoccus* species especially in the 1st instar larvae. The possibility will be discussed that some features and characters of the 1st instar reflect peculiar behavioral traits [3.2, 3.3]. In the 2nd instar male, on the other hand, *E. pustulata* is very similar to *G. secundus* and *G. heckrothi* (the 2nd instar males of *G. anthonyae* and *G. spinigalla* are unknown). This stage, intermediate in ontogeny and exclusively devoted to growth, may be the least affected morphologically in association with behaviour, and the resemblance in it may indicate some phylogenetic affinity. It should be mentioned here that *G. secundus* and *G. spinigalla* appear quite different in the 1st instar males [2.4.6] in contradiction with their close similarities in other stages. Again, their remarkably different morphological characters may be associated with different behaviours peculiar to the male crawlers [3.3].

Echinogalla appears more derivative than *Gallacoccus* in character 1), 2), 4), 6), 8), 11), 12), 14)–19), and 23), whereas it is obviously more primitive in character 5), 10), and 21). In the adult female the combination of character 19) (the retention of a setigerous cellular anal ring) and character 11) (the rudimentary legs) is especially noteworthy. It should be mentioned that the adult female of an unnamed coccoid from Sarawak [91ML-131], which apparently represents another genus of the *Gallacoccus-Echinogalla* group, has a multisetose anal ring and rudimentary legs [1.3, 3.1]. The common ancestor of all these coccoids, if any, should be a fairly primitive form with a completely setigerous anal ring and complete legs in the adult female.

2.7. *Echinogalla pustulata*, sp. nov.

2.7.1. Material examined. Galls were collected at Beserah Forest Reserve, Kuantan, Pahang, Malaya, on saplings of *Shorea falcifera* and *Shorea glauca* in 1990. These galls occur in leaf axils and do not differ in external appearance between the plant species. They are globular and provided with many robust conical spines, which are recurvate and separated from each other except for their bases (Fig. 4). Nine galls, various in size, were collected on *S. falcifera*, 10 July [90ML-182]; from one of these galls were mounted many 1st instar females, some 1st instar males, and some pupae, and from other 6 galls were mounted 6 adult females; no insects were found in the remaining 2 galls. Four galls were obtained from *S. glauca*, 24 July [90ML-307]; 2 adult females were mounted from two of these galls; the adult female of another gall was infested with fungi and was not mounted, and no insect was obtained from the remaining gall. Two galls were obtained from *S. glauca*, 14 Aug. [90ML-510]; from one of these galls, about 2cm in diameter (spines excluded), were mounted 1 adult female, a number of 1st instar females, about 10 1st instar males, a few pupae, and about 40 adult males; no insects were obtained from the other gall, which was very small, about 0.5cm in diameter (spines excluded), and apparently at an incipient stage of formation. Holotype (1st instar female) from 90ML-510.

2.7.2. First instar female (Fig. 19). The examined specimens, apparently at the crawling

stage, are nearly obovate, with the abdomen small and triangular in outline. Dorsal derm slightly sclerotized. Dorsal surface of head, thorax and basal 2 abdominal segments covered with low pustular swellings; dorsal surface of abd III–VII with transverse rows of spiculations. Ventral surface also with pustular swellings on marginal area of head and thorax, and with spiculations on posterior abdominal segments. Dorsal setae bluntly spinous, small except a pair on head and another pair on abd VIII (end of body), which are strong but not conical; similar strong setae occurring on ventral surface of body end in an apical and a subapical pair (in Fig. 19 the subapical pair is represented by 2 setae on one side, which state has been observed not rarely in the examined specimens). Microtubular ducts present, occurring as follows on each side: 5 submedians on dorsal surface, forming a longitudinal series, the posteriormost occurring on abd II; 4 along margin on ventral surface (in Fig. 19 one of them is hidden by the mid femur). Anus situated on dorsal surface, appearing to belong to abd VII, surrounded by a heavily sclerotized thick ring, which bears 2 pairs of conical setae. Spiracles each with a 7-locular disc pore. Antennae 3-segmented; basal segment broader than long, with 2 setae; 2nd segment reduced to a slender ring, with no seta; 3rd segment about twice as long as broad, with 7 setae on distal part, one of them being stiff, longer than the segment. Legs arising near body margin, well developed; tarsi longer than tibiae, about 1.5 times as long as the latter in hind legs; tarsal digitules a little shorter than the segment; claws slightly curved; unguis digitules surpassing claws.

2.7.3. Adult female (Fig. 22). Globular, much simplified in structure. Quinquelocular disc pores abundant, strewn broadly along body margin on both dorsal and ventral surfaces, not occurring anteriorly to anus. Small tubular ducts strewn among 5-locular disc pores on abdomen. Setae spinous, mostly occurring on dorsal surface within the band of 5-locular disc pores, especially numerous between anus and vulva. Antenna 2-segmented; basal segment represented by an incomplete ring or a crescent sclerite, with 2 setae; 2nd segment stump-like, with about 7 setae. Spiracles with an enlarged peritreme. Anus in an elliptical sclerotized area, situated in posterior half of the area; a rudimentary cellular ring enclosing the area, usually with a pair of spinous setae arising near its anterior end. Legs rudimentary; hind legs longest, yet incomplete, with or without claw.

2.7.4. First instar male (Fig. 26). The examined specimens, probably newly hatched, are nearly elliptical. Dorsal surface of head and thorax covered with rudimentary pustular swellings. Abdominal segments with transverse rows of spicules on both surfaces. Body setae hairy except some sharply pointed spinous ones occurring on posterior end of body. Microtubular ducts occurring on each side as follows: 5 submedians on dorsal surface, forming a longitudinal series, the posteriormost occurring on abd II; 4 along margin on ventral surface. Antennae 3-segmented; basal segment well developed, with 2 setae (in Fig. 26 one of these setae is not shown, being situated on the dorsal side); 2nd segment much smaller, with no seta; 3rd segment about twice as long as broad, with 7 setae on its distal part, one of them stiff, about as long as the segment. Spiracles each with a 5-locular disc pore. Anus near posterior end of body on ventral surface. Legs well developed; femora with 1 seta on ventral surface; tarsi longer than tibiae, about 1.5 times as long as the latter in hind legs; tarsal digitules much shorter than the segment; claws elongate, as long as tibiae, nearly straight, and sharp, with a slight denticle near apex on plantar surface; unguis digitules much shorter than claws.

2.7.5. Second instar male (Fig. 29). Elliptical when fully grown. Derm with transverse rows of spicules on meso- and metathorax and abdominal segments. Quinquelocular disc pores present; a few submedians on dorsal surface of head; 6 submedians on each side of

ventral surface, forming a longitudinal series through abd I–VI; others occurring along body margin on both surfaces. Tubular ducts occurring on both surfaces. Anus near posterior end of body on dorsal surface. Antennae obscurely 2-segmented; basal segment broad, with 2 setae and 1 tubercular process (sensillum?); 2nd segment stump-like, with as many as 9 setae various in length. Legs apparently diminished in size when compared with those of the 1st instar male; tarsi about twice as long as tibiae in hind legs; tarsal digitules very short; claws a little curved, with a denticle near apex on plantar surface; unguis digitules not surpassing claws.

2.7.6. Adult male (Fig. 33). Slender and gracile; head with genal area enlarged, occupying a greater part of head, and about 0.6–0.7 times as broad as prothorax; abdomen (excluding genital capsule) subequal to thorax in length. Eyes small, occurring in distal half of head. Head, thorax, and abdomen with tubercular papillae; fore and mid tibiae each also with several papillae. No disc pores (except for glandular pouches on abd VIII [2.1.8]). Transverse rows of spicules on abdominal segments. Antennae set close, arising on sides of produced apex of head, 6-segmented, as long as fore tibia and tarsus combined; basal segment about as long as broad, with 1 or 2 short setae; 2nd segment rather globular, with 1–3 short setae; 3rd segment constricted basally, about 1.5 times as long as broad, with 2 short setae; 4th and 5th segments as long as broad, each with 3 or 4 long setae; 6th segment about 1.5 times as long as broad, with 4 short fleshy setae and 2 long, stiff, apically knobbed setae arising subapically. Midcranial and postoccipital ridges obsolete. Preocular and postocular ridges united, running longitudinally through head; another longitudinal ridge dorsally along margin of gena. Pronotal ridge well represented; post-tergite obsolete. Scutum much shorter than prescutum; scutellum represented by a small sclerite with a membranous spot medially. Postnotal apophysis represented by a short pointed process. Mesosternum with marginal ridge obsolete, and with furca reduced to a small triangular sclerite. Halteres absent. Legs slender; trochanters with basal portion much shorter than distal one; femora not particularly thickened; tarsi longer than tibiae, about 1.3 times as long as the latter in hind legs; fore and mid tarsi each with several papillae; tarsal digitules short; claws gently curved, with a minute denticle near apex on plantar surface; unguis digitules surpassing claws. Genital capsule with distal part elongate and serrate on lateral margins.

2.7.7. Remarks. The echinate gall induced by *Echinogalla pustulata* is very similar to that of *Gallacoccus spinigalla*, whereas these species are not particularly related to each other. The significance of the occurrence of such echinate galls will be discussed in a later section [3.4].

3. FACTS, SPECULATIONS, AND PERSPECTIVES

3.1. Diptercarp-associated gall-inhabiting coccoids (DGC's)

As stated [1.3.4], in addition to the 4 species described above, another form has been available for my study. It is represented by only 1 mounted adult female collected on the diptercarp *Hopea sangal* in Bako National Park, Sarawak (Borneo) [91ML-131]. The gall induced by this female had no spines or other external processes, transversely oblong, 1.5cm long, 2cm wide, and 1.3cm thick, with a series of short and shallow transverse furrows on the ridge. The adult female is similar to that of *Echinogalla pustulata* in the peritremes of spiracles enlarged, in having tubular ducts in addition to 5-locular disc pores, and in having rudimentary legs, but remarkably differs from the latter in the anal ring having about 14 well-developed spinous setae. I am inclined to believe that this form

represents another genus of the *Gallacoccus-Echinogalla* group. Dr P. J. Gullan (in litt.: 6 August, 2001) collected an echinate terminal bud gall, about 3.5cm across, on a dipterocarp sapling in Brunei (Batu Apoi Forest Reserve, Kuala Belalong Field Studies Centre, Temburong), and found an adult female coccoid within. The spines are numerous and elongate, those occurring on the basal half of the gall pointing downwards and those on the apical half tending to curve upwards, creating an apical congestion of spines (Figs. 5, 6). The coccoid, examined by her, is similar to *E. pustulata*, but differs from the latter in the anal ring having 6 setae and in a few other features. These unnamed species encourage the expectation of finding further diverse forms of DGC's.

Anthony (1980) examined herbarium collections deposited at Singapore, Paris, Kew, Leiden, and Kepong (Malaysia) in search of galls similar to those of *Gallacoccus anthonyae* (galls of the *G. anthonyae* type or 'TGa') and *G. secundus* (galls of 'TGs') occurring on *Shorea curtisii*. She discovered such galls on specimens belonging to 24 species of *Shorea* (including *S. curtisii*) from Malaya, Singapore, Sumatra, Borneo, Mindanao, and Luzon. Some of these *Shorea* species bore galls of both types, and *S. leprosula* had in addition galls of an echinate type ('TGs2'). These *Shorea* species mostly belong to the red melanti group (which, according to Jenkins, 1992, is not a taxonomic group). Although the causal organisms are unknown or not exactly known, Anthony assumes that these galls were induced by coccoids of *Gallacoccus*. Then, how many species of coccoids can induce these galls? There is no doubt that different species of causal organisms are responsible for galls of TGa, TGs, and TGs2 occurring on a *Shorea* species, and this was actually the case with *S. leprosula*. Not all the galls of the same types were the same in details of morphological characters, in their sites on the host plants, and in the positions of the inhabiting adult females. The present study shows that, while closely related coccoids do not necessarily induce similar galls (as exemplified by *Gallacoccus secundus* and *G. spinigalla*), coccoids of different species or even of different genera may induce galls of the same types (as illustrated by *G. spinigalla* and *Echinogalla pustulata*). All this considered, there seems to be no good reason to suppose that only a limited number of coccoid species induced the galls of TGa, TGs and TGs2 recorded by Anthony.

In connection with his studies on the echinate gall induced by *Mangalorea hopeae* on *Hopea ponga*, Jenkins (1992) surveyed herbarium collections deposited at London, Leiden, Singapore, and Bogor, and in India, and also literature and some field localities, in an attempt to expand the record of galls across the family Dipterocarpaceae. 'The expansion ...proved to be surprisingly fruitful, both in terms of the number of species and their taxonomic and geographical distributions'. He enumerated 68 species of gall-bearing dipterocarps (excluding *Hopea ponga*)—30 *Shorea*, 16 *Vatica*, 12 *Dipterocarpus*, 7 *Hopea*, and 3 *Monotes* species—from Sri Lanka, southwestern India, Myanmar, Thailand, Vietnam, Malaya, Sumatra, Java, Borneo, Mindanao, Luzon, New Guinea, and tropical Africa. The galls were variable in external appearance, and some of the dipterocarp species bore galls of different types. The greater part of the galls discovered by Jenkins are equipped with eminent appendages, which are spinous or folious and variable in number, shape and size. Galls of Anthony's TGs2 are included (but no galls of TGa and TGs). Galls with wiry rather than spinous appendages are formed on *Hopea novoguineensis* from New Guinea. Hirsute galls, covered with very fine appendages, occur on most of the *Vatica* species recorded, whereas galls with folious or bract-like appendages on the others. The diversity of the gall-bearing dipterocarps and the variety of the galls indicate that the causal organisms of all these galls belong to many different species.

The dipterocarps on which Jenkins discovered the galls come from across the range of the subfamily Dipteroocarpoideae including New Guinea east of Wallace's Line. It is also significant that the genus *Monotes* is included in the gall-bearing dipterocarps. This genus belongs to the subfamily Monotoideae, which is a relatively primitive offshoot remaining in Africa and Madagascar. Assuming that the galls from Africa were 'induced by a coccid similar to those from Asia', Jenkins and Mabblerley (1994) argue: 'The occurrence of the spinose gall within the widely separated subfamilies Monotoideae and Dipteroocarpoideae suggests that the parasitism existed before the division of Gondwanaland'. On the basis of this argument they assert that 'the association between the *Beesonia-Gallacoccus* complex and modern dipterocarps has endured since the early Cretaceous period, approximately 140 million years ago'. They find support for their assertion in the occurrence of a hirsute gall on *Sarcolaena*, 'whose family Sarcolaenaceae, endemic to Madagascar, is considered to be derived from the same dipteroocarpaceous stock'. Their insight, thus, has opened a grand perspective on the study of dipterocarp galls and the causal organisms.

Of the 68 species of gall-bearing dipterocarps recorded by Jenkins (1992), only 7 species of *Shorea* are found in the 24 species of the genus recorded by Anthony (1980). *Shorea oblongifolia* occurring in Sri Lanka, not recorded by them but mentioned by Raman and Takagi (1992), bears a gall similar to that of *Beesonia dipterocarpi*. Eighty-six species of dipterocarps in total, therefore, have been recorded by these authors, bearing galls induced by unknown or unstudied organisms. They still form a small part of the family, which comprises nearly 600 species.

The facies of these galls allow us to think that the causal organisms belong to *Gallacoccus*, *Echinogalla*, *Beesonia*, *Mangalorea*, or other coccoid genera. Anthony (1980) collected galls of 2 different types, 'TGa1' and 'TGa2', on *Shorea macroptera* in Singapore, and the causal organisms were examined and referred to undescribed species of *Gallacoccus* by Dr Beardsley. She discovered galls exactly of these types on herbarium specimens of *S. macroptera* (including subsp. *sandakanensis*) collected in Malaya, Singapore, and Borneo. Jenkins (1992) collected galls with obtuse-angulate spines on *Dipterocarpus indicus* in southern India, and attributed them to a *Beesonia* species on the basis of Dr Beardsley's examination of 'several insect stages' isolated from them. He found galls similar to them on herbarium sheets of *Dipterocarpus palembanicus* and *Shorea ovalis* collected in Borneo. As stated in the beginning of this section, Dr Gullan collected in Brunei an eminently echinate dipterocarp gall (Figs. 5, 6), of which the causal organism is definitely a coccoid and similar to *Echinogalla pustulata*. Jenkins (1992) recorded galls apparently of this type from *Shorea fallax* and *S. havilandii* collected in Borneo. Although similar galls do not necessarily mean similar causal organisms, these examples strongly support the view that the unexamined causal organisms are also coccoids. Putting all the available pieces of information together, we can reasonably conclude that there must be a great number of unknown forms of DGC's. The dipterocarp forest of Asia may be comparable to the eucalyptus forest of Australia or exceed the latter in the diversity of gall-inhabiting coccoids.

The known genera of DGC's have been referred by authors to the families Eriococcidae (*Gallacoccus*) and Beesoniidae (*Beesonia*; *Mangalorea*). In the course of the present study I have been deeply impressed by extraordinary features commonly possessed by the *Gallacoccus-Echinogalla* group and *Mangalorea*: the aliform appendages of the mouthparts in the adult female [2.1.6] and the papillae in the adult male [2.1.7]. The common occurrence of these features in the different groups may be due to convergence associated with gall-inhabitation [for the supposed role of the papillae, see 3.2]. I do not think, however,

that such features are universal in other gall-inhabiting coccoids, and, therefore, I do not exclude the possibility that the common occurrence of these features indicates a close phylogenetic relationship. In fact, Hoy (1963) examined *Beesonia dipterocarpi* and included it tentatively within the family Eriococcidae, because it exhibited 'typical eriococcid features' in 'second-stage nymphs'. Recently Foldi (1995) has presented a different view based on a cladistic analysis of adult female and larval characters. According to him, the South American *Limacoccus* should be united with *Beesonia* and *Mangalorea* in the same family, the Beesoniidae, which should be placed near the Phoenicococcidae, Halimococcidae, and Diaspididae.

In this paper I take no position on the phylogenetic problem for clarifying the relationship between the *Gallacoccus-Echinogalla* group and the *Beesonia-Mangalorea* group. They may tentatively be referred to the family Eriococcidae and the Beesoniidae, respectively, though 'the limits and classification of the Eriococcidae are far from being settled' (Miller and Gimpel, 2000). Koteja (2000) in his review of recent studies on fossil coccoids states: 'the Eriococcidae must have radiated through all Cretaceous and Early Tertiary giving origin to a series of small, specialized groups'. In fact, some derived forms of the family have been found in late Cretaceous amber (Koteja, 2001). Jenkins and Mabblerley (1994) assumed an early Cretaceous origin for the association between dipterocarps and gall-inducing coccoids. In addition to the supposed old origin, the adult females of the known DGC's are highly modified and simplified, suggesting that parallelism and convergence prevail in their characters. The 1st instar larvae of the *Gallacoccus* species exhibit remarkable sexual dimorphism, and must have undergone considerable modifications at least in the females; those of *Echinogalla pustulata* are also peculiarly characterized [3.3]. The known adult males show some characters strikingly different between the *Gallacoccus-Echinogalla* group and the *Beesonia-Mangalorea* group, and this may support the view that these groups belong to the quite different families. No phylogenetic evaluation of adult male characters, however, is attempted in this paper mainly owing to my limited knowledge on this stage across the superfamily. Above all, the known forms of DGC's are very few against the richness of unknown forms indicated by the herbarium galls, which are far from uniform. I expect that diverse forms of DGC's will be found, and that some of them with less modified characters will afford substantial clues to the phylogenetic relationship, which should be involved in critical studies on the Eriococcidae and the Beesoniidae. My expectation of finding less modified forms of DGC's may not be unreasonable. In their overview on gall-inhabiting mealybugs Williams and Miller (1999) state: 'We were surprised to find that several true gall-forming species seem to have no unusual morphological modifications'. Their finding is harmonious with the view that evolution of organisms involves the phase of steady state at various stages resulting in stable hierarchical taxa and giving rise to 'living fossils' [for further comments, see 3.4].

At least 2 oak-associated species in addition to the dipterocarp-associated species are recognized in *Beesonia*, and the dipterocarp-oak combination in host association is not unique to this genus [1.2.1]. Gall-inducing coccoids associated with fagaceous plants in Asia, therefore, should not be excluded from the scope in the study of DGC's. Among the known forms, especially noteworthy are *Fulbrightia* Ferris, 1950 (with *F. gallicola* Ferris, 1950, occurring on *Quercus delavayi* in Yunnan, China) and *Reynvaania* Reyne, 1954 (with *R. gallicola* Reyne, 1954, inducing galls on *Quercus lineata* in Java and Sumatra, and *R. spinata* Hu and Li, 1993 [originally '*Reynvaania spinatus*'], feeding on *Cyclobalanopsis myrsinaefolia* in Jiangxi, China). These coccoids have been referred to the family Kermesidae

(s. str.) by recent authors, but rather provisionally (Miller and Gimpel, 2000). It should be noted that fagaceous plants are abundant in Southeast Asia and especially in montane forests.

3.2. Synchronism between the female crawlers and the adult males

First instar larvae of both sexes and adult males were found together in the examined material of all the 4 species, and in the same galls in certain cases. Anthony (1980) also observed the concurrence of 1st instar females and adult males within the same galls of *Gallacoccus anthonyae* and *G. secundus*. The synchronic emergence of the female crawlers and the adult males in the maternal galls seems to have a special significance when it is combined with the morphological peculiarities of these instars.

The male completes its metamorphosis within the maternal gall (Anthony, 1980, and my observations on the material), and the male crawlers need not disperse out of the gall. In many families of the Coccoidea the 1st instar larvae are generally provided with a pair of long hairy caudal setae, which are supposed to contribute to their dispersal by air currents (Takagi, 2000, Part IV). It is quite natural, therefore, that the 1st instar males of the *Gallacoccus* and *Echinogalla* species have no long caudal setae [2.1.5]. This fact gives support to the view that the absence of long caudal setae indicates, at least generally, the absence of dispersal by air currents (for an exception, see below).

The female crawlers, however, have to disperse out of the maternal gall and to settle on new sites for inducing new galls, yet they also lack long caudal setae. There are at least 2 manners of dispersal, except for pedestrian movement, for crawlers lacking long caudal setae or other particularly developed setae: aerial 'sailing' by the use of wax filaments and phoresy on other animals. Crawlers of *Dactylopius* (Dactylopiidae) have neither caudal setae nor other elongate setae. They disperse by air currents with the aid of long wax filaments, which grow straight up and are used as sails (Moran et al., 1982; Pérez Guerra and Kosztarab, 1992). Cases of phoresy on ants, birds, or other animals have been recorded, but some of them may be incidental especially when the crawlers are provided with well-developed caudal setae. In the gall-inhabiting *Cystococcus* (Eriococcidae), female crawlers make their appearance synchronically with the emergence of adult males in the maternal gall. They are transported by their winged adult brothers, clinging to the abdomens of the latter, from the maternal gall to new sites to induce galls (Gullan and Cockburn, 1986). In accordance with this behaviour, they have only short and weak caudal setae (Raman and Takagi, 1992, p. 30, footnote). The *Cystococcus* adult males have an extremely attenuate and elongate abdomen to facilitate impregnation of a gall-living female positioned at a distance from the gall orifice (Gullan, 1983). This character also enables an adult male to carry as many as 13 female crawlers (Gullan and Cockburn, 1986).

No further case of intersexual phoresy has been known in the Coccoidea, and this manner of phoresy may be thought of as a very rare phenomenon. However, I (in Raman and Takagi, 1992) once suggested the possibility that it occurs in *Mangalorea hopeae*. This species lacks long caudal setae in the 1st instar larvae of both sexes. The adult male has a long abdomen, which is, however, not unusually elongate as in the *Cystococcus* adult males. It is beset with a number of papillae on the body instead. This is also a quite unusual character, which could not have evolved without any peculiar role. I obtained crawlers and adult males, along with specimens of other instars, from the same material. All these facts, when combined, imply that female crawlers are transported by adult males. It is easily imaginable that papillae will help female crawlers cling to adult males and keep them from dropping off. So far as the body size is concerned, an adult male can carry more than

several crawlers on the abdomen and other parts of the body.

Mangalorea hopeae induces spherical galls covered with dense spines. The male insects grow in gaps among the lanceolate spines, which, when fully developed, are tightly appressed together at their thickest parts to enclose the male insects within the galls. When the winged adult males emerge from their pupae, the enlargement of the gall core causes the spines to separate along their whole length. Jenkins and Mabberley (1994) state: 'This allows the males to depart, which they do at night, and *mate with the first instar females that live exclusively on the surface of the host*' (my italics). Actually, however, Jenkins (1992) did not observe mating (needless to say, mating takes place only between the adult male and the adult female). He placed a gall 'in a sealed glass chamber, placed near an open window, and observed for the emergence of the males'. Several dozen adult males emerged at 10.00pm, and 'were readily drawn to a torchlight, placed at one end of the container. By the following morning, all the insects were dead'. The adult males were apparently disturbed by the torchlight, and he failed to observe their normal behaviour. It seems that in his field observations female crawlers appeared outside the maternal gall in advance of the emergence of adult males and remained on the surface of the host plant. He did not discover any airborne individuals. The female crawlers, thus, may have been waiting for the emergence of adult males, but definitely not for a chance for mating.

The species of *Gallacoccus* and *Echinogalla* examined in this study agree with *Mangalorea hopeae* in lacking long caudal setae in the 1st instar larvae, in having papillae in the adult males, which are macropterous, and in the synchronic emergence of the female crawlers and the adult males from the same maternal galls. These conditions are sufficient for the supposition that intersexual phoresy takes place also in these species. This supposition is harmonious with the fact that in the female crawlers of the 3 species except *G. secundus* the legs arise on the side of the body, which state is apparently useful for hugging the abdomen or other body parts of the adult male. The 1st instar female of *G. heckrothi* has deeply excavated femora and hook-shaped claws, and these characters may also have developed in association with this supposed action.

The synchronic occurrence of the female crawlers and the adult males requires sexual dichromism in producing offspring leading to the emergence of the males well before their sisters. However, 1st instar males, and usually also intermediate-instar males, were found together with adult males and 1st instar females in the same galls. The only insect found within the dry full-grown gall examined of *G. heckrothi* [2.5.1] was a half-destroyed body of the 1st instar male, apparently one of the last individuals produced by the mother insect, of which the body was not found (consumed by a predator or a scavenger?). One of the galls examined of *Echinogalla pustulata* was crowded with larvae, especially 1st instar females, and adult males, and yet the body of their mother was full of eggs [2.7.1]. It seems that the male offspring are produced not only before the emergence of the female offspring but also continuously thereafter. It is not knowable, however, from the present material whether the female offspring are produced only once or more during the reproductive period of an adult female. In the latter case, the continuous production of male offspring will secure the encounter of female crawlers with their adult brothers. But there seems to be another reason for the continuous presence of the 1st instar males within the gall as will be discussed in the following section.

3.3. Sexual dimorphism in the 1st instar larvae

In Coccoidea in general the 1st instar male and female are very similar and hardly

distinguishable especially at their crawling stage. In the family Eriococcidae, some species of *Apiomorpha* exhibit larval dimorphism, which is due mainly to the reduction in male crawlers of features associated with dispersal (Cook et al., 2000).

Sexual dimorphism is unusually remarkable in the 1st instar larvae of the 3 species of *Gallacoccus* examined in this study. In these species and *G. anthonyae* the 1st instar females are equipped with strong conical setae and strange dermal processes over the dorsum, and also with peculiar dorsal pits except in *G. heckrothi*. The latter two of these features are quite unusual and apparently specialized. All these features are restricted to the females and must be relevant to some behavioral trait peculiar to them. I am inclined to believe that these features have developed in association with the supposed phoretic dispersal [3.2], but I will keep from going farther with this possibility, which is a speculation built on another speculation.

The 1st instar males of the 3 examined species of *Gallacoccus* are much simpler than the females of the same instar in the dorsal makeup, having no specialized features. Because dispersal is the main role in the 1st instar larvae, the remarkable sexual dimorphism suggests that they are different in behaviour at their crawling stage, and are harmonious with the supposition that only the female crawlers are transported by the adult males [3.2]. Lacking the specialized features of the females, the males may represent a generalized character pattern for the 1st instar larva in the *Gallacoccus-Echinogalla* group. However, they are generalized not in all features. In *G. secundus* the legs are unusually thickened and the fore femora are especially robust, and in *G. spinigalla* and *G. heckrothi* the claws are unusually elongated to form slender, sharp processes in all the legs.

Sexual dimorphism is less pronounced in the 1st instar of *Echinogalla pustulata*. There is no trace of the specialized features of the *Gallacoccus* females in the 1st instar female of *E. pustulata*, which is covered with low pustular swellings instead. Compared with the state in *Gallacoccus*, the dorsal setae are modified in shape (being bluntly spinous), much reduced in size (except a pair on the frons and some around the posterior end of the body), and decreased in number (being lost in the intermediate area). Pustular swellings are also present in the 1st instar male of *E. pustulata*, though they are rudimentary and occur less extensively than in the female. Thus the 1st instar female and male of this species are not much different from each other, and yet deviate from the supposed generalized type of the instar. This may reflect some behavioral trait peculiar to *E. pustulata* and common to both sexes. This species, however, agrees with *G. spinigalla* and *G. heckrothi* in having unusually elongate claws in the 1st instar male.

In Fig. 34 is shown sexual dimorphism in the 1st instar larvae exhibited in some linear dimensions of legs. Even in these simple features, the patterns of dimorphism are not uniform among the species, suggesting somewhat different behavioral traits. The 1st instar male of *Gallacoccus secundus* is quite peculiar in having enlarged and robust legs. The 4 species, however, agree in the claws obviously longer in the males than in the females. It appears that in *G. secundus* the large size of the male claws is due, at least partly, to the enlargement of the whole legs, but in the other species the elongate claws in the males are not associated with enlarged (or much enlarged) legs. In *G. heckrothi* and *Echinogalla pustulata* the claws are not only elongate but also nearly straight.

It should be emphasized again that the males complete their metamorphosis within the maternal galls. What is, then, the use of the unusually thickened legs and unusually elongated claws of the 1st instar males? Apparently they are not especially useful to the larvae for walking around or clinging to the wall of the gall. Drawing an analogy between

the robust legs and wrestlers' limbs and also between the elongate claws and awls or sharp spear heads may be too hasty for the problem. Nothing other than one idea, however, comes across my mind—these 'strangling' legs and 'piercing' claws should be used for defence against invading natural enemies. This idea is not wholly groundless. Defensive behaviour and defensive morphs, fertile or sterile, are now known in about 30 species of aphidoids belonging to gall-inducing groups in the families Hormaphididae and Pemphigidae. Foster and Northcott (1994) summarized information about the behaviour of these aphidoids. Gall-inhabitation is neither a necessary nor a sufficient condition for the evolution of defence. But the gall is important in providing a resource that can be readily defended and in providing a ring-fence around the inhabitants, increasing the likelihood that they are related to their close neighbours, and those galls that are relatively long-lived might encourage the emergence of defensive behaviour and defensive morphs. I wonder why their generalization should be restricted to aphidoids. Recently, defensive morphs have been found in other animals including gall-inhabiting species of Thysanoptera (Crespi, 1992).

A few natural enemies of DGC's were recorded, but not identified. The gall induced by *Mangalorea hopeae* is covered with dense strong spines, which harbour growing male coccoids in their closed spaces and thus are probably useful for protecting the males (and also the inhabitants *within* the gall) from parasites and predators [3.2]. Jenkins and Maberley (1994) discussed another effect of the spines: 'The effectiveness of the spines is such that as soon as they fully part, other insects are able to gain access to the nutrient rich core, which is rapidly consumed'. The galls induced by the known *Gallacoccus* and *Echinogalla* species, echinate and non-echinate, are not guarded by such dense spines, and are apparently easily accessible to gall consumers and less protective against parasites and predators. In preparing specimens for the present study I was shocked to find empty small-sized galls, because I had expected to get from immature galls compact specimens of young adult females suitable for mounting. Predacious natural enemies may be responsible for the absence of gall inhabitants. Anthony (1974a) referred to 'parasitic wasps' found in galls of *G. secundus*: 'The galls attacked by parasitic wasps ... never reach their maximum size. ... [in the attacked galls] coccids are present but in very small numbers'.

The development of the gall continues 5 or 6 months in *Gallacoccus secundus* and more than 7 months in *G. anthonyae* (Anthony, 1980). The material at hand is not sufficient to show how long the galls of *Gallacoccus* and *Echinogalla* persist after the start of offspring production. There is, however, some evidence to support the view that an adult female produces offspring for a long duration and, in particular, male offspring continuously [3.2]. Thus the galls may meet the condition presumed by Foster and Northcott (1994) to be necessary for the emergence of defensive behaviour—persistence for a relatively long time. Above all, if the continuous production of male offspring is real, it must have a special significance. In the preceding section the possibility is suggested that it will secure the encounter of female crawlers with their adult brothers. But when it is combined with the morphological peculiarities of the 1st instar males, what it secures must be the defence of the galls and gall inhabitants by the armed male larvae against invading enemies (parasites, predators, and gall consumers). This is not incompatible with the former possibility. In each species only a single form of the 1st instar male is known. There may be no sterile defensive morph, and all male larvae may grow into adult males unless they are lost by accidents (including the invasion of natural enemies, which should cause the defensive reactions of 1st instar males). The full-grown males, now winged, may fill another familial

role—transportation of their immature sisters [3.2].

3.4. Atavism and evolution

Anthony (1977, 1980) compared the galls induced by *Gallacoccus anthonyae* and *G. secundus* with the normal vegetative buds of *Shorea curtisii*, and found corresponding parts between them. The gall of *G. anthonyae* is very similar to the young normal inflorescence of *S. curtisii* and comparable to a sterile inflorescence. The mature gall of *G. secundus* resembles apterous fruits (with short sepals), which are found in many dipterocarps.

Jenkins and Mabberley (1994) relate how the echinate gall induced by *Mangalorea hopeae* on *Hopea ponga* was mistaken for a fruit, especially one of a species of the breadfruit genus *Artocarpus* (Moraceae). The dense spines covering the gall, which are useful for the protection of the gall and probably also of the coccoid, are unknown in the normal ontogeny of dipterocarps. Jenkins and Mabberley searched for the origin of this feature. They state: 'It may be hypothesized that most, if not all of the Gondwanic malvalean/dipterocarpaceous ancestors bore large, capsular fruits with an impressive armour of spines, from which have evolved those with indehiscent, non-spiny pericarps, containing exarillate seeds. Only a few modern taxa in this group display these ancestral characters, but it appears that, in the Dipterocarpaceae at least, the genetic potential to express the spine remains—realized by a cecidogenous parasite'.

What *Mangalorea hopeae* unlocks is, according to Jenkins and Mabberley, an ancestral phenotype of the pericarp. However, the spines of the gall are marvellously fitted to the life history of the parasitic coccoid. They are so shaped and developed as to provide a protected space, in which male insects can complete their metamorphosis [3.2]. Their development and ultimate shape and size may, therefore, be manipulated by the parasitic coccoid unless the coccoid has adapted itself to the original state of plant phenotype. *Gallacoccus spinigalla* and *Echinogalla pustulata* also induce echinate galls, which, however, differ from the gall induced by *M. hopeae* in the spines being not lanceolate but conical, thus not appressed together when fully developed (Fig. 4). Their galls are more closely similar to some breadfruits (fruits of *Artocarpus* spp.) and durians (fruits of *Durio* spp., Bombacaceae) in external appearance except for size. Galls of this type were recorded by Anthony (1980) on *Shorea leprosula* and by Jenkins (1992) on that species and some other species of *Shorea* [1.2.4, 3.1]. In contrast, the galls of *G. anthonyae* and *G. secundus* are induced by utilizing the developmental pathways that, when working in the normal ontogeny, lead to the current phenotypes of the inflorescence and fruit.

It is not knowable at present whether any atavistic change in the chemical composition of the parasite's saliva takes part in the formation of the echinate galls found in the *Gallacoccus-Echinogalla* group, which induces galls of non-echinate types, too. However, morphological patterns that can be interpreted as atavistic are known in the Diaspididae, another family of the Coccoidea. There are 2 principal types of the 2nd instar larvae in the Diaspididae, the homomorphic and the heteromorphic type. Both types occur in the tribes Diaspidini (subfamily Diaspidinae) and Odonaspidini (Aspidiotinae) and also in certain odd genera, whereas only the homomorphic type is known in the other tribes. The larvae of the homomorphic type are similar to the adult females of the same species, whereas those of the heteromorphic type greatly differ in principal characters from the adult females (except in pupillarial forms, of which the adult females are generally modified and often much simplified). Homomorphism involves the females, and occasionally also the males, of the 2nd instar, and the known heteromorphic larvae are mostly males. Homo- and

heteromorphic 2nd instar males sometimes occur in species that are supposed to be closely related because of their closely similar adult females. It follows that the 2 types are easily interchangeable in the course of speciation. We have taxonomic evidence in favour of the supposition that the character patterns of the heteromorphic larvae have their origins in remote ancestors of the tribes or genera concerned. The heteromorphic 2nd instar males of many Diaspidini are more or less similar to *Ulucooccus*, a very primitive form of the family. The 2nd instar males of some Odonaspidini I have examined exhibit the character pattern of the other tribe Parlatoriini, which does not appear to be closely related to the Odonaspidini so far as based on adult female characters. Rutherford (1915, p. 113, not 114) described '*Parlatoria zeylanica*', which had been collected together with '*Chionaspis simplex*, Gr., and *Aspidiotus secretus*, Gr.' on the same plant (a small bamboo). In my view, the 'Adult insect' (adult female) described as such by him is, in reality, the 2nd instar male of *Odonaspis secreta* (= *Aspidiotus secretus*) or *O. greeni* (which was treated as a variety of *A. secretus* by authors in his time). All unawares, by confusing the developmental stages, he strongly implied the presence of an ancestor-descendant relationship between the Parlatoriini and the Odonaspidini. Apparently, in the Odonaspidini as well as in the Diaspidini, the developmental pathways of the ancestral character patterns have not been lost. They are currently at work in forming the character patterns of the heteromorphic 2nd instar larvae. Occasionally they are suppressed, causing a switchover from the heteromorphic to the homomorphic phenotype. The reverse change is also possible, and it is atavistic. I hold the view that the interchange between the 2nd instar larval types takes place as an effect of genetic change caused by the evolving adult female, having no adaptive significance by itself. Actually, however, the distinction between the homo- and heteromorphic phenotypes is not always clear. The 2nd instar males of Diaspidini show a broad range of variation especially in the development of marginal appendages of the pygidium. They vary from one extreme, in which they approach the state of the supposed remote ancestral form (represented by the extant *Ulucooccus*), to the other, in which they are rather similar to the relatively advanced patterns of the adult females. The ancestral developmental pathways may work independently or along with the homomorphic pathways, thus producing a broad spectrum of phenotypes (for an introduction to this phenomenon, see Takagi, 1990 and 1998).

Atavism may also be involved in adult female characters. 'Rugaspidotine-patterned' forms of the adult female, arising independently in a wide range of diaspidids, suggest that phenotypic reversals of considerable magnitude are not unusual in the evolution within the family (Takagi et al., 1997). Atavism may occur in ecophenotypes, too. In some diaspidid genera the adult females are remarkably different between the conspecific bark- and leaf-associated forms, thus having caused considerable taxonomic confusion, and the character patterns characteristic of the leaf-associated forms are interpreted to be atavistic (Takagi, 1990). There is no reason to believe that atavism does not take place in the other families of the Coccoidea and in physiological features such as the chemical composition of the saliva.

Hall (1984) examined experimental atavisms from the viewpoint of developmental biology. He strictly defined the concept of atavism in accordance with the objects of his surveys, yet his generalizations have a broad biological significance: 'Such atavisms are *not* based on heritable genetic changes. They indicate the developmental plasticity that exists within embryos and the relative ease with which development can be switched from one programme to another'; 'They are the outward and visible sign of a hidden potential for morphology change possessed by all organisms. Neither basic capacity to form the

organ nor patterning information is lost’.

The occurrence of atavism in nature may have been much underestimated as pointed out by Hall. Atavism may be involved in the evolution of many organisms and in various aspects—including phenomena difficult to explain. The presence of sterile morphs in social insects has been a special difficulty to the theory of natural selection. Thorne (1997) reviewed studies on the social evolution of Isoptera. Being diploid in both sexes, the Isoptera have no concern with the asymmetric genetic relatedness of nestmates that has been emphasized in the study of social evolution in haplodiploid Hymenoptera. Her discussions have convinced me that eusociality should eventually be understood in terms of developmental pathways and their responses to a variety of life-historical elements and selective pressures generated thereby. In this view, eusociality does not essentially differ from other biological phenomena in which development plays a crucial role. I wonder, then, why the mechanism responsible for atavism should not be invoked here. Once social behaviour has started to develop, the emergence and evolution of sterile social morphs will be possible by this mechanism. The potential of the developmental pathways that lead to the morphological and behavioral phenotypes of the sterile morphs can be inherited by this mechanism through the generations of fertile individuals, and any changes in the pathways that modify the phenotypic traits of the sterile morphs will undergo group selection. If the supposed defensive behaviour of the 1st instar males of the *Gallacoccus* and *Echinogalla* species is real, we may expect to discover sterile defensive morphs in gall-inhabiting coccoids and should be cautious about the potential problem of misinterpreting them.

Atavism is ‘an embarrassment to the evolutionary biologists’ (Hall, 1984) who base their thought on changes in DNA compositions combined with natural selection. Raff (1996) emphasizes that ‘apparent evolutionary reversals in developmental mode must be evaluated critically’, because they may result from different causes. Yet he admits ‘evolutionary reactivation of morphogenetic processes’, and accepts the occurrence of ‘reversals over relatively short evolutionary distances’, 0.5–6 million years, ‘but not in time frames over 10 million years *unless the gene in question is maintained by active selection*’ (my italics). ‘Nevertheless, genes no longer expressed in one pathway may be used in another, so that there is in fact a mechanism that could permit much longer periods of atavistic recovery’ (Brock, 2000). Actually, Jenkins and Maberley (1994) require a time frame of 140 million years for the cryptic maintenance of the ancestral pericarpial phenotype [3.1].

‘Living fossils’ are also great difficulties to the conventional theory of evolution. Generally they have been regarded as phenomena of low evolutionary rates associated with eurytopy or other adaptive factors (for a recent interpretation, see Brock, 2000). Schopf (1992) presents examples of stasis held for extremely long periods in prokaryotes. On ample evidence he states: ‘the size, shape, and cellular organization of cyanobacteria have remained unchanged over periods of more than one, and in some cases more than two billion years’. Any stasis held over 2000 million (‘two billion’) years cannot simply be a matter of evolutionary rate! On the other hand, domestic animals and cultivated plants have been adopted to show how easily and greatly animals and plants can change. Ironically they have not changed their taxic positions (except for the creation of new plants by crossing different species) in spite of their great variations, which, if these organisms were wild, could be of specific or even generic value.

Reversals, long-persistent phenotypes, and stable taxa are, thus, real phenomena in spite of changing DNA. They agree in implying that DNA compositions or genes alone cannot be crucial. A genome may hardly be more than the sum of its genes, but it does its

work in the hierarchical structure of the organism, in which genes can perform multiple functions including compensation for inactivated genes. ‘This multiple action of genes, their involvement in very different processes, is not arbitrary: it is because the genes and their products have particular properties that they carry out these multiple functions’. ‘The most difficult will be to understand ... how the simple elementary functions of the genes are organized to generate the complex functions of organisms’ (Morange, 2001). Gene expression should be organized in some hierarchical way to maintain potential of ancestral phenotypes. Hierarchical patterns of gene expression thus organized should persist for a long geological time. They should underlie the generating process of, so to say, *grand developmental schemes* that are responsible for the occurrence of hierarchical taxa and robust enough to accommodate genetic and phenetic variations arising within taxa.

The multifunctionality of genes and the hierarchical organization of gene expression require that evolutionary changes should be far from uniform. When hierarchical patterns of gene expression change, they must do in a relatively short time, because any evolving pattern should rapidly reach a stable state, otherwise being easily lost. The greater the change, the more rapid should it be. ‘Cryptic maintenance of phenotypic potential can only be one side of the coin. Changes in regulatory schemes that alter the timing of expression or even the nature of association between individual genes can result in entirely new, large-scale phenotypic experiments’ (Hunkapillar et al., 1982). Ohno (1996) proposed the occurrence of nearly identical genomes in the animals radiated to display a multitude of distinct body plans at the Cambrian explosion—real large-scale evolutionary experiments, provided these animals appeared in the fossil record shortly after they first evolved. Recent paleontological discoveries support the view that the Cambrian explosion was a biological event. ‘Crown group bilaterians may yet be demonstrated in terminal Proterozoic rocks, but the diversification of crown groups was principally a Cambrian event’ (Knoll and Carroll, 1999). Ohno’s hypothesis (‘the Cambrian pananimalia genome’) supposes differential usage of the same set of genes accounting for the great disparity in body forms.

We may need, therefore, a theory that can explain not only the recurrence of ancestral phenotypes but also the expected rapid process in the emergence of higher and lower taxa and the stability and persistence of established taxa *all consistently*. Developmental mechanisms should constitute the nucleus of the theory, while regulatory genes and the regulatory function of other genes, alone, may not be sufficient for the underlying genetic mechanisms. We may agree in the belief that ‘acceptance of a broader concept of heredity, which includes multiple inheritance systems, will have far reaching consequences of our understanding of evolutionary processes’ (Jablonka and Lamb, 1995).

Disparity and diversity among organisms have been explained by evolutionary theories. On the other hand, taxonomy with its unending refinement requires a better evolutionary theory, which should not be incompatible with what it discovers. In doing so, taxonomy is significant in promoting the study of evolutionary patterns and mechanisms of organisms. As far as the arguments developed in this study are accepted, DGC’s with their long evolutionary histories, abundant species, familial behaviours associated with gall-inhabitation, and diverse gall phenotypes including atavistic ones may be promising for undertaking such an approach to evolution.

4. POSTSCRIPT

My stories of intersexual phoresy [3.2] and defensive larvae [3.3] will readily be

confirmed (or rejected) by field observations. (If they are rejected, we have to look for other explanations for the synchronic occurrence of the female crawlers and the adult males, their morphological peculiarities, and the remarkable sexual dimorphism in the 1st instar larvae. What explanations are then possible?) The supposed phoresy, however, may be performed at night. Rearing gall-bearing twigs indoors, kept away from light at night [3.2], may be substituted for field observations. But the most serious problem is how to find galls. In my trips in tropical Asia I rarely came across dipterocarp galls. This may be due to my concentration on collecting diaspidids, but there seems to be another reason. Although the galls and insect specimens examined in this study were mostly collected on saplings, the main domain of DGC's is probably in the forest canopy. It is generally admitted that in the tropical rain forest an unknown number of insect species inhabit the canopy.

When I visited Singapore in 1992 and got a close view of the summit of Bukit Timah, composed of 2 small peaks and a short ridge between, I understood why Anthony (1974a) had succeeded with her gall surveys in that limited area [1.2.3]. The forest stand on the summit was once cleared to a considerable degree. When, years after, Anthony made her surveys, the crowns of saplings growing in the area must have been easily accessible to her. She states: 'One should note that a large number of *Shorea curtisii* King saplings which compose the undergrowth in my field area, is the result of the germination of anemochorous and heliophilic seeds. This testifies to a recent thinning of the forest'. Jenkins and Mabberley (1994) state: '*Hopea ponga* (Dennst.) Mabberley (Dipterocarpaceae) is most commonly encountered as the dominant component of cleared forest sites in the wet zone of South West India, where it persists in dense coppiced stands, rarely exceeding 50cm high, which are grazed regularly and cut for firewood'. These stands bear abundant galls induced by *Mangalorea hopeae*. Giving the impression of a fruit, the gall has been known to European botanists since the late 17th century.

In my Malaysia trips, surveys in primeval and natural forests were largely confined to the lower storeys, yet I got a good amount of diaspidid material from seedlings, saplings, and lower branches of young trees. Diaspidid crawlers are generally provided with long caudal setae, which fact implies that they disperse by air currents. In the course of wind dispersal, part of crawlers leaving their natal sites in the canopy will drop onto the lower storeys inevitably and frequently, thus founding colonies in the lower storeys. Needless to say, it is impossible at present to compare the diaspidid fauna of the lower storeys with that of the canopy and to evaluate how much it reflects the latter, which is unknown.

In the present study the view is adopted that the crawlers of the species of *Mangalorea*, *Gallacoccus*, and *Echinogalla* do not disperse by air currents, lacking long caudal setae. The synchronic appearance of the female crawlers and the adult males from the same maternal galls, combined with their morphological peculiarities, enables us to think that the female crawlers are transported by their winged adult brothers from the maternal galls to new sites favourable for inducing galls [3.2]. Assuming that these coccoids mainly inhabit the canopy, which abounds with shoots suitable for gall formation, the occurrence of their galls in the lower storeys should be due to the occasional landing of adult males carrying female crawlers and flying astray.

If this supposition is correct, spots once cleared and grown with saplings in the dipterocarp forest may be suitable for collecting and observing DGC's. In such a place the crowns of saplings form the canopy, which is low enough for our access.

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Dr Hans Peter Heckroth, Johann Wolfgang Goethe-Universität, Frankfurt am Main, sent to me the material of the 2 new species of *Gallacoccus*. This study began with my intention of settling his material, which had been left aside for years because of the unidentified host plant. In the course of the present study I have come to believe that the host plant is a *Shorea* species. Now I think I have sighted the coast of another *terra incognita*—the regnum of DGC's, of which the existence was predicted by Dr Anthony and Dr Jenkins. I am deeply thankful to Dr Heckroth for giving me the material and the chance to do this study.

Dr Ming Anthony favoured me with a copy of her thesis. The Document Supply Department, Radcliffe Science Library, University of Oxford, supplied me with a copy of Jenkins' thesis. These works are and will remain valuable resources for information about dipterocarp galls.

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REFERENCES

- Affi, S. F., 1968. Morphology and taxonomy of the adult males of the families Pseudococcidae and Eriococcidae (Homoptera: Coccoidea). Bulletin of the British Museum (Natural History), Entomology, Supplement 13, 210 pp.
- Anthony, M., 1974a. Contribution to the knowledge of cecidia of Singapore. Gardens' Bulletin, Singapore 27: 17–65, 13 plates.
- Anthony, M., 1974b. Cécidogénèse comparée de deux galles de coccides (*Gallacoccus anthonyae* Beardsley et *Galloccoccus secundus* Beardsley) développées sur le *Shorea curtisii* Dyer ex King (Dipterocarpaceae). Marcellia 38: 99–144.
- Anthony, M., 1977. Morphological and anatomical comparison of normal and cecidial shoots in *Shorea curtisii* Dyer ex King. Marcellia 40: 181–192.
- Anthony, M., 1980. Étude des Bourgeonnements Épiphylls Déterminés par l'Action

- d'Ériococcides Cécidogènes chez les Diptero-carpaceae du Genre *Shorea*. Thèse d'État ès Sciences Naturelles, Université Louis Pasteur, Strasbourg. [Besides the author's studies on the galls of *Gallacoccus anthonyae* and *G. secundus*, the results of her surveys of herbarium specimens for galls similar to those of the *Gallacoccus* species are given in the part titled 'Les galles en bourgeon néoformé chez les diptero-carpacees asiatiques, leur distribution phytogéographique et ses implications'.]
- Beardsley, J. W., Jr., 1971. A new genus of gall-inhabiting Eriococcidae from Singapore (Homoptera: Coccoidea). *Proceedings of the Hawaiian Entomological Society* 21: 31–39.
- Beardsley, J. W., Jr., 1984. Gall-forming Coccoidea. In: Ananthakrishnan, T. K. (ed.), *Biology of Gall Insects*, p. 79–106.
- Brock, J. P., 2000. *The Evolution of Adaptive Systems*. Academic Press, xiii+642 pp.
- Cook, L. G., Gullan, P. J., and Stewart, A. C., 2000. First-instar morphology and sexual dimorphism in the gall-inducing scale insect *Apiomorpha* Rübsaamen (Hemiptera: Coccoidea: Eriococcidae). *Journal of Natural History* 34: 879–894.
- Crespi, B. J., 1992. Eusociality in Australian gall thrips. *Nature* 359: 724–726.
- Cronquist, A., 1981. *An Integrated System of Classification of Flowering Plants*. Columbia University Press, xvii+1262 pp.
- Ferris, G. F., 1950. Report upon scale insects collected in China (Homoptera: Coccoidea). Part I. *Microentomology* 15: 1–34.
- Foldi, I., 1995. A taxonomic revision of *Limacoccus* Bondar with a cladistic analysis of its relationships with other scale insects (Hemiptera: Coccoidea). *Systematic Entomology* 20: 265–288.
- Foster, W. A. and Northcott, P. A., 1994. Galls and the evolution of social behaviour in aphids. In: Williams, M. A. J. (ed.), *Plant Galls: Organisms, Interactions, Populations, Systematic Association Special Volume 49*, Clarendon Press, p. 161–182.
- Green, E. E., 1926. On some new genera and species of Coccidae. *Bulletin of Entomological Research* 17: 55–65.
- Green, E. E., 1928. Further observations on *Beesonia diptero-carpi*, Green. *Bulletin of Entomological Research* 19: 205–207.
- Gullan, P. J., 1983. Taxonomy and biology of Australian gall-forming Coccoidea. *Verh. SIEEC X, Budapest*: 381–383.
- Gullan, P. J. and Cockburn, A., 1986. Sexual dichromism and intersexual phoresy in gall-forming coccoids. *Oecologia* (Berlin) 68: 632–634.
- Hall, B.K., 1984. Developmental mechanisms underlying the formation of atavisms. *Biological Reviews of Cambridge Philosophical Society* 59: 89–124.
- Hoy, J. M., 1963. *A Catalogue of the Eriococcidae* (Homoptera: Coccoidea) of the World. New Zealand Department of Scientific and Industrial Research, Bulletin 150, 260 pp.
- Hu X. and Li S., 1993. On a newly recorded genus and a new species of Kermesidae (Homoptera: Coccoidea) from China. *Scientia Silvae Sinicae* 29: 110–114.
- Hu X., Li S., and Prokopy, R., 1995. Studies on the morphology and taxonomy of the male of *Beesonia napiformis* (Kuwana) (Coccoidea: Beesonidae). *Israel Journal of Entomology* 29: 85–91.
- Hunkapillar, T., Huang, H., Hood, L., and Campbell, J. H., 1982. The impact of modern genetics on evolutionary theory. In: Milkman, R. (ed.), *Perspectives on Evolution*, Sinauer Associates, Inc., p. 164–189.
- Jablonka, E. and Lamb, M. J., 1995. *Epigenetic Inheritance and Evolution: The Lamarckian Dimension*. Oxford University Press, xiii+346 pp.
- Jenkins, R. M., 1992. *Taxonomic Character Change and the Significance of Galls*. Thesis submitted for the degree of Doctor of Philosophy in the University of Oxford. [This thesis is composed of Section I–III and Appendix I–V. The results of the author's studies

- on the echinate gall induced by the coccoid now known as *Mangalorea hopeae* and the life history of the coccoid are given in Section II titled 'The spinose gall of the Dipterothripidae'. The results of his surveys for echinate galls across the family Dipterothripidae are given in Part B of Section II and Appendices. (Section I is titled 'The origin of the fagaceous cupule', and III 'The inherited gall and the ant-plant tuber', with 'Thesis overview and conclusions'.)]
- Jenkins, R. M. and Mabblerley, D. J., 1994. A breadfruit amongst the dipterothrips: galls and atavism. In: Williams, M. A. J. (ed.), Plant Galls: Organisms, Interactions, Populations, Systematic Association Special Volume 49, Clarendon Press, p. 183–199.
- Knoll, A. H. and Carroll, S. B., 1999. Early animal evolution: Emerging views from comparative biology and geology. *Science* 284: 2129–2137.
- Koteja, J., 2000. Advances in the study of fossil coccids (Hemiptera: Coccinea). *Polskie Pismo Entomologiczne* 69: 187–218.
- Koteja, J., 2001. Essays on coccids (Hemiptera: Coccinea): Paleontology without fossils? *Prace Museum Ziemi* 46: 41–53.
- Larew, H. G., 1990. Gall Formation. In: Rosen, D. (ed.), Armored Scale Insects: Their Biology, Natural Enemies and Control, Vol. A., Elsevier, p. 293–300.
- Miller, D. R. and Gimpel, M. E., 2000. A Systematic Catalogue of the Eriococcidae (Felt Scales) (Hemiptera: Coccoidea) of the World. Intercept, 589 pp.
- Moran, V. C., Gunn, B. H., and Walter, G. H., 1982. Wind dispersal and settling of first-instar crawlers of the cochineal insect *Dactylopius austrinus* (Homoptera: Coccoidea: Dactylopiidae). *Ecological Entomology* 7: 409–419.
- Morange, M., 2001 (translated by Cobb, M.). The Misunderstood Gene. Harvard University Press, ix+222pp. [Originally published in 1998 under the title 'La Part des Gènes'.]
- Morley, R. J., 2000. Origin and Evolution of Tropical Rain Forests. John Wiley & Sons Ltd, xv+362 pp.
- Ohno, S., 1996. The notion of the Cambrian pananimalia genome. *Proceedings of the National Academy of Sciences of the United States of America* 93: 8475–8478.
- Pérez Guerra, G. and Kosztarab, M., 1992. Biosystematics of the family Dactylopiidae (Homoptera: Coccinea) with emphasis on the life cycle of *Dactylopius coccus* Costa. Virginia Polytechnic Institute and State University, Bulletin 92-1, vi+90 pp.
- Raff, R. A., 1996. The Shape of Life: Genes, Development, and the Evolution of Animal Form. University of Chicago Press, xxiii+520 pp.
- Raman, A. and Takagi, S., 1992. Galls induced on *Hopea ponga* (Dipterothripidae) in southern India and the gall-maker belonging to the Beesoniidae (Homoptera: Coccoidea). *Insecta Matsumurana New Series* 47: 1–32.
- Reyne, A., 1954. *Reynvaania gallicola*, a new eriococcid causing galls on *Quercus lineata* Bl. *Tijdschrift voor Entomologie* 97: 233–241.
- Rohfritsch, O. and Anthony, M., 1992. Strategies in gall induction in two groups of Homoptera. In: Shorthouse, J. D. and Rohfritsch, O. (eds.), *Biology of Insect-Induced Galls*, Oxford University Press, p. 102–117.
- Rutherford, A., 1915. Some new Ceylon Coccidae. *Journal of the Bombay Natural History Society* 24: 111–118.
- Schopf, J. W., 1992. The oldest fossils and what they mean. In: Schopf, J. W. (ed.), *Major Events in the History of Life*, Jones and Bartlett Publishers, Inc., p. 29–63.
- Takagi, S., 1987. Notes on the Beesoniidae (Homoptera: Coccoidea). *Insecta Matsumurana New Series* 37: 27–41.
- Takagi, S., 1990. Polymorphism. In: Rosen, D. (ed.), *Armored Scale Insects: Their Biology, Natural Enemies and Control Vol. A (World Crop Pest Vol. 4A)*, Elsevier, p. 59–64.
- Takagi, S., 1995. A new species of *Beesonia* with larval polymorphism, inducing a stem gall on *Shorea curtisii* in Singapore (Homoptera: Coccoidea: Beesoniidae). *Insecta*

- Matsumurana New Series 52: 1–19.
- Takagi, S., 1998. A further study of *Uluccoccus* (Homoptera: Coccoidea: Diaspididae). *Species Diversity* 3: 105–116.
- Takagi, S., 2000. Four extraordinary diaspidids (Homoptera: Coccoidea). *Insecta Matsumurana New Series* 57: 39–87.
- Takagi, S., Tang F.-t., Yasar, B., and Kondo, T., 1997. Further forms of the Rugaspidiotini-problem (Homoptera: Coccoidea: Diaspididae). *Insecta Matsumurana New Series* 53: 81–116.
- Tang F.-D. and Hao J.-J., 1955. The Margarodidae and Others of China (Homoptera: Coccinea of Insecta). Chinese Agricultural Science Technology Press, 738 pp. [in Chinese with English Summary].
- Thorne, B. L., 1997. Evolution of eusociality in termites. *Annual Review of Ecology and Systematics* 28: 27–54.
- Veevers-Carter, W., 1984. *Riches of the Rain Forest*. Oxford University Press, xvi+103 pp.
- Williams, D. J. and Miller, D. R., 1999. Two new genera and species of mealybugs (Hemiptera: Coccoidea: Pseudococcidae) that produce plant galls. *Proceedings of the Entomological Society of Washington* 101: 522–539.



Fig. 1. *Gallacoccus anthonyae*, galls. Bukit Timah, Singapore, on *Shorea curtisii*. Courtesy: Dr D. H. Murphy.



Fig. 2. *Gallacoccus anthonyae*, gall, cut open to show the inhabiting adult female. Bukit Timah, Singapore, on *Shorea curtisii*. Courtesy: Dr D. H. Murphy.



Fig. 3. *Gallacoccus secundus*, gall, cut open to show the inhabiting adult female. Bukit Timah, Singapore, on *Shorea curtisii*. Courtesy: Dr D. H. Murphy.



Fig. 4. *Echinogalla pustulata*, galls [90ML-182].



Fig. 5. Gall collected on a dipterocarp sapling in Brunei [see text: 3.1]. Courtesy: Dr P. J. Gullan.



Fig. 6. Same as Fig. 5, cut open. Courtesy: Dr P. J. Gullan.

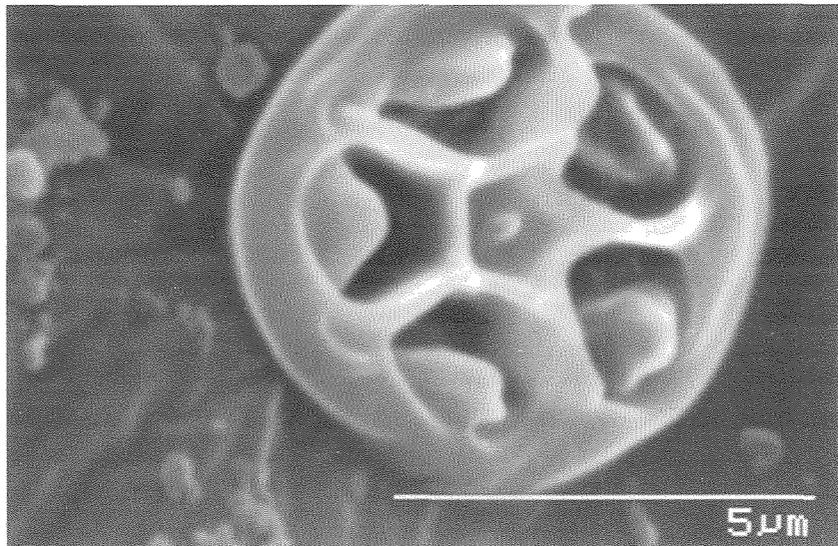


Fig. 7. *Gallacoccus heckrothi*, adult female: 5-locular disc pore with a linguiform process in each locule.

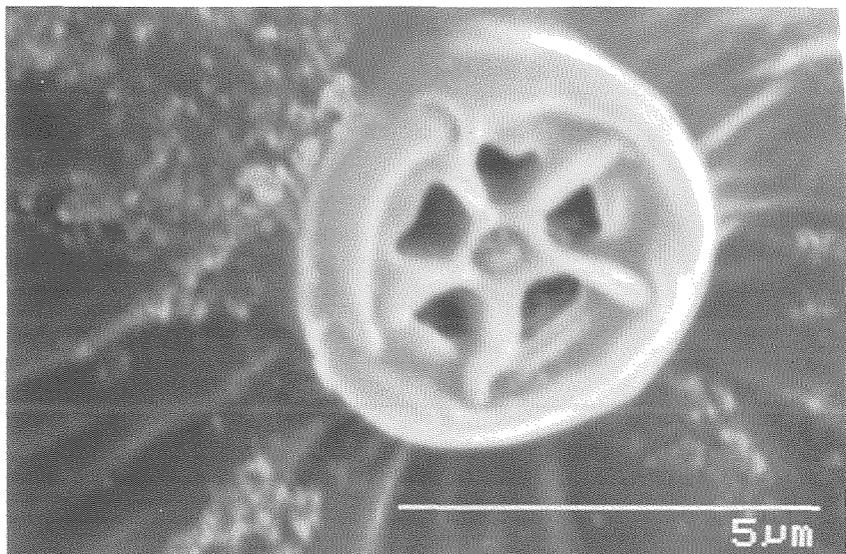


Fig. 8. *Gallacoccus heckrothi*, adult female: 5-locular disc pore without linguiform process.

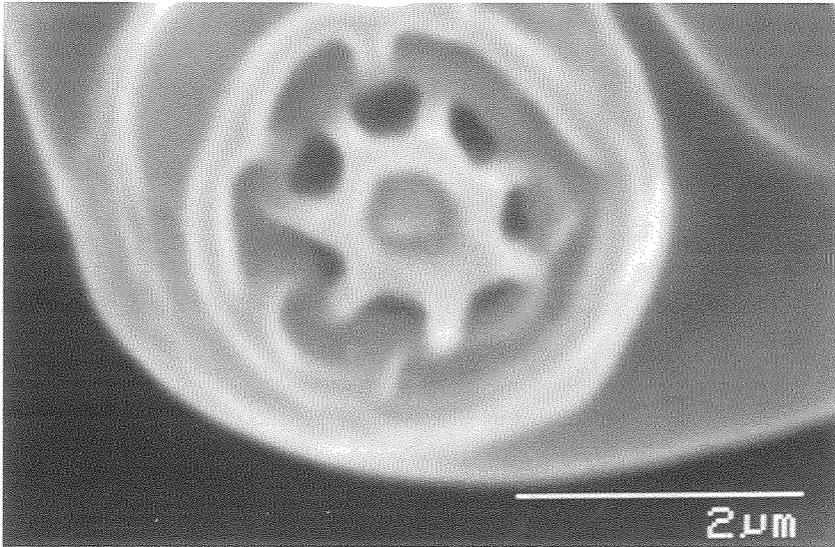


Fig. 9. *Gallacoccus heckrothi*, 1st instar female: 7-locular spiracular disc pore.

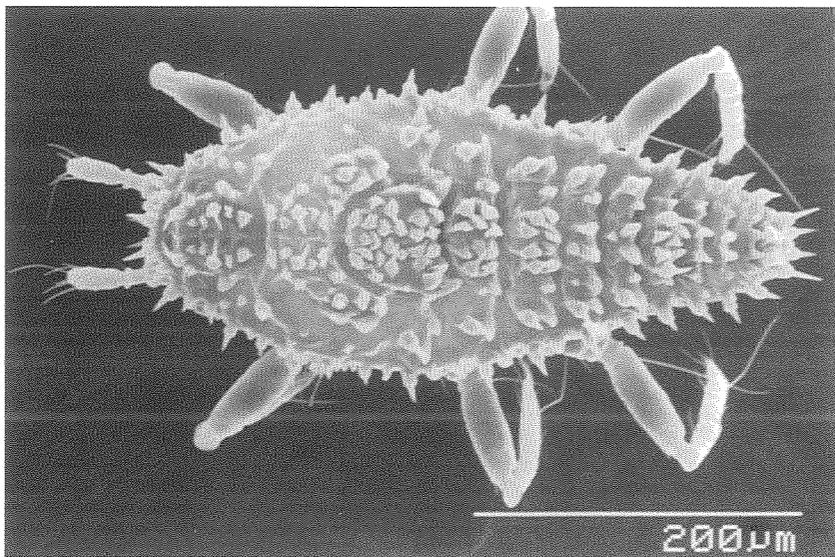


Fig. 10. *Gallacoccus heckrothi*, 1st instar female: dorsal view.

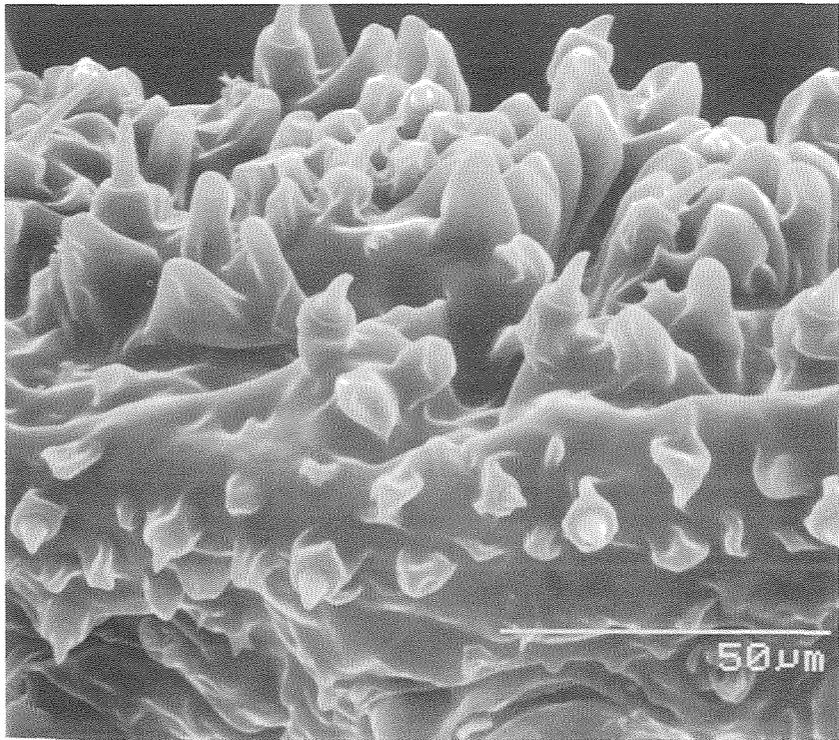
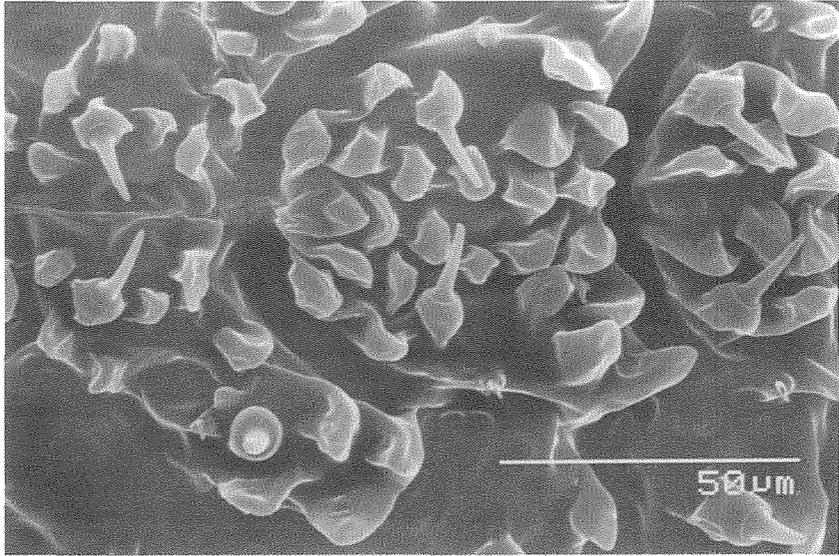


Fig. 11 (upper). *Gallacoccus heckrothi*, 1st instar female: thoracic region, dorsal view.
Fig. 12 (lower). Same as Fig. 11, lateral view.

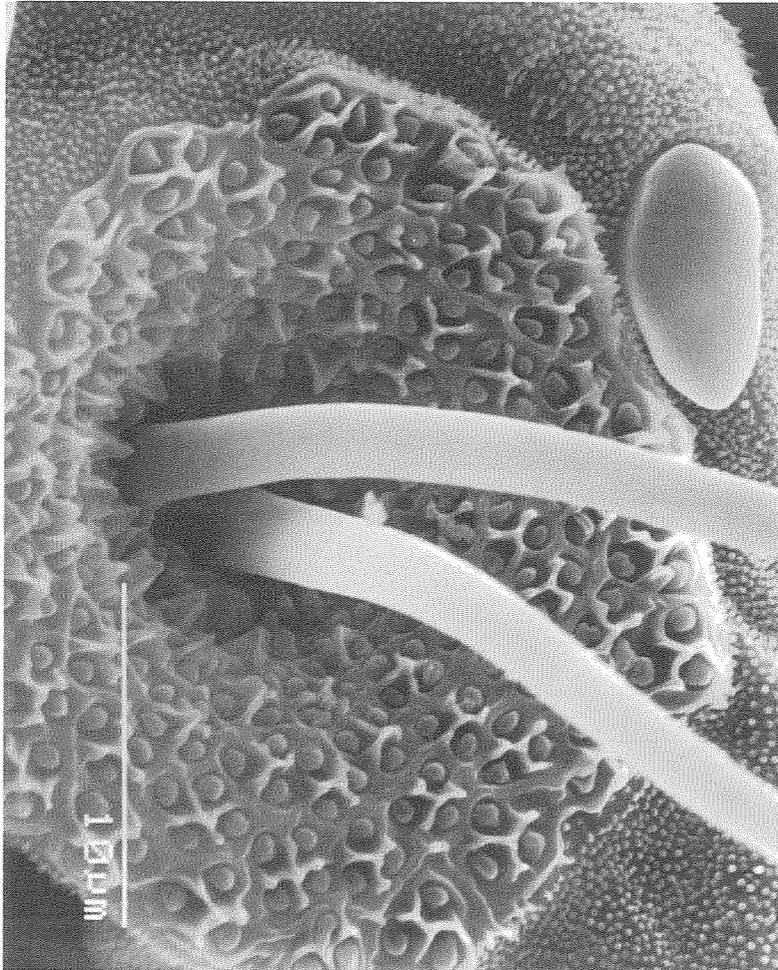


Fig. 13. *Gallacoccus heckrothi*, adult male: glandular pouch on abd VIII. Note shining 3-furcate patterns each representing the interocular septa of a 3-locular disc pore. One papilla is shown in the upper right corner of the picture.

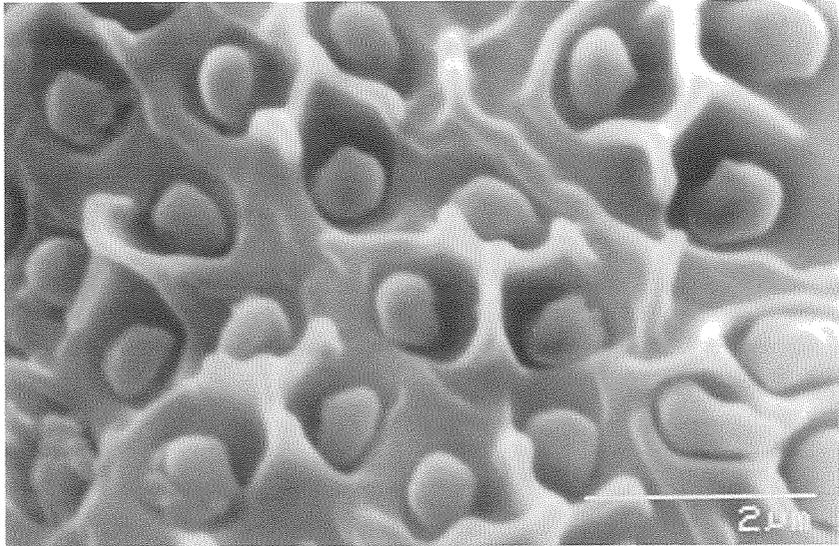


Fig. 14. *Gallacoccus heckrothi*, adult male: trilocular disc pores in glandular pouch viewed from above.

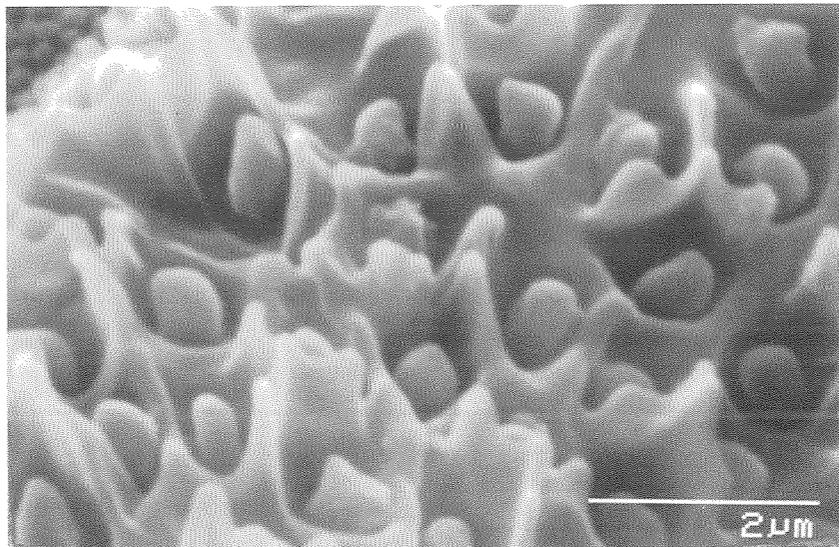


Fig. 15. Same as Fig. 14, viewed obliquely. Note interocular septa produced beyond the level of the surrounding wall of a 3-locular pore.

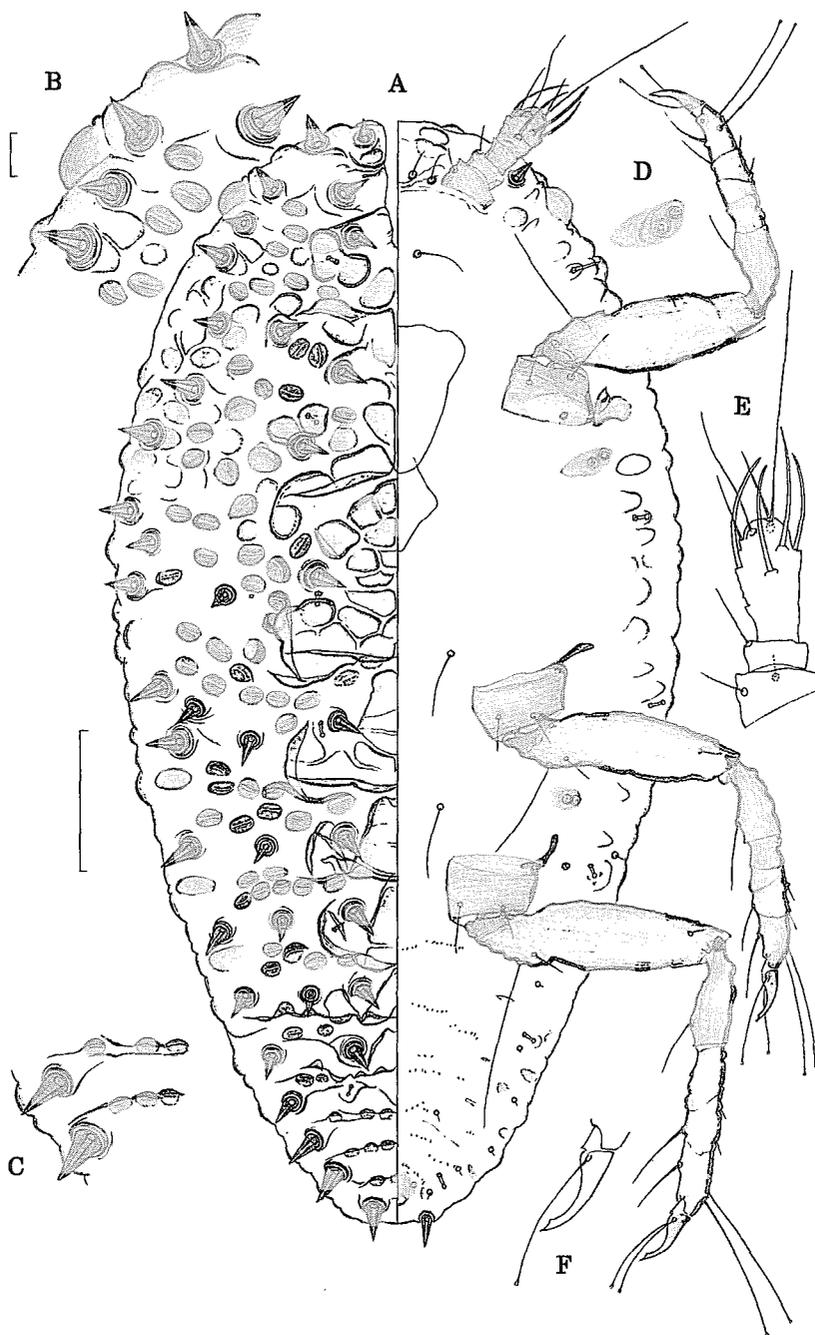


Fig. 16. *Gallacoccus secundus*, 1st instar female: B, part of head, dorsal view; C, abd VI and VII, dorsal view; D, anterior spiracle; E, antenna, ventral side; F, claw of hind leg. Scales: A, 50 μ m; B, 10 μ m (C–F magnified at the same rate as B).



Fig. 17. *Gallacoccus spinigalla*, 1st instar female: B, part of head, dorsal view; C, abd I and II, dorsal view; D, claw of hind leg. Scales: A, 50 μ m; B, 10 μ m (C and D magnified at the same rate as B).

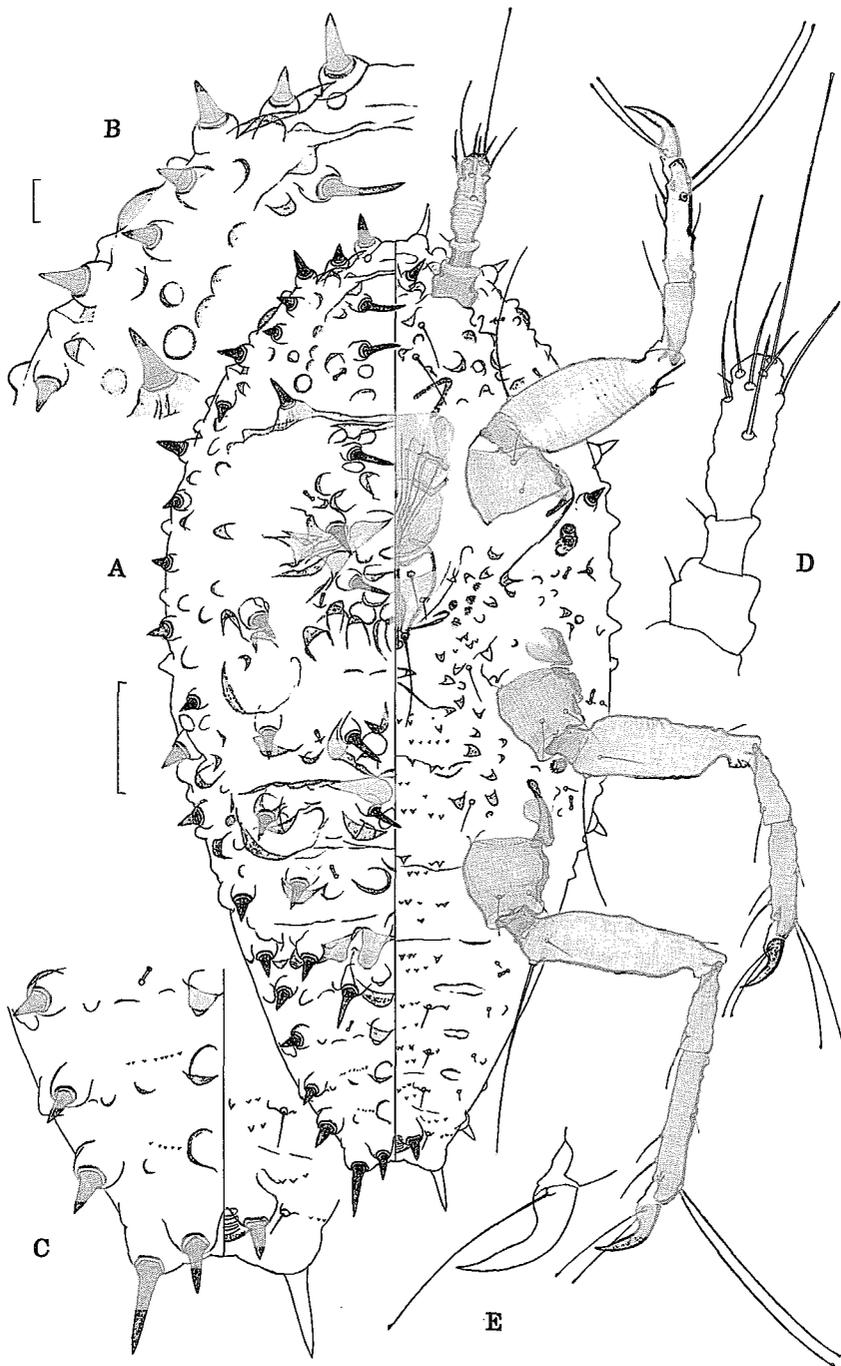


Fig. 18. *Gallacoccus heckrothi*, 1st instar female: B, part of head, dorsal view; C, posterior end of abdomen; D, antenna; E, claw of hind leg. Scales: A, 50 μ m; B, 10 μ m (C-E magnified at the same rate as B).

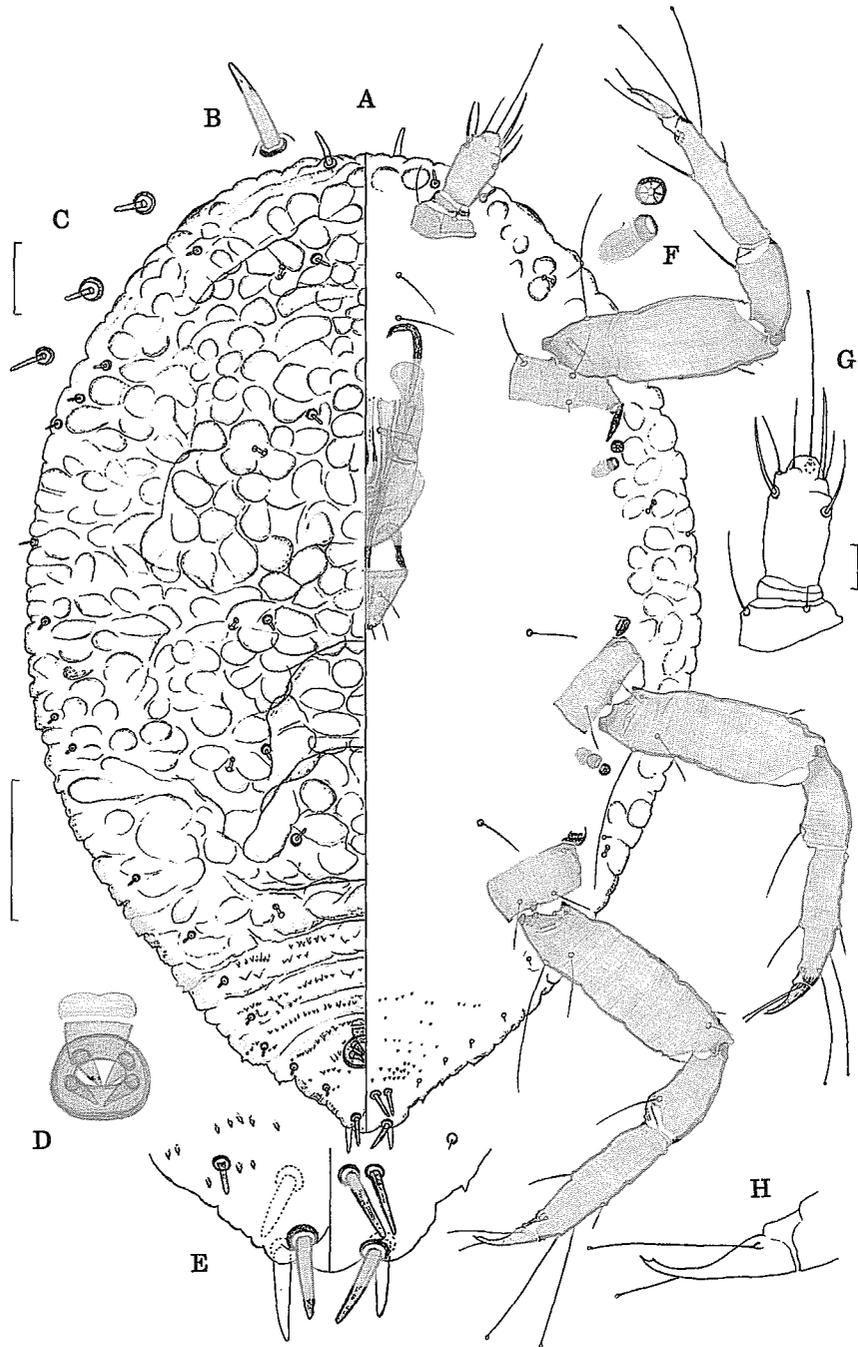


Fig. 19. *Echinogalla pustulata*, 1st instar female [90ML-510]: B, frontal seta; C, dorsal setae on margin; D, anus; E, posterior end of abdomen; F, anterior spiracle; G, antenna; H, claw of hind leg. Scales: A, 50 μ m; C, 10 μ m (B, D–F, and H magnified at the same rate as C); G, 10 μ m.

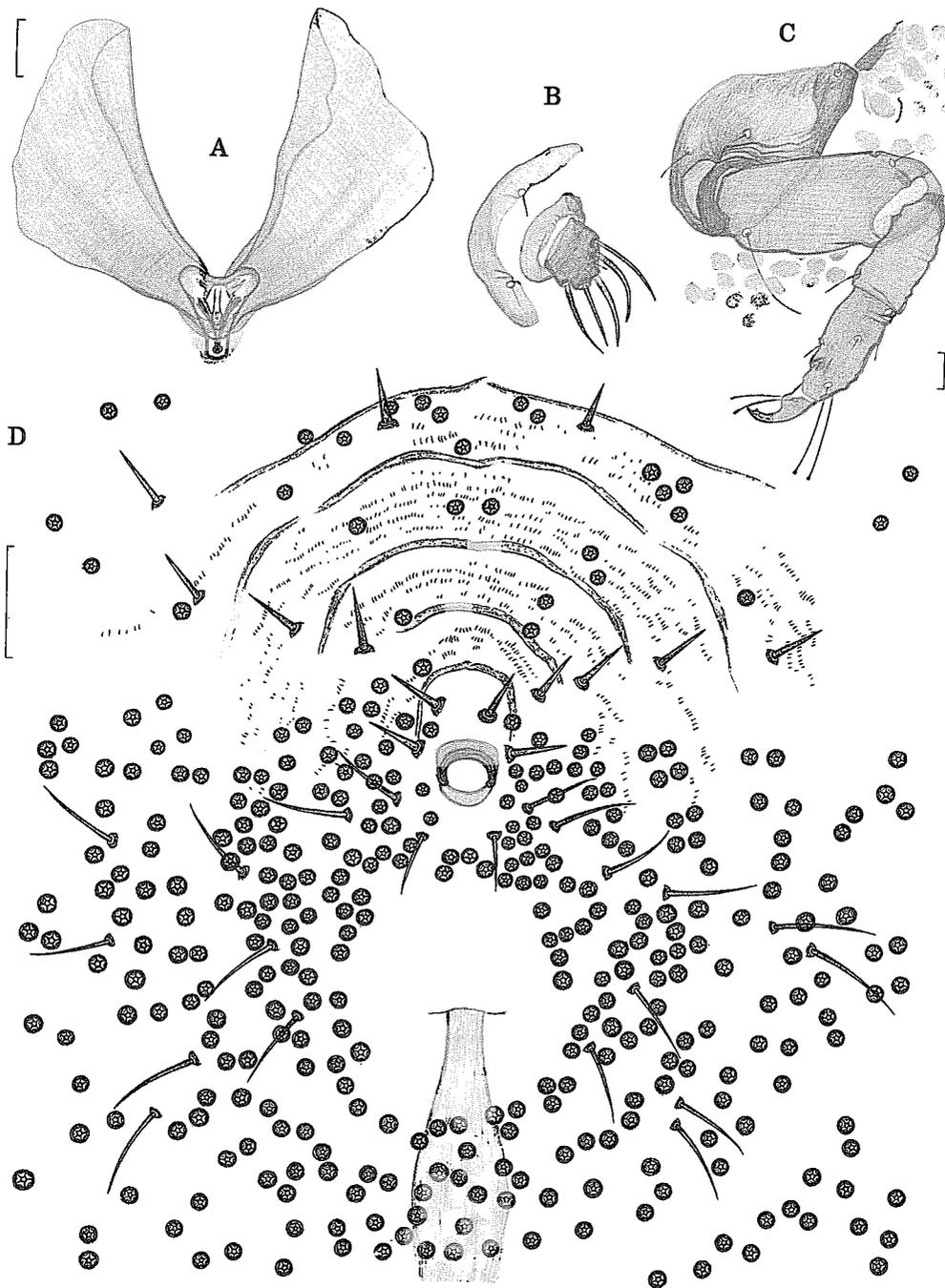


Fig. 20. *Gallacoccus spinigalla*, adult female: A, mouth-parts, showing aliform appendages; B, antenna; C, hind leg; D, posterior region of body around anus and vulva. Scales: A, 100 μ m; C, 10 μ m (B magnified at the same rate as C); D, 50 μ m.

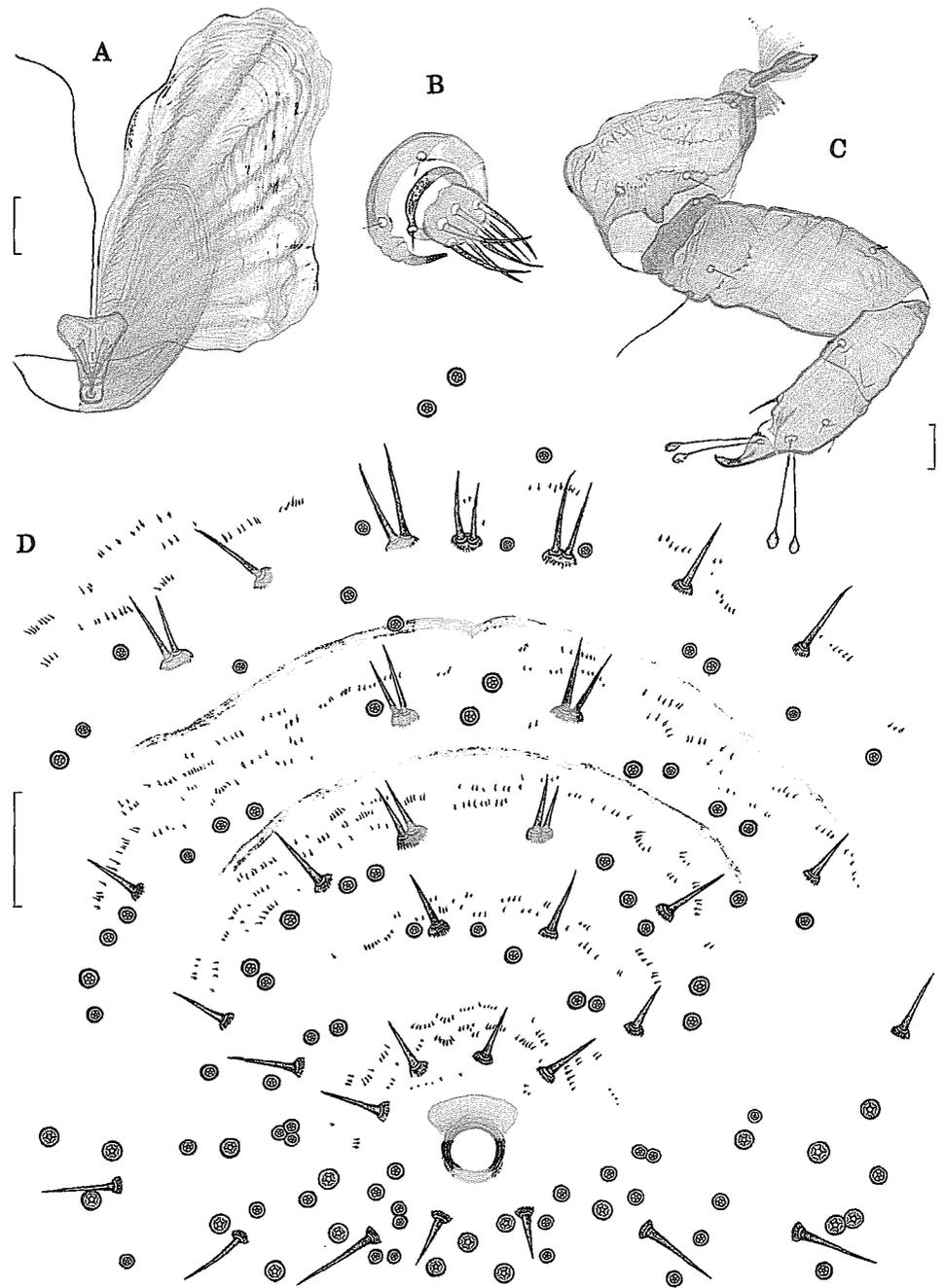


Fig. 21. *Gallacoccus heckrothi*, adult female: A, mouth-parts, showing aliform appendages; B, antenna; C, hind leg; D, posterior region of body around anus. Scales: A, 100 μ m; C, 10 μ m (B magnified at the same rate as C); D, 50 μ m.

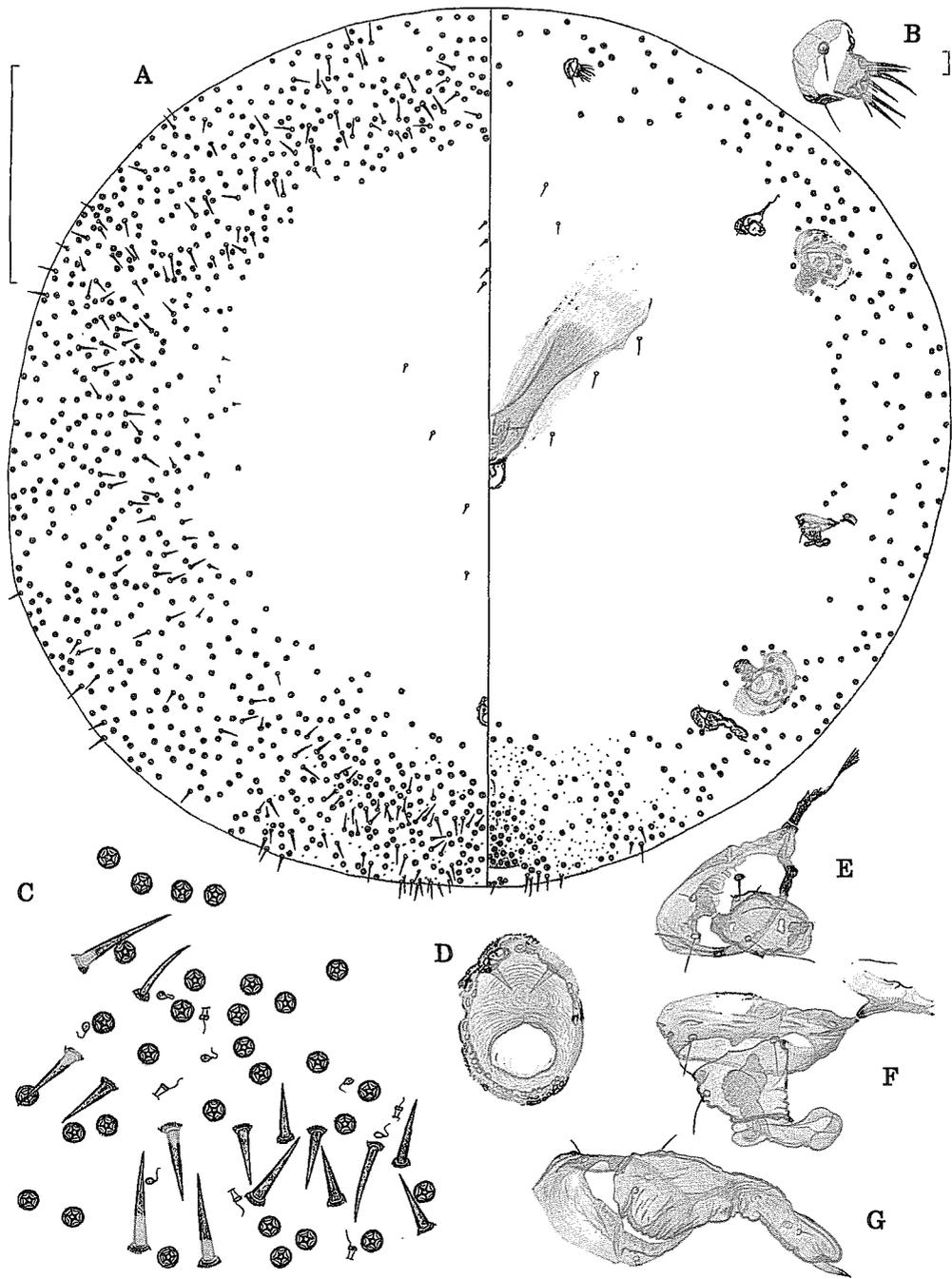


Fig. 22. *Echinogalla pustulata*, adult female, figured from a young specimen [90ML-307]: B, antenna; C, posterior region of body, dorsal surface, showing 5-locular disc pores, tubular ducts, and spinous setae; D, anus; E, fore leg; F, mid leg; G, hind leg. Scales: A, 500 μ m; B, 10 μ m (C-G magnified at the same rate as B).

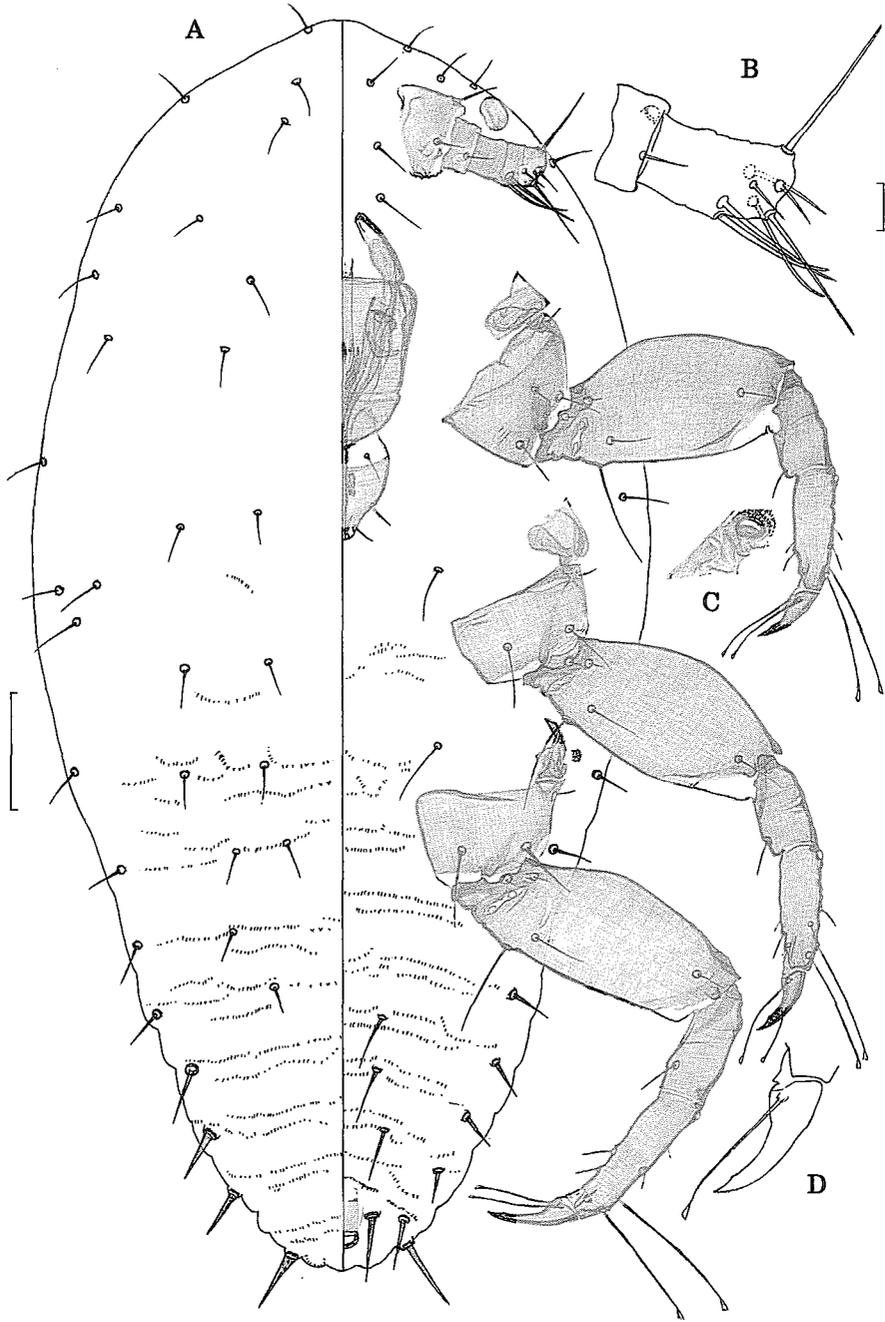


Fig. 23. *Gallacoccus secundus*, 1st instar male: B, antenna; C, anterior spiracle; D, claw of hind leg. Scales: A, 50 μ m; B, 10 μ m (C and D magnified at the same rate as B).

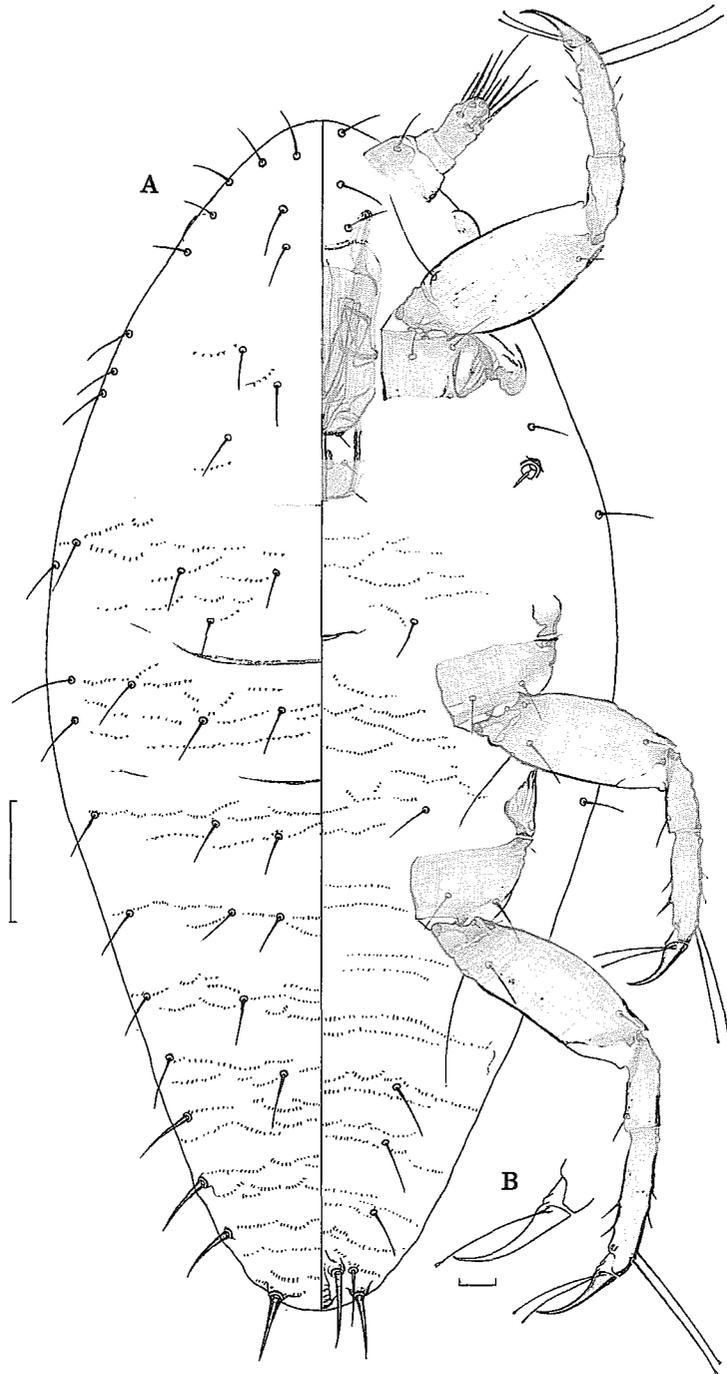


Fig. 24. *Gallacoccus spinigalla*, 1st instar male: B, claw of hind leg. Scales: A, 50 μ m; B, 10 μ m.

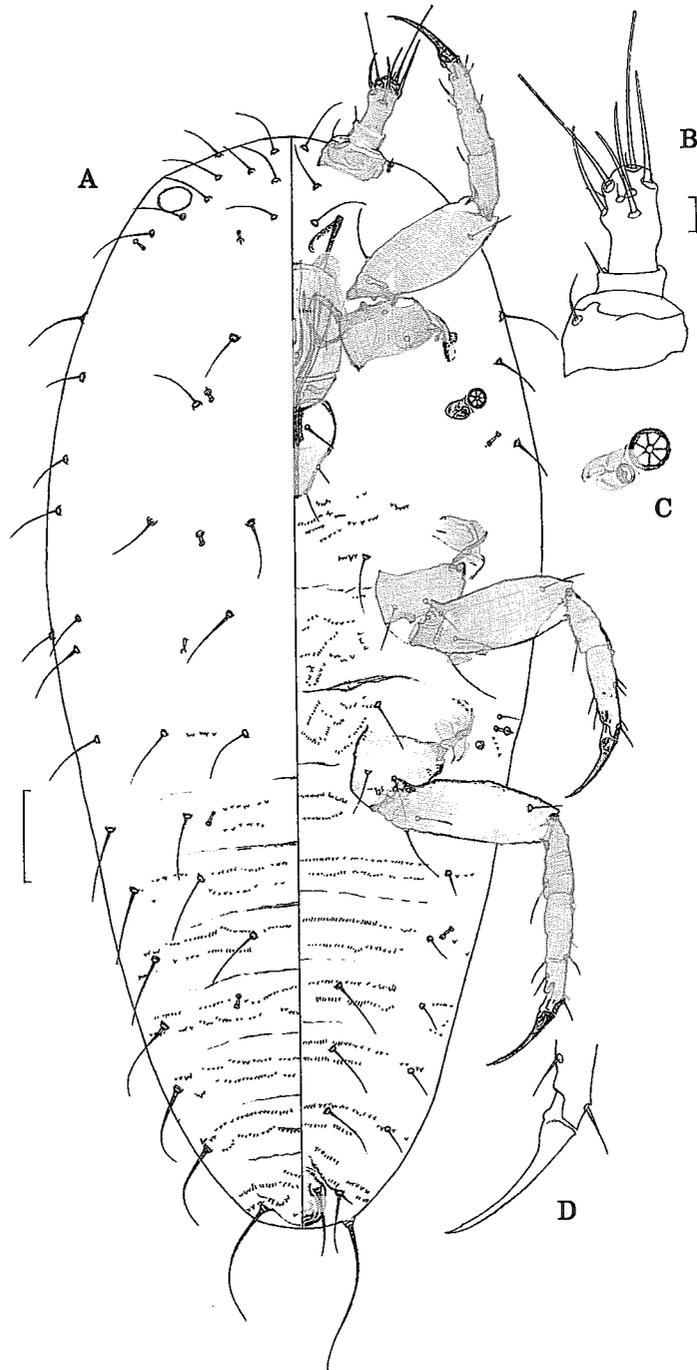


Fig. 25. *Gallacoccus heckrothi*, 1st instar male: B, antenna; C, anterior spiracle; D, claw of hind leg. Scales: A, 50 μ m; B, 10 μ m (C and D magnified at the same rate as B).

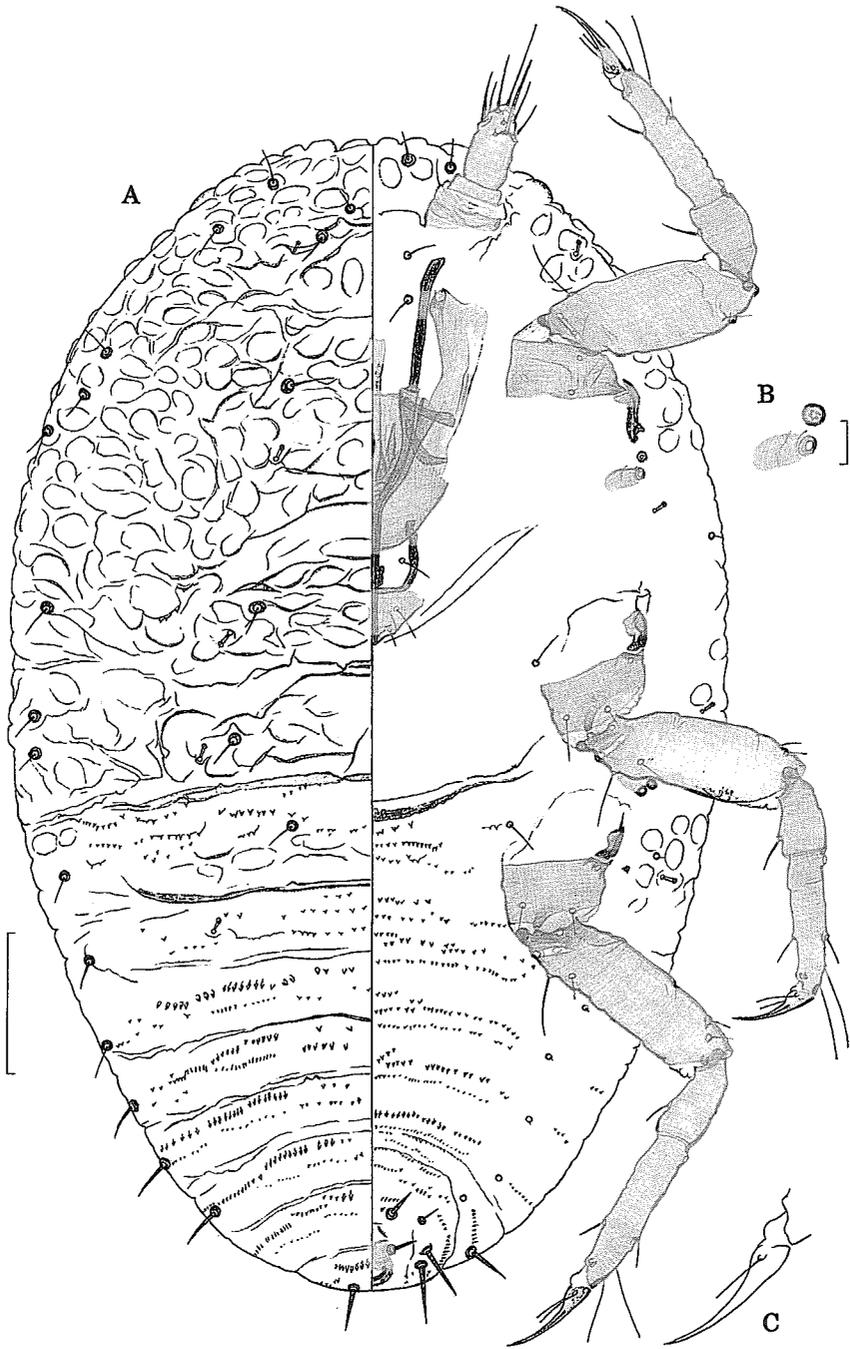


Fig. 26. *Echinogalla pustulata*, 1st instar male [90ML-510]: B, anterior spiracle; C, claw of hind leg. Scales: A, 50 μ m; B, 10 μ m (C magnified at the same rate as B).

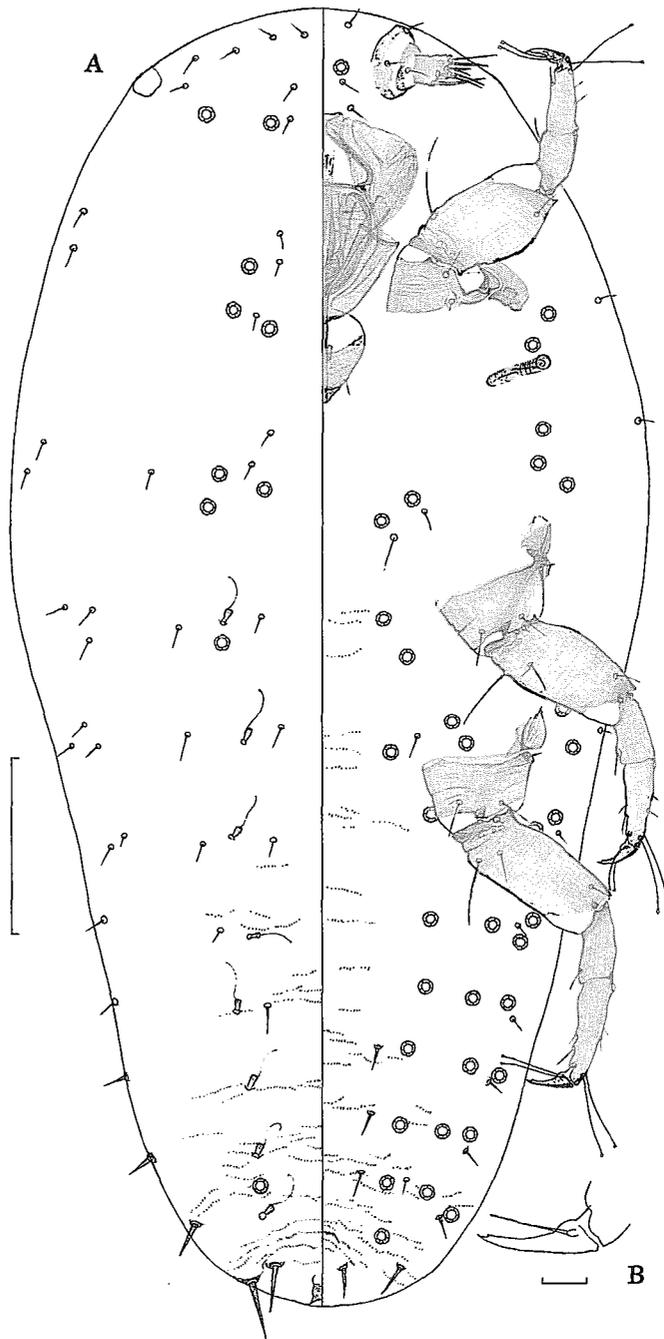


Fig. 27. *Gallacoccus secundus*, 2nd instar male: B, claw of hind leg. Scales: A, 100 μ m; B, 10 μ m.

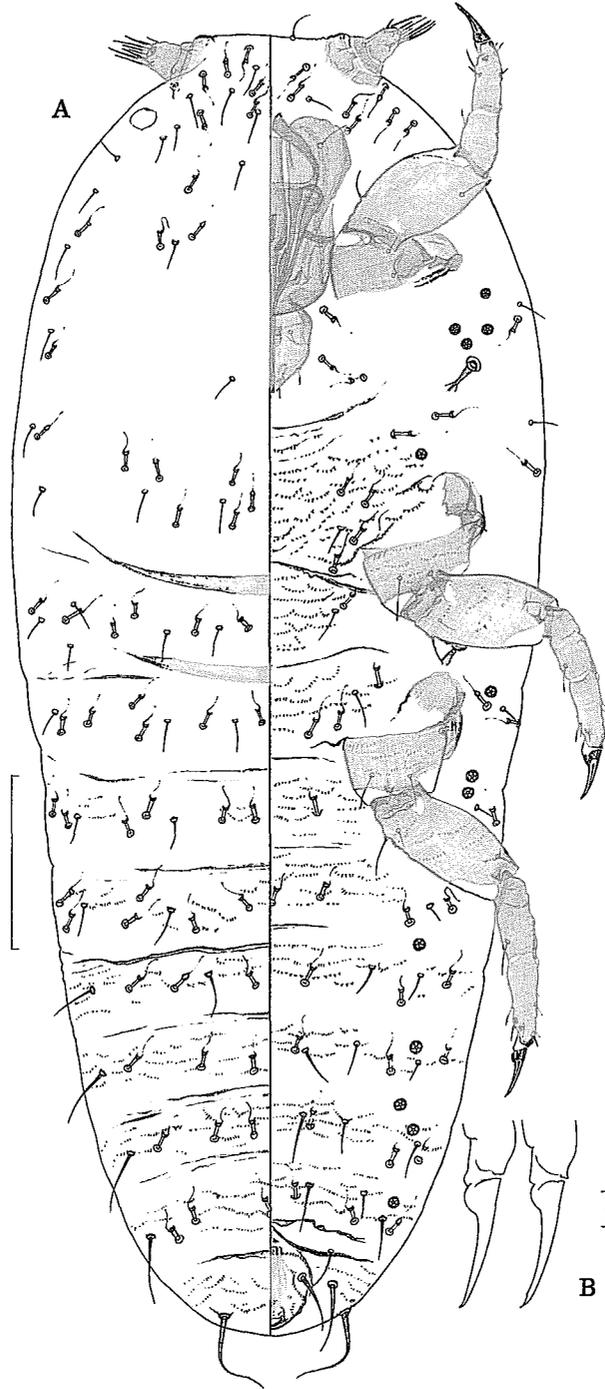


Fig. 28. *Gallacoccus heckrothi*, 2nd instar male: B, claws of hind leg with (right) or without (left) denticle. Scales: A, 100 μ m; B, 10 μ m.



Fig. 29. *Echinogalla pustulata*, 2nd instar male [90ML-510]: B, claw of hind leg. Scales: A, 100 μ m; B, 10 μ m.

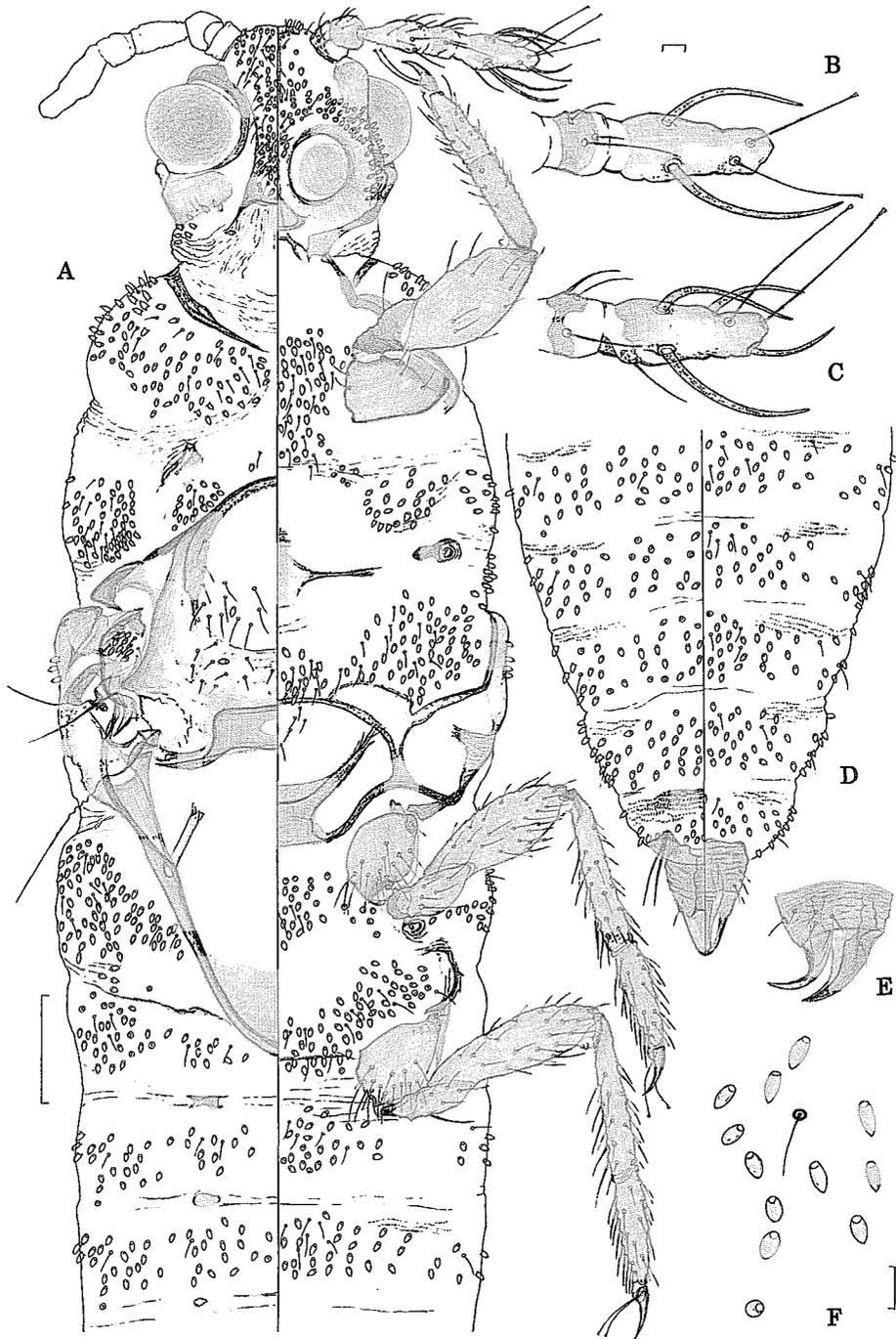


Fig. 30. *Gallacoccus secundus*, adult male: A and D, body; B, 4th and 5th antennal segments, ventral surface; C, 4th and 5th antennal segments, dorsal surface; E, genital capsule, lateral view (right side: dorsal); F, papillae. Scales: A, 100 μ m (D and E magnified at the same rate as A); B, 10 μ m (C magnified at the same rate as B); F, 10 μ m.

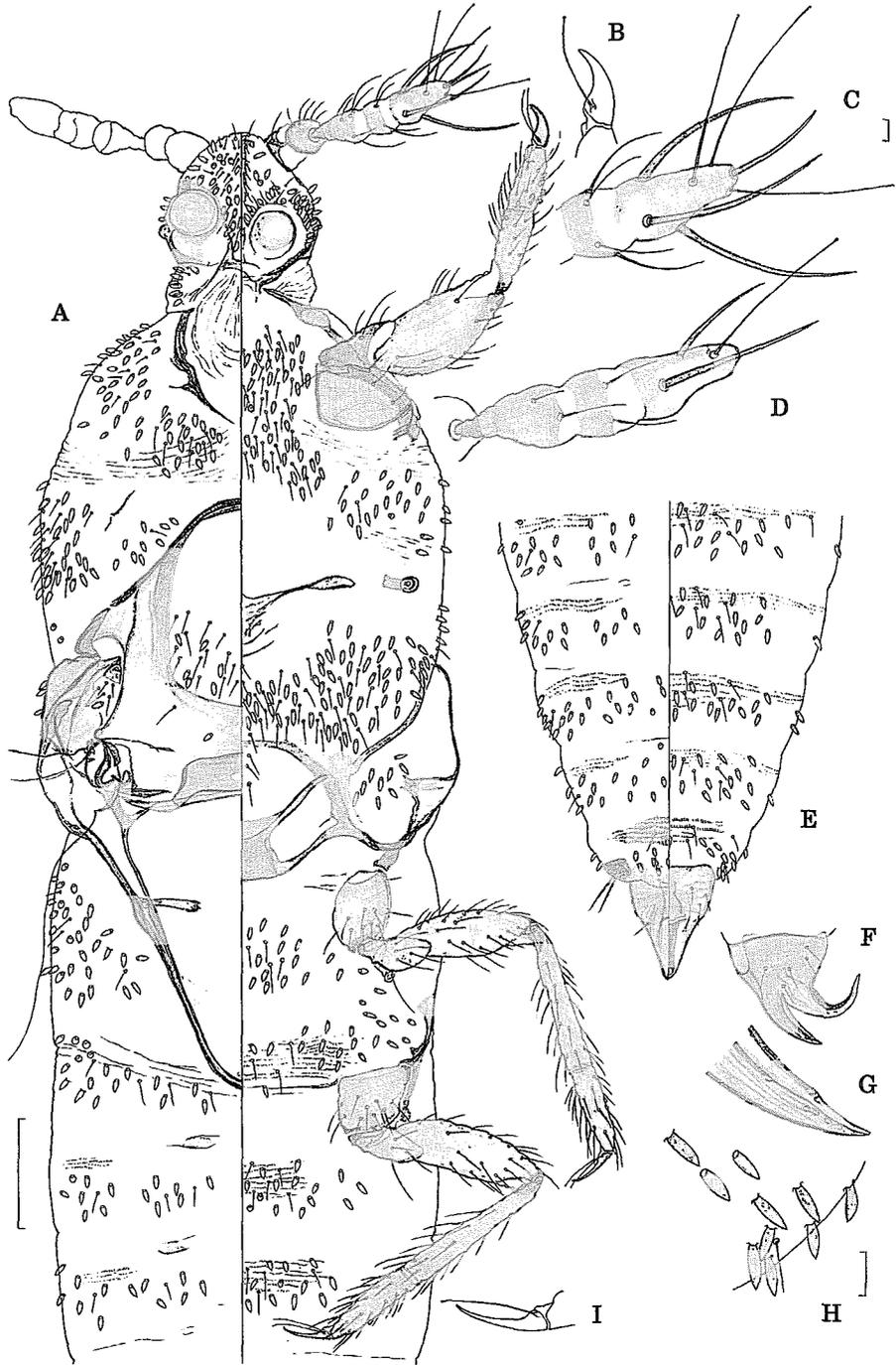


Fig. 31. *Gallacoccus spinigalla*, adult male: A and E, body; B, claw of fore leg; C, 4th and 5th antennal segments, ventral surface; D, 3rd-5th antennal segments, dorsal surface; F, genital capsule, lateral view (right side: ventral); G, penis sheath, apex, lateral view; H, papillae; I, claw of hind leg. Scales: A, 100 μ m (E and F magnified at the same rate as A); C, 10 μ m (B, D, and I magnified at the same rate as C); H, 10 μ m (G magnified at the same rate as H).

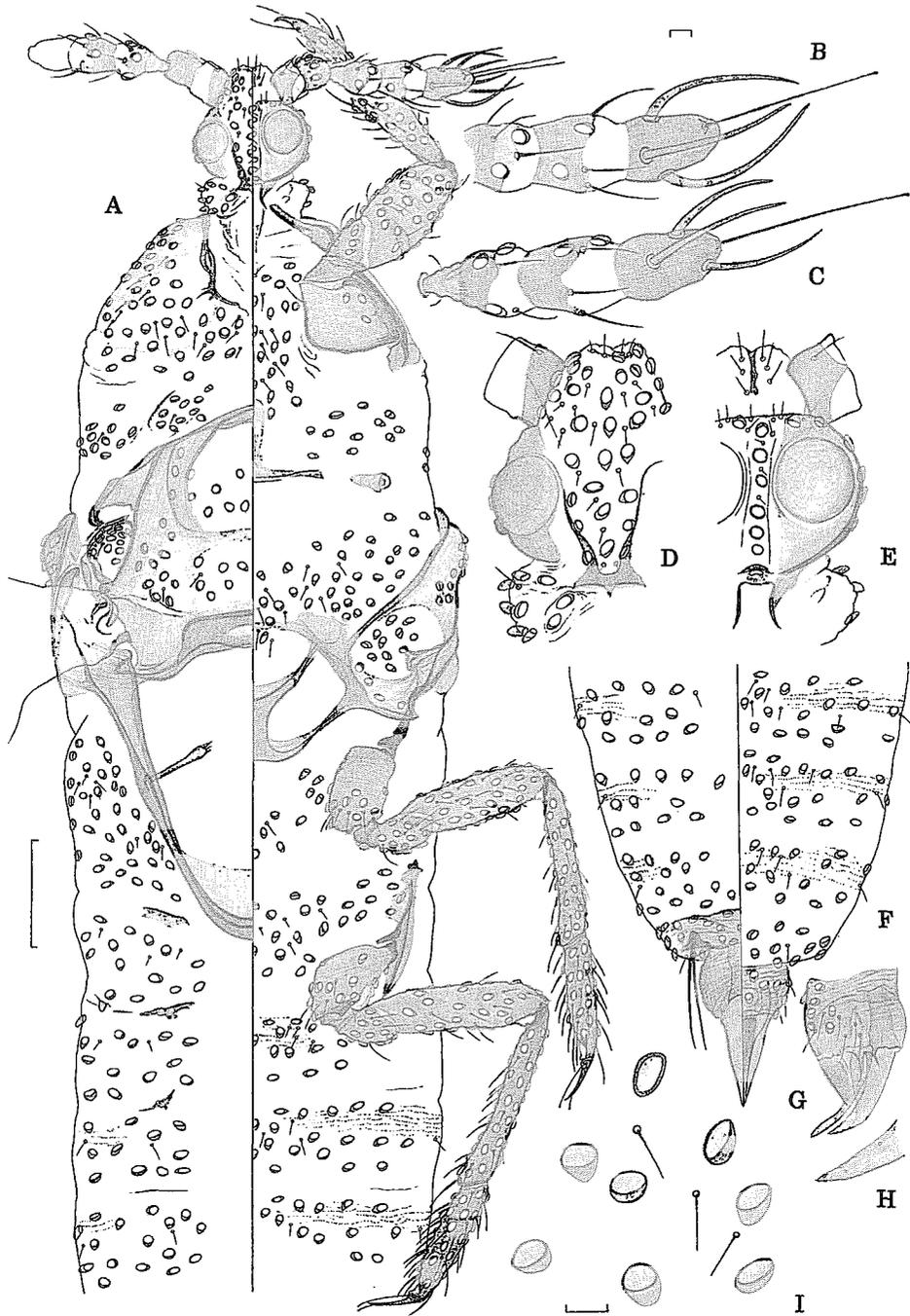


Fig. 32. *Gallacoccus heckrothi*, adult male: A and F, body; B, 3rd–5th antennal segments, ventral surface; C, 3rd–5th antennal segments, dorsal surface; D, head, dorsal surface; E, head, ventral surface; G, genital capsule, lateral view (right side: dorsal); H, penis sheath, apex, lateral view; I, papillae. Scales: A, 100 μ m (F and G magnified at the same rate as A); B, 10 μ m (C–E and H magnified at the same rate as B); I, 10 μ m.



Fig. 33. *Echinogalla pustulata*, adult male [90ML-510]: A and F, body; B, head (with dorsal eyes within head margin); C, antenna, ventral surface; D, papillae; E, tarsus (part) and claw of mid leg; G, genital capsule, distal half. Scales: A, 100 μ m (B and F magnified at the same rate as A); C, 10 μ m (E and G magnified at the same rate as C); D, 10 μ m.

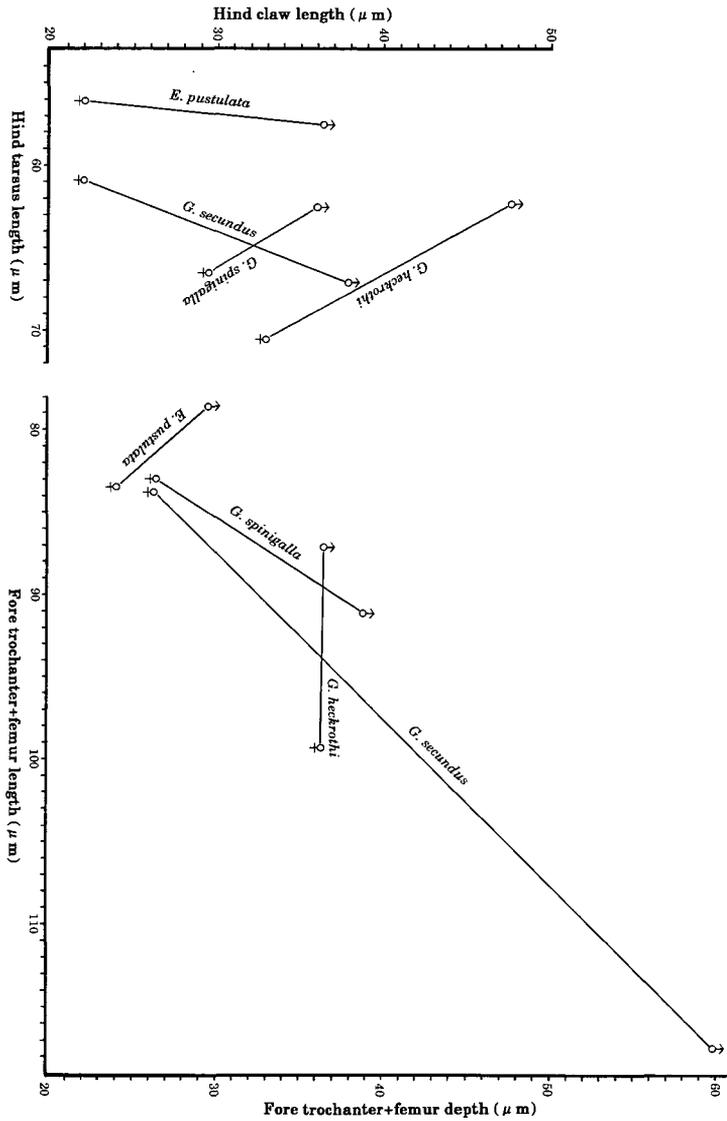


Fig. 34. Sexual dimorphism in the 1st instar larvae, exhibited in linear dimensions of legs: length of hind leg claw against length of hind tarsus, and depth against length of fore trochanter+femur. Mean values are plotted, and those of the conspecific male and female are connected by a line. Each mean value is based on 10 legs of 10 individuals except for the 1st instar female of *Gallacoccus secundus*, in which 4 legs of 2 individuals were measured.