INSECTA MATSUMURANA

NEW SERIES 75: 29–79 OCTOBER 2019

CHIONASPIS IN THE TROPICS (STERNORRHYNCHA: COCCOIDEA: DIASPIDIDAE)

By SADAO TAKAGI

Abstract

TAKAGI, S. 2019. *Chionaspis* in the tropics (Sternorrhyncha: Coccoidea: Diaspididae). *Ins. matsum. n. s.* 75: 29–79, 23 figs.

Taxonomic studies on *Chionaspis* in the past are briefly summarized with emphasis on the confusion they caused. Thirteen species of *Chionaspis* are described, 12 from Malaya and Sabah and one from Luzón. They are deemed to be new to science, but one of them is not formally named. They were collected in montane areas from plants of the family Fagaceae (ten of the *Chionaspis* species), Anacardiaceae (one), or Melastomataceae (two). The females of five species, and possibly also of two others, occurring on fagaceous trees burrow under the upper epidermal layer on the lower surface of leaves, having the macroduct system remarkably incomplete. At least one species occurring in Malaya on fagaceous plants is closely related to three species inhabiting the Himalayas. The second instar males of eight species were examined; those of the two species associated with melastomataceous plants are noteworthy for their occurring patterns of modified macroducts. The first instar exuvial casts, examined in 12 species, have six-segmented antennae. The 13 species are: *Chionaspis trigonobalani*, *C. lithocarporum*, *C. quercea*, *C. oligocera*, *C. rhombifera*, *C. rhombiphora*, *C.* sp.TN*L*, *C. berincangensis*, *C. kinabaluana*, and *C. samatana*, these species occurring on fagaceous plants, the last in Luzón; *C. glutae* on an anacardiaceous plant; *C. melastomatis* and *C. pogonantherae* on melastomataceous plants.

Author's address. Hukuzumi 3-3-4-16, Toyohira-ku, Sapporo, 062-0043 Japan (E-mail: s7d4-tkg@jcom.zaq.ne.jp).

Contents

Scientific paper for the united projects: Hokkaidô University Expeditions to the Himalaya; Research Trips for Agricultural and Forest Insects in the Subcontinent of India; Systematic and Ecological Surveys on Some Plant-parasitic Microarthropods in Southeast Asia.

Introduction

In the present paper, 13 species of scale insects are described as members of *Chionaspis*, 12 from Malaya (Malay Peninsula) and Sabah (northeastern Borneo), Malaysia, and the other one from Luzón, the Philippines. All these species are deemed to be new to science but one of them, from Malaya, is not formally named owing to the condition of the mounted specimens. So far as examined in my revision of *Chionaspis* made in 1985, the genus was mainly Holarctic in distribution, and in eastern Asia it was represented well in and north of the Himalayan Region. The species described in the present paper are probably true members of *Chionaspis*, at least one of them being connectable with northern species of the genus inhabiting the Himalayas. Provided this interpretation is correct, this paper presents the first document for the definite occurrence of the genus in the equatorial climate zone.

These species were collected in montane oak forests in areas distantly separated by lowlands and seas, but some of them suggest that there were interflows of species between Malaya and Sabah (probably through montane areas in northwestern Borneo) and possibly also between Sabah and Luzón (possibly through Palawan) during the not remote past. Further species of *Chionaspis*, therefore, may be expected to exist in other montane areas in this region, the Sundaland in the Glacial Periods.

I started my study on the species from Malaysia about 30 years ago, but I soon stopped the study owing to the circumstances I explained on p.147 in my paper published in 1999. I have not yet cleared up the question I had at that time: how to discriminate between species of *Chionaspis* and some species probably referable to another genus, which I named *Myrtaspis* in 1999, in the stage of the adult female. The 13 species described in this paper seem to belong to *Chionaspis* not only in their morphological characters but also in their habitats. They are published here with my unsettled question left aside.

It should be added that in my study published in 1999, I adopted as a trial the view that *Chionaspis* species should have six-segmented antennae in the first instar without exception. In the present study on the tropical species, I have come across no exceptional case.

Terms. The term ‘trullae’ is used in place of ‘pygidial lobes’ in authors. The abbreviations ‘abd I’, ‘abd II’ and so on stand for abdominal segments.

Numbers of wax-secreting organs. The numbers of main wax-secreting organs (disc pores, macroducts, and gland spines) are given for each side of the body except for their total numbers (and, needless to say, also median perivulvar disc pores). The total number of dorsal macroducts means that of submedian and submarginal macroducts combined, not including marginal macroducts (even on the third abdominal segment). For each sample are given: the lowest, mean, and highest values; the lowest and highest values; or values in individuals; ‘[*n*]’ standing for the sample size or frequency.

Depositories of the holotypes. The holotypes of the 11 formally named species from Malaysia are deposited in the collection of the Entomology Division, Forest Research Institute of Malaysia, Kepong, Kuala Lumpur, Malaysia; the holotype of the species from the Philippines is deposited in the collection of the Museum of Natural History, University of the Philippines at Los Baños, Laguna, Philippines.

Taxonomic studies on Chionaspis in confusion

The genus *Chionaspis* was proposed in 1868 and 69, when the classification of armoured scale insects was in its incipient stage. It was in a great confusion for a century not only because diverse forms were described in combination with this generic name (as was usual with early named genera) but also because the occurrence of polymorphic variation in association with different feeding sites on the host plant body, a kind of polyphenism, was overlooked for a long time in many species closely related to the type species (designated in 1899) of the genus and also in certain other diaspidines. In these scale insects, foliicolous (leaf-feeding) and ramicolous (branch-feeding) forms of the same species are, in not a few cases, remarkably different especially in the state of the trullae (pygidial lobes) and in the numbers of wax-secreting organs. In 1899 and 1903, the foliicolous form of such a species was supposed to represent not only a different species but also a different genus, which was named *Phenacaspis* and, after that time, stuffed not only with the foliicolous forms of other species but also with many diverse forms all on the basis of similarity especially in the median trullae. In the middle of the 20th century and particularly around 1955 and 56, *Phenacaspis* was regarded as a well-established genus and, in 1965 and 66, even the subtribe Phenacaspidina was proposed in opposition to the Chionaspidina, having some other genera added. *Chionaspis*, *Phenacaspis*, and the higher groups concerned all composed at that time were, in reality, confused assemblages of related and unrelated forms, involving polyphenism, convergence, and parallelism all intermingled intricately.

The confusion began with a simple mistake in interpreting a polyphenistic form. At that time, scale insect taxonomy may have been still in its early stage. However, mistakes were repeated thereafter during half a century in many scale insects. It seems that, in those days, no one was aware of the biological significance of the occurrence of different forms on different feeding sites, especially branches and leaves, on the same plant bodies in spite of the fact that the host plants of those scale insects included not a few deciduous ones.

In 1952 and 53, an attempt to reveal the confusion was made in some diaspidines by carrying out observations on ramicolous and foliicolous individuals occurring in the same colonies at the same times, and the conclusion was drawn that *Phenacaspis* was not to be separated from *Chionaspis*. It was the first challenge to *Phenacaspis*, but it was not concerned with the 'type species' of *Phenacaspis*, so that the conclusion it presented was not fully convincing. The attempt was not positively evaluated at that time, and the conclusion was not accepted generally.

In 1967, a morphometric analysis of a series of median trullae indicated that the 'type species' of *Phenacaspis* was nothing other than the foliicolous form of a species which was recognized as a member of *Chionaspis* on the basis of the ramicolous form occurring on the same deciduous plant. In 1976, a transplant experiment was led to the same conclusion. These studies made the occurrence of feeding-site polyphenism an established fact, and gave a compelling reason to make a critical re-examination on the long-held concepts of *Chionaspis* and *Phenacaspis*. This examination furnished a suitable occasion to exclude from *Chionaspis* under reformation many unrelated species, which had been included especially in *Phenacaspis*. Since that time, the concept and composition of *Chionaspis* have undergone remarkable but reasonable changes.

In my revision of the genus *Chionaspis* made in 1985, I examined 383 specific names which had been used in combination with *Chionaspis* or *Phenacaspis*, and

enumerated 59 species as members of *Chionaspis*. My revision was restricted to literature as to many species, and the recognition of the members of *Chionaspis* was no more than tentative as to some species. The genus thus recomposed was mainly Holarctic in distribution, with species mostly occurring in temperate climates. No species described from the Southern Hemisphere were retained in the genus.

After 1985, some species were newly described in *Chionaspis* and a few were excluded from the genus as given below. New questions have also arisen, and remain to be investigated.

Chionaspis montanoides, occurring on *Salix* and *Populus* (both genera belonging to Salicaceae), was described from Xinjiang (Sinkiang), Central Asia (Tang, 1986).

Chionaspis hamoni occurring on *Salix* (Salicaceae) and *C. gilli* on *Tamarix* (Tamaricaceae) were described from North America (Liu and Kosztarab, 1987). The latter is probably an introduced insect in North America.

Chionaspis broughae, *C. comys*, and *C. keravatana* were described from New Guinea, the former two from undetermined plants and the third from *Eucalyptus* (Myrtaceae); *Chionaspis freycinetiae*, *C. pandanicola*, and *C. rhaphidophorae* were described from Fiji, the host plants belonging to *Freycinetia* (Pandanaceae), *Pandanus* (Pandanaceae), and *Rhaphidophora* (Araceae), respectively. These six species were 'described in *Chionaspis* for the time being' (Williams and Watson, 1988), thus requiring further study for their generic positions. Above all, they occur in the South Pacific Region far from the main distribution range of *Chionaspis* and in lowland or marine tropical climates. The three species from Fiji are all associated with monocotyledonous plants. So far as presumed from the figures presented by Williams and Watson (fig. 38, 40, 41), they agree also in having dorsal submedian setae forming a longitudinal row on each side of the body through the postsoma from the metathorax to the seventh abdominal segment. Among the three species from New Guinea, *C. keravatana* is characteristic in having 'usually a single submedian duct … on segment 7'. Otherwise, no particularly noteworthy characters are found in the descriptions and figures given to the three species.

Chionaspis styracis was described from *Styrax* (Styracaceae) in North America (Liu and Kosztarab, 1989).

Chionaspis syzygii and *C. lumbiniana*, both occurring on *Syzygium* (=*Eugenia*, Myrtaceae) at low altitudes in the Himalayan Region and having five-segmented antennae in the first instar (Takagi, 1985), were excluded from *Chionaspis*. The former was removed to the newly erected genus *Myrtaspis*, and the latter was left pending as to its generic position (Takagi, 1999). *Myrtaspis syzygii*, however, has a close counterpart, *Chionaspis trochodendri* (=*Phenacaspis trochodendri* Takahashi), which occurs on *Trochodendron* (Trochodendraceae) in Taiwan. These two species are very closely similar to each other in the adult females, whereas *C. trochodendri* is provided with six-segmented antennae in the first instar as is usual with *Chionaspis* species (Takagi, 1985). The exclusion of *C. lumbiniana* from *Chionaspis* suggests the exclusion of another species, *Chionaspis ramakrishnai* Rao. This species occurs on *Eugenia* in South India at an altitude of about 1000m on the Nilgiris. So far as based on the description (Rao, 1953), it is closely similar to *C. lumbiniana* in the adult female, but no information is available as to the number of antennal segments in the first instar.

Chionaspis brachycephalon, *C. caudata*, *C. sonorae*, and *C. torreyanae* were described from *Pinus* (Pinaceae), the former three occurring in Mexico and the fourth in California. *C. caudata* is not referable to *Chionaspis* or any related genus so far as based

on some morphological characters, but molecular analyses 'unambiguously place' it in *Chionaspis* (Vea et al., 2012, with the authorship of the specific names attributed to Vea).

In addition to the list above, C*hionaspis lepineyi* Balachowsky, 1928, and *Chionaspis parastigma* Balachowsky, 1954, should be mentioned here. They have been treated by recent authors as belonging to one and the same species. These forms combined together are broadly distributed in western Eurasia to northwestern Africa in association with some fagaceous plants. Among the members of *Chionaspis*, they are peculiar in having a claviform sclerosis arising at the lateral base of the mesal lobule of the second trulla; moreover, so far as presumed from the figures in Balachowsky (1954, fig. 75, 76), they have dorsal submedian setae forming a longitudinal row on each side of the body through the postsoma from the metathorax to the seventh abdominal segment. These characters combined together may be sufficient for excluding them from *Chionaspis*. Bodenheimer (1951) erected a new genus, *Marchaliella*, for *C. lepineyi*, but he adopted other characters as generic. Authors have not accepted his genus. The occurrence of dorsal submedian setae, in general, has received little attention as a taxonomic feature, either (see, in this connection, comments on *Chionaspis freycinetiae* and two other species from Fiji given above in this section).

Descriptions of the species

Chionaspis trigonobalani, n.sp. (Fig. 1)

Material examined

Collected on Mt. Kinabalu, alt. ca. 1500m, Sabah, Borneo, on *Trigonobalanus verticillata* (Fagaceae), 7–13.X.1988, Sample 1–3. Adult females available: 3 individuals from Sample 1, 1 from Sample 2, and 15 from Sample 3. Holotype: adult female specimen from Sample 3.

Females and males occurring on both surfaces of leaves. Female tests rounded in outline.

Wax-secreting organs in adult females

Spiracular disc pores. Associated with each anterior spiracle: 7–11 <Sample 1>; 6, 9 <2>; 6–11.8–17 [*n*=23] <3>. With each posterior spiracle: 2–4 <1>; 3, 4 <2>; 2–3.9–6 [28] <3>.

Perivulvar disc pores. In median group: 10, 11, 13 <Sample 1>; 14 <2>; 8–14 <3>. In each anterolateral group: 15–23 <1>; 21, 25 <2>; 16–26 <3>. In each posterolateral group: 12–17 <1>; 15, 16 <2>; 12–20 <3>. Total: 82, 83, 90 <1>; 91 <2>; 66–86.6–101 [*n*=14] <3>.

Dorsal macroducts. Submedian macroducts occurring usually on abd III–VI, absent occasionally on III and rarely on VI; submarginal macroducts on III–V.

<Sample 1>. Submedian macroducts: 2–5 on III; 2–5 on IV; 2–4 on V; 1 [*n*=4], 2 [2] on VI. Submarginal macroducts: 3–5 on III; 3–5 on IV; 3 [3], 4 [3] on V. Total: 31, 41, 56.

<2>. Submedian macroducts: 4 [2] on III; 4 [2] on IV; 2, 3 on V; 2 [2] on VI. Submarginal macroducts: 4 [2] on III; 5, 7 on IV; 4 [2] on V. Total: 53.

<3>. Submedian macroducts: 0 [5], 1–4 [23] on III; 1–4 on IV; 1–4 on V; 0 [1], 1 [13], 2 [14] on VI. Submarginal macroducts: 1–6 on III; 1–5 on IV; 2–5 on V. Total: 19–39.9–56 [14].

Lateral macroducts. Occurring on metathorax to abd III, rarely also on prothorax.

<Sample 1>. 2–5 on mesothorax; 5–8 on metathorax; 4–7 on I; 4 [*n*=4], 5 [2] on II; 2 [2], 3 [4] on III. Total: 43, 46, 49.

<2>. 5 [2] on mesothorax; 6, 7 on metathorax; 6, 7 on I; 3, 5 on II, 3, 5 on III. Total: 52.

<3>. 0 [26], 1 [1], 2 [1] on prothorax; 1–5 on mesothorax; 5–10 on metathorax; 4–9 on I; 4–7 on II, 2–5 on III. Total on mesothorax to III: 37–50.7–59 [14].

Gland spines. Lateral gland spines occurring on abd I–III, occasionally absent on I; marginal gland spines on IV–VIII, single on V–VIII.

<Sample 1>. 0 [*n*=1], 2 [2], 3 [3] on I; 1–3 on II; 2 [4], 3 [2] on III; 1 [1], 2 [5] on IV. Total on I–IV: 12, 15, 18.

<2>. 1 [2] on I; 1, 2 on II; 2 [2] on III; 1, 2 on IV. Total on I–IV: 12.

<3>. 0 [2], 1–3 [24] on I; 1–4 on II; 1–4 on III; 1 [1], 2 [24], 3 [3] on IV. Total on I–IV: 10–15.1–24 [13].

Recognition characters

Adult female. Body fusiform at full growth. Anterior spiracles each with a small to moderately large cluster of disc pores; posterior spiracle each with a smaller cluster. Perivulvar disc pores moderate in number. Dorsal macroducts in submedian and submarginal rows; submedian macroducts usually occurring on abd III–VI, absent occasionally on III and rarely on VI, usually 1 or 2 on VI; submarginal ones on III–V. Lateral macroducts on meso- and metathorax and abd I–III, rarely a few small ones on prothorax. Lateral gland spines on abd I–III, few on each segment, very small and occasionally absent on I. Marginal gland spines 1–3, usually 2, on abd IV. Median trullae sunken into pygidial apex almost entirely, divergent, basally united through a slender but distinct sclerosis, which is produced anteriorly beyond the bases of the trullae in an inverted V-shape; each trulla slender, serrate on mesal margin. Second trullae well developed; mesal lobule robust, flatly roundish on apical margin, basally with a pair of long linear scleroses extending anteriorly; lateral lobule smaller, but well represented. Third trullae with lobules replaced with serrate sections of pygidial margin.

Second instar female. Marginal macroducts 4 or 5 on each side, occurring on abd IV–VII or III–VII.

Chionaspis lithocarporum, n.sp. (Fig. 2, 3; 20, C, D)

Material examined

Collected in two montane localities, Ulu Kali and the Cameron Highlands, in Pahang, Malaya, on *Lithocarpus* spp. (Fagaceae) including *L. kingianus* and *L. cyclophorus*.

Sample 1–5: Ulu Kali, alt. ca. 1700m, 28.XI.1985 (Sample 1); 23.IX.1986 (on *L. kingianus*, Sample 2); 5.X.1986 (Sample 3); 15.XI.1986 (Sample 4, 5). Sample 6 and 7: Tanah Rata, Cameron Highlands, alt. ca. 1500m, 30.XI.1985 (Sample 6); 13.X.1986 (on *L. cyclophorus*, Sample 7). Adult females examined: 155 individuals in total. Holotype: adult female specimen from Sample 1.

Females and males occurring on the upper surface of leaves, females often along the midrib. Female tests elongate, thin and translucent.

Wax-secreting organs in adult females

Spiracular disc pores. Associated with each anterior spiracle: 9–11.3–15 [n=27]

<Sample 1>; 6–9.7–14 [27] <2>; 7–10.9–18 [28] <3>; 6–10.6–15 [16] <4>; 7–10.8–19 [13] <5>; 4–6.6–10 [26] <6>; 2–4.0–7 [52] <7>. With each posterior spiracle: 1–3.5–8 [59] <1>; 1–2.8–4 [42] <2>; 2–3.8–5 [58] <3>; 2–4.1–7 [26] <4>; 2–4.2–5 [25] <5>; 0 [2], 1–1.9–3 [26] <6>; 0 [4], 1 [40], 2 [11], 3 [2] <7>.

Perivulvar disc pores. In median group: 6–16 <Sample 1>; 8–15 <2>; 8–16 <3>; 8–16 <4>; 8–16 <5>; 7–10 <6>; 7–14 <7>. In each anterolateral group: 13–26 <1>; 13–26 <2>; 17–27 <3>; 17–28 <4>; 18–26 <5>; 14–24 <6>; 11–20 <7>. In each posterolateral group: 13–30 <1>; 12–24 <2>; 11–22 <3>; 15–23 <4>; 14–24 <5>; 9–16 <6>; 7–16 <7>. Total: 68–85.7–105 [*n*=30] <1>; 67–84.6–103 [20] <2>; 80–93.7–109 [30] <3>; 83–96.3–108 [12] <4>; 85–91.9–101 [14] <5>; 58–68.8–80 [13] <6>; 46–60.9–80 [30] <7>.

Dorsal macroducts. Submedian macroducts occurring on abd III–V usually and on VI very rarely; submarginal macroducts on III–V.

<Sample 1>. Submedian macroducts: 1–3 on III; 1–4 on IV; 0 [*n*=1], 1 [18], 2 [41] on V. Submarginal macroducts: 2–7 on III; 1–5 on IV; 2 [32], 3 [28] on V. Total: 25–30.9–35 [30].

<2>. Submedian macroducts: 1–3 on III; 1–3 on IV; 0 [1], 1[33], 2 [8] on V. Submarginal macroducts: 1–5 on III; 2–4 on IV; 1–3 on V. Total: 23–25.5–30 [21].

<3>. Submedian macroducts: 0 [4], 1–3 [56] on III; 1–3 on IV; 1–3 on V. Submarginal macroducts: 3–7 on III; 3–6 on IV; 1–3 on V. Total: 22–31.3–44 [30].

<4>. Submedian macroducts: 0 [1], 1–8 [25] on III; 0 [1], 1–7 [25] on IV; 0 [2], 1–5 [23] on V; 0 [20], 1[4], 2 [1] on VI. Submarginal macroducts: 3–11 on III; 2–8 on IV; 2–6 on V. Total: 26–35.1–81 [12].

<5>. Submedian macroducts: 1–3 on III; 1–3 on IV; 1 [11], 2 [18] on V. Submarginal macroducts: 3–5 on III; 2–4 on IV; 1–3 on V. Total: 25–29.6–33 [14].

<6>. Submedian macroducts: 0 [4], 1–3 [24] on III; 0 [1], 1 [17], 2 [10] on IV; 0 [1], 1 [21], 2 [6] on V. Submarginal macroducts: 1–4 on III; 2 [12], 3 [14] on IV; 1–3 on V. Total: 11–20.5–27 [13].

<7>. Submedian macroducts: 0 [11], 1 [34], 2 [9], 3 [2] on III; 1 [33], 2 [23] on IV; 1 [44], 2 [12] on V. Submarginal macroducts: 1–4 on III; 1–4 on IV; 1–3 on V. Total: 11–21.1–31 [27]

In addition to the macroducts given above, there occur microducts on the dorsal surface of the abdomen not always but frequently. These microducts are variable in number and in the extent of occurrence. When abundant, they occur on the first to fourth abdominal segments submedially and on the first and second segments submarginally (Fig. 3, A). More often, they are not numerous and irregularly scattered.

Lateral macroducts. Occurring on metathorax to abd III, occasionally absent on metathorax; occurring also on mesothorax very rarely.

<Sample 1>. 2–5 on metathorax; 3–7 on I; 3–6 on II; 2–5 on III. Total: 23–32.4–37 [*n*=30].

<2>. 0 [2], 1–5 [40] on metathorax; 3–6 on I; 3–6 on II; 1–4 on III. Total: 22–29.1–37 [21].

<3>. 1–6 on metathorax; 3–8 on I; 4–6 on II; 2–4 on III. Total: 26–33.0–43 [30].

<4>. 0 [21], 1 [1], 2[2] on mesothorax; 2–6 on metathorax; 3–9 on I; 4–7 on II; 2–10 on III. Total on metathorax to III: 29–33.2–58 [12].

<5>. 1–5 on metathorax; 1–7 on I; 3–6 on II; 3 [27], 4 [3] on III. Total: 23–31.1–39 [14].

<6>. 0 [1], 1–4 [25] on metathorax; 2–5 on I; 2–5 on II; 1–4 on III. Total: 18–25.6–30 [13].

<7>. 0 [4], 1–5 [49] on metathorax; 1–4 on I; 2–4 on II; 1–4 on III. Total: 12–23.8–30 [23].

Gland spines. Lateral gland spines on abd I–III, sometimes absent on I; a rudimentary lateral gland spine occurring on metathorax occasionally; marginal gland spines on IV–VIII, single on V– VIII.

<Sample 1>. 1–3 on I; 1–4 II; 2–5 on III; 2–4 on IV. Total on I–IV: 18–23.1–27 [*n*=29].

<2>. 0 [1], 1–3 [41] on I; 1–5 on II; 3–5 on III; 2–4 on IV. Total on I–IV: 17–22.8–29]21].

<3>. 1–3 on I; 2–5 on II; 3–6 on III; 2–4 on IV. Total on I–IV: 19–25.0–28 [30].

<4>. 0 [1], 1–3 [23] on I; 2–4 on II; 2–5 on III; 3 [23], 4 [1] on IV. Total on I–IV: 19–22.8–26 [12].

<5>. 0 [1], 1–3 [28] on I; 1–5 on II; 3–5 on III; 2 [3], 3 [27] on IV. Total on I–IV: 20–23.6–29 [14].

<6>. 0 [13], 1 [7], 2 [6] on I; 1–4 on II; 2–4 on III; 1–4 on IV. Total on I–IV: 13–17.3–23 [13].

<7>. 0 [16], 1–3 [38] on I; 1–4 on II; 2–5 on III; 2 [39], 3 [15] on 1V. Total on I–IV: 10–17.3–27 [24].

Recognition characters

Adult female. Body growing to be much elongated and nearly parallel-sided, becoming about twice to thrice as long as wide. Anterior spiracles each with a cluster of disc pores variable in number and tending to form an arched row; posterior spiracles each with a much smaller cluster, at times without disc pores. Perivulvar disc pores moderate in number. Submedian macroducts occurring on abd III–V but not always on all of these segments, few on each segment usually; occurring also on VI very rarely. Submarginal macroducts on III–V, few to rather numerous on each segment. Lateral macroducts occurring on metathorax to abd III usually, a few to several ones on each segment; a few on mesothorax very rarely. Lateral gland spines on abd I–III but at times none on I. Marginal gland spines 1–4 on abd IV. Median trullae sunken into pygidium almost entirely, divergent, basally united through a distinct sclerosis, which is produced anteriorly much beyond the bases of the trullae in an inverted V-shape; each trulla narrow, serrate on mesal margin. Second trullae well developed; mesal lobule oblong, lateral lobule smaller. Third trullae with mesal lobule well developed, lateral lobule represented by a serrate process.

Second instar female. Marginal macroducts 4 on each side, occurring on abd IV–VII.

Chionaspis quercea, n.sp. (Fig. 4)

Material examined

Collected on Tanah Rata, alt. ca. 1400m, Cameron Highlands, Pahang, Malaya, on *Quercus lineata* (Fagaceae), 14.X.1986, Sample 1; 17.X.1986, Sample 2. Adult females examined: 30 individuals from Sample 1 and another 30 from Sample 2. Holotype: adult female specimen from Sample 2.

Females and males occurring on the lower surface of leaves. Females burrowing under a thin upper layer of the epidermis, tests elongate, thin, and translucent.

Wax-secreting organs in adult females

Spiracular disc pores. Associated with each anterior spiracle: 1–3.6–6 [*n*=50] <Sample 1>; 1–3.3–6 [40] <2>. None with posterior spiracles.

Perivulvar disc pores. In median group: 5–12 <Sample 1>; 5–13 <2>. In each anterolateral group: 9–17 <1>; 8–16 <2>. In each posterolateral group: 7–13 <1>; 7–12 <2>. Total: 43–53.9–62 [*n*=30] <1>; 42–51.9–63 [30] <2>.

Dorsal macroducts. Absent submedially. Submarginal macroducts occurring on abd III and IV usually and on V occasionally.

<Sample 1>. Submarginal macroducts: 0 [*n*=6], 1 [46], 2 [8] on III; 0 [1], 1 [31], 2 [28] on IV; 0 [56], 1 [4] on V. Total: 2–5.0–8 [30].

<2>. Submarginal macroducts: 0 [1], 1 [48], 2 [11] on III; 1 [38], 2 [22] on IV; 0 [57], 1 [3] on V. Total: 2–5.1–8 [30].

Lateral macroducts. Occurring on metathorax and abd I–III, bu not always on all of them.

<Sample 1>. 0 [*n*=56], 1 [4] on metathorax; 0 [3], 1 [48], 2 [8] on I; 1 [18], 2 [39], 3 [2] on II; 1 [20], 2 [39] on III. Total: 6–9.1–13 [28].

<2>. 0 [29], 1 [30] on metathorax; 0 [1], 1 [56], 2 [2] on I; 1 [35], 2 [24] on II; 0 [1], 1 [38], 2 [21] on III. Total: 6–8.2–12 [28].

Gland spines. Lateral gland spines occurring on abd II and III usually and on I very rarely; marginal gland spines on IV–VIII, single on V–VIII.

<Sample 1>. 0 [*n*=7], 1 [42], 2 [8] on II; 1 [9], 2 [47], 3 [3] on III; 2 [59] on IV. Total on II–IV: 8–9.9–13 [26].

<2>. 0 [59], 1 [1] on I; 0 [1], 1 [38], 2 [19] on II; 1 [1], 2 [56], 3 [2] on III; 1 [3], 2 [56] on IV. Total on II–IV: 6–9.9–13 [28].

Recognition characters

Adult female. Body growing to be much elongated and nearly parallel-sided. Anterior spiracles each with disc pores usually few; posterior spiracles without disc pores. Perivulvar disc pores not numerous. Dorsal macroducts usually restricted to a few ones occurring submarginally on each of abd III and IV, occasionally absent on III or on both III and IV; 1 submarginal macroduct occurring on V very rarely. Lateral macroducts occurring on abd I–III but not always on all of these segments, few on each of them; 1 present or absent on metathorax. Lateral gland spines occurring on abd II and III and few on each of the segments, occasionally absent on II; 1 lateral gland spine on I very rarely. Marginal gland spines usually 2, occasionally 1, on abd IV. Median trullae sunken into pygidium almost entirely, divergent, basally united through a small but distinct sclerosis, which is produced anteriorly beyond the bases of the trullae; each trulla large and elongate, serrate on mesal margin. Second trullae well represented; mesal lobule broadly roundish on apical margin, the lateral smaller. Third trullae with lobules replaced with serrate sections of pygidial margin.

Second instar female. Marginal macroducts 4 on each side, occurring on abd IV–VII.

Chionaspis oligocera, n.sp. (Fig. 5)

Material examined

Collected on Tanah Rata, alt. ca. 1500m, Cameron Highlands, Pahang, Malaya, on *Lithocarpus* sp. (Fagaceae), 20.X.1986. Adult females examined: 38 individuals. Holotype: adult female specimen.

Females occurring on the lower surface of leaves, burrowing under a thin upper layer of the epidermis; tests very thin and translucent.

Wax-secreting organs in adult females

Spiracular disc pores. Associated with each anterior spiracle: 0 [*n*=1], 1–2.7–5 [70]. None with posterior spiracles.

Perivulvar disc pores. In median group: 5–9. In each anterolateral group: 9–17. In each posterolateral group: 8–14. Total: 44–53.4–67 [*n*=38].

Dorsal macroducts. No macroducts have been observed in both submedian and submarginal areas in all the examined adult females.

Lateral macroducts. Occurring on abd II and III usually. 0 [n=72], 1 [4] on I; 0 [1], 1 [7], 2 [39], 3 [28] on II; 1 [1], 2 [16], 3 [59] on III. Total: 6–10.5–14 [37].

Marginal macroducts. 0 on abd III [*n*=76]; 1 [6], 2 [70] on IV; 2 on each of V and VI and 1 on VII [76].

Gland spines. Lateral gland spines occurring on abd II and III not always but frequently; marginal gland spines on IV–VIII and single on V–VIII. 0 [n=15], 1 [60] on II; 0 [4] 1 [72] on III; 1 [2], 2 [73] on IV. Total on II–IV: 5–7.2–8 [36].

Recognition characters

Adult female. Body growing to be much elongated and nearly parallel-sided. Anterior spiracles each with a few disc pores usually; posterior spiracles without disc pores. Dorsal macroducts absent both submedially and submarginally. Lateral macroducts occurring on abd II and III usually and on I occasionally, few on each segment. Marginal macroducts reduced in number to 7 or even 6 on each side, being absent on abd III always and in the outer position on IV sometimes. Lateral gland spines occurring frequently on abd II and III, single. Marginal gland spines much shortened on abd IV and V, usually 2 on IV. Median trullae sunken into pygidium almost entirely, divergent, basally united through a robust sclerosis, which is produced anteriorly beyond the bases of the trullae in an inverted V-shape; each trulla rather robust, serrate on mesal margin. Second trullae with both lobules well represented, the lateral lobule smaller than the mesal. Third trullae with lobules reduced into broad shortened processes, which are well sclerotized and serrate.

Second instar female. Marginal macroducts 3 on each side, belonging to V–VII.

Chionaspis rhombifera, n.sp. (Fig. 6, 7)

Material examined

Collected on Mt. Kinabalu, alt. ca. 1700m, Sabah, Borneo, on *Castanopsis acuminatissima* (Fagaceae), 12.X.1988. Adult females available: 16 individuals. Holotype: adult female specimen.

Females occurring on the lower surface of the leaves, burrowing under a thin upper layer of the epidermis.

Wax-secreting organs in adult females

Spiracular disc pores. Associated with each anterior spiracle: 2–7 [*n*=32] (2 [7], 3 [16], 4 [6], 5 [1], 6 [1], 7 [1]). None with posterior spiracles.

Perivulvar disc pores. In median group: 6–9. In each anterolateral group: 14–20. In each posterolateral group: 9–19. Total: 56–65.6–77 [*n*=16].

Dorsal macroducts. Absent submedially. Submarginal macroducts absent or few on abd III–V each: 0 [*n*=28], 1 [4] on III; 0 [3], 1 [23], 2 [5], 3 [1] on IV; 0 [30], 1 [2] on V. Total: 0 [1], 1–8 [15] (1 [1], 2 [9], 3 [1], 4 [3], 8 [1]).

Lateral macroducts. Occurring on abd I–III usually and on metathorax rarely. 0 [*n*=31], 1 [1] on metathorax; 3–6 [30] (3 [2], 4 [21], 5 [6], 6 [1]) on I; 3–5 [31] (3 [2], 4 [25], 5 [4]) on II; 2 [1], 3 [30] on III. Total: 21–22.6–27 [14].

Gland spines. Lateral gland spines occurring on abd I–III, at times absent on I. 0 [*n*=7], 1 [22], 2 [1] on I; 1–4 [31] (1 [5], 2 [23], 3 [2], 4 [1]) on II; 2 [21], 3 [10] on III. Total: 6–9.7–12 [15]. Marginal gland spines: 0 [4], 1 [28] on IV; 1 on each of V–VIII.

Recognition characters

Adult female. Body growing to be much elongated and nearly parallel-sided, becoming about thrice as long as wide. Anterior spiracles each with a small cluster of disc pores; posterior spiracles without disc pores. Perivulvar disc pores not numerous. Dorsal macroduct absent submedially; submarginal macroducts restricted to abd III–V and few on each, absent on III and V frequently and also on IV occasionally. Lateral macroducts occurring on abd I–III, rarely also on metathorax. Marginal macroducts in a complete set, occurring on abd III–VII. Lateral gland spines on abd I–III, occasionally absent on I. Marginal gland spines single and much shortened on abd IV and V, occasionally absent on IV. Median trullae with their posterior halves produced beyond pygidial margin, basally united through a strong sclerosis, which is produced anteriorly beyond the bases of the trullae in an inverted V-shape; each trulla robust, rhomboid, serrate along free margin. Second trullae with lobules small but distinct and sclerotized. Third trullae reduced into sclerotized processes.

Second instar female. Marginal macroducts 3 on each side, occurring on abd V–VII.

Chionaspis rhombiphora, n.sp. (Fig. 8, 9)

Material examined

Collected in montane localities in Malaya and Sabah on fagaceous plants.

Sample 1 and 2: Gg. Hijau via Bukit Larut, alt. ca. 1400m, Perak, Malaya, on unidentified trees of *Lithocarpus*, 8.X.1986. Sample 3–5: Mt. Kinabalu, alt. ca. 1500–1600m, Sabah, Borneo, on *Castanopsis* sp. (Sample 3), *Castanopsis acuminatissima* (Sample 4), and *Quercus gemilliflora* (Sample 5), 5–8.X.1988. Adult females available: 16 and 14 individuals from Sample 1 and 2; 23, 8, 26 from Sample 3, 4, and 5. Holotyp: adult female specimen from Sample 5.

Females and males occurring on the lower surface of leaves. Females burrowing under a thin upper layer of the epidermis; tests thin.

Wax-secreting organs in adult females

Spiracular disc pores. Associated with each anterior spiracle: 0 [*n*=1], 1–3 [26] (1 [15], 2 [6], 3 [5]) <Sample 1> ; 1–3 [25] (1 [2], 2 [12], 3 [11]) <2>; 2–3.3–6 [42] <3>;

2–4 [16] (2 [6], 3 [8], 4 [2]) <4>; 1–2.7–5 [52] <5>. None with posterior spiracles.

Perivulvar disc pores. In median group: 3–11 <Sample 1>; 5–8 <2>; 5–9 <3>; 4–8 <4>; 4–8 <5>. In each anterolateral group: 9–13 <1>; 10–13 <2>; 9–17 <3>; 10–16 <4>; 8–15 <5>. In each posterolateral group: 7–10 <1>; 7–9 <2>; 7–15 <3>; 7–12 <4>; 6–10 <5>. Total: 43–47.1–50 [*n*=16] <1>; 40–46.2–49 [14] <2>; 46–52.7–60 [23] <3>; 40–58 [8] <4>; 43–48.2–55 [26] <5>.

Dorsal macroducts. Absent submedially. Submarginal macroducts absent except for rare occurrence on abd IV or V: 0 [*n*=28], 1 [4] on abd IV <Sample 1>; 0 [38], 1 [8] on IV, 0 [45], 1 [1] on V <3>.

Lateral macroducts. Occurring on abd I–III.

<Sample 1>. 2 [*n*=2], 3 [25], 4 [5] on I; 3 [32] on II; 2 [3], 3 [29] on III. Total: 17–18.0–20 [16].

<2>. 2 [4], 3 [22], 4 [2] on I; 2 [2], 3 [24], 4 [2] on II; 2 [4], 3 [23], 4 [1] on III. Total: 14–17.6–19 [14].

<3>. 3 [31], 4 [12], 5 [2] on I; 2 [2], 3 [42], 4 [2] on II; 2 [2], 3 [44] on III. Total: 17–18.5–21 [22].

<4>. 2 [1], 3 [13], 4 [1] on I; 2 [2], 3 [13] on II; 3 [15], 4 [1] on III. Total: 17–19 [7] (17 [1], 18 [5], 19 [1]).

<5>. 1 [1], 2 [8], 3 [40], 4 [2] on I; 2 [4], 3 [45], 4 [1] on II; 1 [1], 2 [6], 3 [45] on III. Total: 14–17.3–19 [24].

Marginal macroducts. Absent on abd III in all the samples; outer one of the pair on IV and also on V rarely absent. 1 [*n*=1], 2 [31] on abd IV and also on V <Sample 1>; 1 [2], 2 [26] on IV <2>; 1 [2], 2 [44] on IV, 1 [1], 2 [45] on V <3>; 1 [1], 2 [51] on IV, (0 [1]: abnormality rather than normal variation?), 2 [51] on V <5>.

Gland spines. Lateral gland spines occurring on abd I–III, occasionally absent on I; marginal gland spines single on IV–VIII, rarely absent on IV.

<Sample 1>. 1 [*n*=26], 2 [6] on I; 1 [2], 2 [30] on II; 2 [32] III; 0 [2], 1 [30] on IV. Total on I–III: 9–10.3–12 [16].

<2>. 0 [2], 1 [24], 2 [2] on I; 1 [4], 2 [24] on II; 2 [28] on III. Total on I–III: 9–9.7–11 [14].

<3>. 0 [5], 1 [40], 2 [1] on I; 1 [2], 2 [44] on II; 2 [42], 3 [4] on III. Total on I–III: 7–9.9–11 [23].

<4>. 0 [3], 1 [10] on I; 1 [1], 2 [12] on II; 2 [15] on III. Total on I–III: 9 [1], 10 [3], 11 [1].

<5>. 0 [13], 1 [38] on I; 1 [12], 2 [39] on II; 1 [1], 2 [50], 3 [1] on III; 0 [1], 1 [51] on IV. Total on I–III: 5–9.0–10 [24].

Recognition characters

Adult female. Body growing to be much elongated and nearly parallel-sided, becoming about thrice as long as wide. Anterior spiracles each with disc pores usually few, rarely no disc pores. Posterior spiracles without disc pores. Perivulvar disc pores not numerous. Dorsal macroducts absent submedially and submarginally except for rare occurrence of a single submarginal one on abd IV or V. Lateral macroducts occurring on abd I–III, usually few on each. Abd III without marginal macroduct; pair of marginal macroducts on IV and also on V lacking the outer one at times. Lateral gland spines restricted to abd I–III, occasionally absent on I. Marginal gland spines single and much shortened on abd IV and V, rarely absent on IV. Median trullae with their posterior halves

produced beyond pygidial margin, basally united through a strong sclerosis, which is produced anteriorly beyond the bases of the trullae; each trulla robust, rhomboid, serrate along free margin. Second trullae with both lobules small but distinct and sclerotized. Third trullae reduced to serrate processes.

Second instar female. Marginal macroducts 3 on each side, occurring on abd V–VII.

Chionaspis sp.TR*L* (Fig. 10)

Material examined

Collected on Tanah Rata, alt. ca. 1500m, Cameron Highlands, Malaya, on *Lithocarpus* sp. (Fagaceae), 20.X.1986. Found together with individuals of *Chionaspis oligocera*. Mounted material includes 7 individuals of the adult female all not in good condition.

Females occurring on the lower surface of leaves, closely along veins; tests slender, very thin, and translucent.

Wax-secreting organs in adult females

Spiracular disc pores. Associated with each anterior spiracle: 0 [*n*=5], 1 [7]. None with posterior spiracles.

Perivulvar disc pores. In median group: 4 [*n*=7]. In each anterolateral group: 9 [7], 10 [7]. In each posterolateral group: 7 [1], 8 [12], 11 [1]. Total: 38 [1], 39 [4], 40 [1], 41 [1].

Dorsal macroducts. No macroducts in both submedian and submarginal areas.

Lateral macroducts. Occurring on abd I–III. 4 [*n*=9], 5 [3], 6 [2] on I; 3 [1], 4 [11], 5 [2] on II; 2 [1], 3 [12], 4 [1] on III. Total: 22 [4], 24 [1], 25 [2].

Marginal macroducts. 0 [*n*=14] on abd III; 2, 2, 2, 1 [14] on IV–VII.

Gland spines. Lateral gland spines occurring on abd I–III; marginal gland spines on IV–VIII, single on V–VIII. 2 [*n*=13] on abd I; 2 [12], 3 [1] on II; 2 [12] on III; 1 [2], 2[9] on IV. Total on I–IV: 15 [2], 16 [2] 17 [1].

Recognition characters

Adult female. Anterior spiracles with a single or no disc pore; posterior spiracles without disc pores. Perivulvar disc pores not numerous. Dorsal macroducts absent both submedially and submarginally. Abd III without marginal macroduct. Lateral macroducts and lateral gland spines occurring on abd I–III. Marginal gland spines shortened on abd IV and V, 1 or 2 in number on IV; those on VI and VII becoming broader basally. Median trullae with their posterior halves produced beyond pygidial margin, basally united through a sclerosis, which is produced anteriorly beyond the bases of the trullae in an inverted V-shape; each trulla robust, nearly rhomboid, serrate along free margin. Second and third trullae rudimentary, represented by minute processes.

Second instar female. Marginal macroducts 3 on each side, occurring on abd V–VII.

Chionaspis berincangensis, n.sp. (Fig. 11, 12)

Material examined

Collected on Gg. Berincang [Mt. Brinchang] (summit: 2031m), alt. ca. 2000m, Cameron Highlands, Pahang, Malaya, on an unidentified tree of *Lithocarpus* (Fagaceae), 16.X.1986, Sample 1; on an unidentified tree of *Lithocarpus*, 21.X.1986, Sample 2. Adult females examined: 30

individuals from Sample 1; 17 from 2. Holotype: adult female specimen from Sample 1.

Females and males occurring on the upper surface of leaves. Females mostly situated along midrib and other veins; female tests elongate, white and opaque.

Wax-secreting organs in adult females

Spiracular disc pores. Associated with each anterior spiracle (usually clustering together too closely): ca. 11–23 <Sample 1>; ca. 11–23 <2>. With each posterior spiracle: 7–13.0–16 [*n*=45] <1>; 8–10.9–16 [19] <2>.

Perivulvar disc pores. In median group: 14–32 <Sample 1>; 12–17 <2>. In each anterolateral group: 26–51 <1>; 22–37 <2>. In each posterolateral group: 17–31 <1>; 17–34 <2>. Total: 113–133.7–181 [*n*=30] <1>; 91–120.4–139 [17] <2>.

Dorsal macroducts. Submedian macroducts occurring on abd III–VI usually; submarginal macroducts on III–V.

<Sample 1>. Submedian macroducts: 1–6 on III; 2–6 on IV; 1–4 on V; 1–3 on VI. Submarginal macroducts: 7–14 on III; 5–11 on IV; 3–8 on V. Total: 60–69.9–89 [*n*=29].

<2>. Submedian macroducts: 1–5 on III; 1–4 on IV; 2–4 on V; 0 [2], 1–3 [32] on VI. Submarginal macroducts: 4–11 on III; 3–10 on IV; 2– 8 on V. Total: 32–55.7–67 [17].

In addition to the macroducts, there occur microducts on the dorsal surface of the abdomen not always but frequently. These microducts are greatly variable in number and in the extent of occurrence (Fig. 11, A; Fig. 12, A).

Lateral macroducts. Occurring on metathorax and abd I–III, occasionally also on mesothorax.

<Sample 1>. 0 [*n*=55], 1 [4], 4 [1] on mesothorax; 2–11 on metathorax; 5–13 on I; 3–9 on II; 3–8 on III. Total on metathorax to III: 34–54.3–71 [28].

<2>. 0 [27], 1 [4], 2 [1] on mesothorax; 3–10 on metathorax; 5–12 on I; 4–8 on II; 2–5 on III. Total on metathorax to III: 33–46.4–58 [17].

Gland spines. Lateral gland spines occurring on abd I–III; marginal gland spines variable in number on IV and V, single on VI–VIII.

<Sample 1>. 2–7 on I; 3–10 on II; 5–9 on III; 4–8 on IV; 1 [*n*=38], 2 [18], 3 [2] on V. Total on I–V: 37–47.0–57 [28].

<2>. 1–5 on I; 2–6 on II; 2–8 on III; 3–6 on IV; 1 [23], 2 [8], 3 [1] on V. Total on I–V: 32–36.9–45 [17].

Recognition characters

Adult female. Body growing to be elongated, about 2.5 times as long as wide, with prepygidial region gradually broader posteriorly, at full growth. Interantennal swelling often discernible. Anterior and posterior spiracles each with a compact cluster of disc pores. Dorsal macroducts in submedian and submarginal rows; submedian macroducts on abd III–VI, 1–3 or rarely absent on VI; submarginal macroducts on III–V, forming single or irregularly double rows. Lateral macroducts occurring on metathorax and abd I–III and occasionally also on mesothorax. Lateral gland spines on abd I–III, short on I and II, much elongated on III. Marginal gland spines strong on IV and V, 3–8 on IV, 1–3 on V. Median trullae largely produced beyond pygidial margin, set close together, basally united through a strong sclerosis, which is produced anteriorly much beyond the bases of the trullae; each trulla robust, broadly rounded along apical margin. Second trullae with lobules well developed, the lateral lobule smaller than the mesal. Third trullae with lobules represented by serrate processes.

Second instar female. Marginal macroducts 4 on each side, occurring on abd IV–VII.

Chionaspis kinabaluana, n.sp. (Fig. 13)

Material examined

Collected on Mt. Kinabalu, alt. ca. 1500m, Sabah, Borneo, on *Lithocarpus* sp. (Fagaceae), 13.X.1988. Adult females examined: 30 individuals. Holotype: adult female specimen.

Females and males occurring on the lower surface of leaves; females burrowing under a thin upper layer of the epidermis, the tests thin. Some individuals of both sexes were found on the upper surface of leaves, on which the females did not appear to be burrowing.

Wax-secreting organs in adult females

Spiracular disc pores. Associated with each anterior spiracle: 1–2.8–7 [*n*=60]. With each posterior spiracle: 0 [17], 1 [41], 2 [2].

Perivulvar disc pores: In median group: 4–16. In each anterolateral group: 8–16. In each posterolateral group: 7–13. Total: 47–53.3–61 [*n*=30].

Dorsal macroducts. Absent submedially. Submarginal macroducts occurring on abd III and IV, rarely absent on III: 0 [*n*=1], 1 [57], 2 [2] on III; 1 [57], 2 [3] on IV. Total: 3 [1], 4 [25], 5 [3], 6 [1].

Lateral macroducts. Occurring on metathorax and abd I–III, occasionally absent on metathorax and III. 0 [*n*=5], 1 [55] on metathorax; 2 [4], 3 [56] on I; 2 [10], 3 [49] on II; 0 [1], 1 [34], 2 [25] on III. Total: 14–16.2–18 [29].

Gland spines. Lateral gland spines occurring on abd I–III; marginal gland spines on IV–VIII, single on V–VIII. 1 [*n*=4], 2 [54], 3 [2] on I; 2 [59], 3 [1] on II; 1 [1], 2 [58], 3 [1] on III; 1 [2], 2 [58] on IV. Total on I–IV: 15 [5], 16 [23], 17 [1], 18 [1].

Recognition characters

Adult female. Body growing to be much elongated and nearly parallel-sided, becoming about thrice as long as wide. Interantennal swelling frequently discernible. Anterior spiracles each with a few or several disc pores; posterior spiracles each with 1 or 2 disc pores, at times with none. Perivulvar disc pores not numerous. Dorsal macroducts absent in submedian area; a few submarginal ones on each of abd III and IV, rarely none on III. Lateral macroducts on metathorax and abd I–III, few on each of the segments, rarely absent on metathorax or III. Lateral gland spines on abd I–III, few on each of the segments. Marginal gland spines well developed on abd IV and V, 2 or rarely 1 on IV. Median trullae largely produced beyond pygidial margin, basally separated from each other by a narrow space and united through a strong sclerosis, which is produced anteriorly beyond the bases of the trullae in an inverted V-shape; each trulla robust, broadly rounded apically, finely serrate marginally. Lateral trullae replaced with serrate sections of pygidial margin.

Second instar female. Marginal macroducts 4 on each side, occurring on abd IV–VII.

Chionaspis samatana, n.sp. (Fig. 14, 15)

Material examined

Collected on Samat Hill (top: 555m), Mt. Mariveles (summit: 1420m), Bataan Peninsula,

Luzón, *Lithocarpus* sp. (Fagaceae), 18.VIII.1994. The altitude of the collection spot was not recorded. Adult females examined: 30 individuals. Holotype: adult female specimen.

Females and males occurring on the lower surface of leaves. Female tests slender.

Wax-secreting organs in adult females

Spiracular disc pores. Associated with each anterior spiracle: 3–5.2–10 [*n*=56]. With each posterior spiracle: 1 [21], 2 [35], 3 [2], 4 [1].

Perivulvar disc pores. In median group: 3–5. In each anterolateral group: 8–12. In each posterolateral group: 6–10. Total: 35–40.4–44 [*n*=30].

Dorsal macroducts. Absent submedially. Submarginal macroducts occurring on abd III and IV, rarely absent on III. 0 [*n*=1], 1 [47], 2 [12] on III; 1 [43], 2 [17] on IV. Total: 3–4.9–8 [30].

Lateral macroducts. Occurring on metathorax and abd I–III, rarely absent on III. 4–7 on metathorax; 3–7 on I; 2–4 on II; 0 [*n*=2], 1 [56], 2 [2] on III. Total: 25–28.9–34 [26].

Gland spines. Lateral gland spines occurring on abd I–III; marginal gland spines on IV–VIII, single on V–VIII. 3–6 on I; 2–4 on II; 2 [*n*=43], 3 [17] on III; 2 [60] on IV. Total on I–IV: 18–21.9–25 [30].

Recognition characters

Adult female. Body growing to be much elongated and nearly parallel-sided, becoming about thrice as long as wide. Anterior spiracles each with a small cluster of disc pores; posterior spircles each with a few disc pores. Perivulvar disc pores not numerous. Dorsal macroducts absent submedially; a few submarginal ones on each of abd III and IV, rarely none on III. Lateral macroducts occurring on metathorax to abd III, rarely none on III. Lateral gland spines occurring on abd I–III. Marginal gland spines 2 on abd IV. Median trullae largely produced beyond pygidial margin, basally separated from each other by a narrow space and united through a distinct sclerosis, which is produced anteriorly to make a low prominence beyond the bases of the trullae; each trulla robust, rounded apically, serrate on both sides. Second trullae with lobules each represented by a small, slender, and membranous process. Third trullae replaced with serrate sections of pygidial margin.

Second instar female. Marginal macroducts 4 on each side, occurring on abd IV–VII.

Chionaspis glutae, n.sp. (Fig. 16)

Material examined

Collected on Ulu Kali, alt. ca. 1700m, Pahang, Malaya, on *Gluta* sp. (Anacardiaceae), 28.XI.1985. Mounted material includes 5 individuals of the adult female. Holotype: adult female specimen.

Adult females occurring on the upper surface of leaves.

Wax-secreting organs in adult females

Spiracular disc pores. Associated with each anterior spiracle: 2 [*n*=1], 3 [1], 10 [1], 13 [3], 14 [2]. With each posterior spiracle: 5–8.6–14 [10].

Perivulvar disc pores. In median group: 16–23. In each anterolateral group: 26–44.

In each posterolateral group: 18–29. Total: 115–169 [*n*=5].

Dorsal macroducts. Submedian macroducts occurring on abd IV and V and occasionally also on III; submarginal macroducts on III–V. Submedian macroducts: 0 [*n*=7], 1 [3] on III; 1 [1], 2 [9] on IV; 1 [10] on V. Submarginal macroducts: 2 [1], 3 [7], 4 [2] on III; 0 [1], 3 [7], 4 [2] on IV; 1 [3], 2 [6], 3 [1] on V. Total: 17–24 [5].

Lateral macroducts. Occurring on metathorax and abd I–III. 4–7 on metathorax; 6–8 on I; 5–7 on II, 3–6 on III. Total: 38–52 [*n*=5].

Gland spines. Lateral gland spines on abd I–III; 2 gland spines, much reduced in size, were observed twice on the metathorax. Marginal gland spines variable in number on IV, single on V–VIII. 1 [*n*=2], 2 [8] on I; 2 [3], 3 [6] 4 [1] on II; 3 [3], 4 [5], 5 [2] on III; 3 [2], 4 [7], 5 [1] on IV. Total on I–IV: 22–28 [5].

Recognition characters

Adult female. Body narrowly fusiform. Anterior and posterior spiracles each with a cluster of disc pores, which are variable in number rather broadly. Dorsal macroducts occurring on abd III–V, few both submedially and submarginally, often absent submedially on III. Lateral macroducts occurring on metathorax and abd I–III. Lateral gland spines occurring on abd I–III. Marginal gland spines 3–5 on abd IV. Median trullae largely sunken into pygidium with their certain apical parts produced, robust, with mesal margins set close to each other on basal halves and divergent and serrate on apical halves, basally united through a sclerosis, which is produced anteriorly to make a low prominence beyond the bases of the trullae. Second and third trullae with both lobules well developed.

Second instar female. Marginal macroducts 4 on each side, occurring on abd IV–VII.

Chionaspis melastomatis, n.sp. (Fig. 17)

Material examined

Collected on Mt. Kinabalu and Gg. Rinangsan (near Mt. Kinabalu), Sabah, Borneo, on unidentified plants of *Melastoma* (Melastomataceae).

Mt. Kinabalu, alt. ca. 1900m, 29.IX.1988, Sample 1; Mt. Kinabalu, alt. ca. 1500m, 5.X.1988, Sample 2; Gg. Rinangsan, alt. 1300–1400m, 8.XI.1988, Sample 3. Adult females available: 18, 24, and 18 individuals from Sample 1, 2, and 3. Holotype: adult female specimen from Sample 2.

Females and males occurring on the lower surface of leaves.

Wax-secreting organs in adult females

Spiracular disc pores. Associated with each anterior spiracle: 3–6.4–10 [*n*=32] <Sample 1>; 4–6.9–12 [39] <2>; 3–7.2–13 [30] <3>. With each posterior spiracle: 0 [2], 2–3.0–4 [32] <1>; 0 [1], 1–2.8–4 [44] <2>; 2 [19], 3 [9], 4 [5] <3>.

Perivulvar disc pores. In median group: 5–10 <Sample 1>; 5–9 <2>; 5–8 <3>. In each anterolateral group: 9–13 <1>; 7–13 <2>; 8–13 <3>. In each posterolateral group: 7 [4], 8 [32] <1>; 6–9 <2>; 6–13 <3>. Total: 42–45.0–48 [*n*=18] <1>; 41–44.3–48 [24] <2>; 42–46.1–53 [18] <3>.

Dorsal macroducts. Submedian macroducts occurring on abd III–VI and submarginal ones on III–V, but not always on all of these segments.

<Sample 1>. Submedian macroducts: 0 [*n*=30], 1 [5] on III; 1 [13], 2 [20], 3 [1] on IV; 1 [7], 2 [20] 3 [8] on V; 1 [18], 2 [16], 3 [1] on VI. Submarginal macroducts: 1 [9], 2 [19], 3 [7] on III; 2 [29], 3 [4] on IV; 1 [3], 2 [30], 3 [2] on V. Total: 15–22.5–27 [15].

<2>. Submedian macroducts: 0 [38], 1[9], 2 [1] on III; 1 [9], 2 [32], 3 [7] on IV; 0 [1], 1 [9], 2 [12], 3 [24], 4 [2] on V; 1 [21], 2 [27] on VI. Submarginal macroducts: 0 [1], 1 [7], 2 [35], 3 [4] on IV; 1 [10], 2 [32], 3 [6] on V. Total: 12–24.0–29 [23].

<3>. Submedian macroducts: 0 [10], 1 [15], 2 [9], 3 [2] on III; 0 [1], 1 [2], 2 [26], 3 [7] on IV; 1 [10], 2 [12], 3 [14] on V; 0 [1], 1 [5], 2 [30], on VI. Submarginal macroducts: 0 [1], 1 [2], 2 [12], 3 [16], 4 [4], 5 [1] on III; 2 [19], 3 [14] on IV; 1 [2], 2 [29], 3 [5] on V. Total: 22–28.6–36 [16].

Lateral macroducts. Occurring on mesothorax to abd III.

<Sample 1>. 2–7 on mesothorax; 5–11 on metathorax; 5–11 on I; 3–7 on II; 2–4 on III. Total: 46–55.4–69 [*n*=17].

<2>. 2–7 on mesothorax; 5–12 on metathorax; 4–9 on I; 3–7 on II; 2–4 on III. Total: 38–52.1–64 [24].

<3>. 1–4 on mesothorax; 5–11 on metathorax; 4–8 on I; 3–7 on II; 2–4 on III. Total: 42–49.1–59 [16].

Gland spines. Lateral gland spines occurring on abd II and III frequently. Marginal gland spines variable in number on IV, single on V–VIII.

<Sample 1>. 0 [*n*=9], 1 [24], 2 [1] on II; 0 [1], 1 [31], 2 [3] on III; 1 [3], 2 [31], 3 [1] on IV. Total on II–IV: 6–7.6–10 [16].

<2>. 0 [29], 1 [18] on II; 0 [3], 1 [40], 2 [4] on III; 0 [1], 1 [8], 2 [37], 3 [1] on IV. Total on II–IV: 3–6.4–8 [23].

<3>. 0 [5], 1 [29] on II; 1 [32], 2 [4] on III; 1 [4], 2 [32] on IV. Total on II–IV: 6–7.6–10 [18].

Recognition characters

Adult female. Body fusiform, narrowing anteriorly on head, rounded along free margin of pygidium. Anterior spiracles each with a small cluster of disc pores; posterior spiracles each with a few disc pores, rarely with none. Perivulvar disc pores not numerous. Dorsal macroducts occurring in submedian and submarginal rows, few in each row; submedian macroducts on abd III–VI, absent frequently on III and rarely on the other segments; submarginal macroducts on abd III–V, rarely absent on III. Lateral macroducts occurring on mesothorax to abd III. Lateral gland spines few on abd II and III, absent on II occasionally and on III rarely. Marginal gland spines 1–3, or rarely absent, on abd IV; single gland spines occurring on abd V–VIII elongate and slender. Median trullae sunken into pygidium nearly entirely, divergent, basally united through a small sclerosis, which is curved in an inverted U- or V-shape; each trulla slender, serrate on mesal margin. Second trullae with both lobules well developed; mesal lobule with a pair of short linear scleroses basally. Third trullae replaced with serrate sections of pygidial margin.

Second instar female. Marginal macroducts 4 or 5 on each side, occurring on abd IV–VII or III–VII.

Chionaspis pogonantherae, n.sp. (Fig. 18, 19)

Material examined

Collected on the Cameron Highlands, Pahang, Malaya, on plants of the family Melastomataceae.

Gg. Berincang [Mt. Brinchang] (summit: 2031m), alt. ca. 2000m, on *Medinilla* sp., 16.X.1986, Sample 1; Tanah Rata, alt. ca. 1500m, on *Pogonanthera* sp., 13.X.1986, Sample 2. Adult females available from leaves: 8 individuals from Sample 1; 32 from Sample 2, 29 of them from leaf blades (Sample 2·Subsample 1: <2·1> in the list below) and 3 from petioles (Sample 2·Subsample 2: <2·2>). Holotype: adult female specimen from Sample 2·Subsample 1.

Females and males occurring on the lower surface of leaves, females also on the upper surface. In Sample 2, females were found mostly on the lower surface of leaves and along the midrib; leaf blades with scales were irregularly but so curved downward as to form a half-opened space enclosed within the lower surface.

Wax-secreting organs in adult females

Spiracular disc pores. Associated with each anterior spiracle: ca. 15–31 <Sample 1>; 15–20.9–29 [*n*=40] <2·1>; ca. 14–23 <2·2>. With each posterior spiracle: 6–8.2–13 [13] <1>; 2–8.0–13 [55] <2·1>; 4–9 <2·2>.

Perivulvar disc pores. In median group: 12–22 <Sample 1>; 9–18 <2·1>; 14, 16, 17 <2·2>. In each anterolateral group: 28–42 <1>; 23–39 <2·1>; 27–34 <2·2>. In each posterolateral group: 21–51 <1>; 15–34 <2·1>; 20–26 <2·2>. Total: 123–145.7–169 [*n*=7] <1>; 109–130.8–147 [29] <2·1>; 110, 127, 135 <2·2>.

Dorsal macroducts. Submedian macroducts occurring on abd III–VI; submarginal macroducts on III–V.

<Sample 1>. Submedian macroducts: 2–6 on III; 3–6 on IV; 1–3 on V; 1 [*n*=7], 2 [9] on VI. Submarginal macroducts: 4–9 on III; 4–7 on IV; 3–6 on V. Total: 47–54.8–64 [8].

<2·1>. Submedian macroducts: 1–6 on III; 2–6 on IV; 1–5 on V; 1–4 on VI. Submarginal macroducts: 5–10 on III; 4–8 on IV; 3–7 on V. Total: 47–57.8–70 [29].

<2·2>. Submedian macroducts: 2–4 on III; 3–4 on IV; 2 on V; 2 on VI. Submarginal macroducts: 6, 7 on III; 4–6 on IV; 3, 4 on V. Total: 51, 53, 57.

Lateral macroducts. Occurring on mesothorax to abd III.

<Sample 1>. 1–3 on mesothorax; 5–8 on metathorax; 5–8 on I; 4–9 on II; 2–5 on III. Total: 41–46.4–57 [*n*=7].

<2·1>. 1–4 on mesothorax; 5–9 on metathorax; 5–10 on I; 3–7 on II; 2–8 on III. Total: 38–47.9–61 [27].

<2·2>. 2, 3 on mesothorax; 4–7 on metathorax; 5–7 on I; 4, 5 on II; 3–5 on III. Total: 43, 44, 46.

Gland spines. Lateral gland spines occurring on abd I–III; a few ones, much reduced in size, on metathorax occasionally. Marginal gland spines variable in number on IV, single on V–VIII.

<Sample 1>. 1–3 on I; 2–4 on II; 3–5 on III; 2–4 on IV. Total on I–IV: 25–27.4–30 [*n*=7].

<2·1>. 1–5 on I; 3–6 on II; 3–8 on III; 2–6 IV. Total on I–IV: 27–33.5–39 [28].

<2·2>. 2–4 on I; 3–7 on II; 4–6 on III; 4, 5 on IV. Total on I–IV: 30, 36, 37.

Recognition characters

Adult female. Body fusiform at full growth. Anterior spiracles each with disc pores clustered in an arc; posterior spiracles each with a much smaller cluster. Perivulvar disc pores abundant. Dorsal macroducts occurring on abd III–VI submedially and III–V submarginally; 1–4 submedian macroducts on VI. Lateral macroducts occurring on mesothorax to abd III. Lateral gland spines occurring on abd I–III, a few ones present or absent on metathorax. Marginal gland spines 2–6 on abd IV. Median trullae sunken into pygidium nearly entirely, divergent, basally united through a sclerosis, which is produced anteriorly distinctly beyond the bases of the trullae in an inverted V-shape; each trulla narrow, roughly serrate on mesal margin. Second trullae with both lobules well developed, the mesal lobule basally with a pair of linear scleroses extending anteriorly, the lateral lobule somewhat smaller. Third trullae also well developed, the lateral lobule slanting on lateral margin.

Second instar female. Marginal macroducts 4 on each side, occurring on abd IV–VII.

Diagnostic table for distinguishing among the species

1(12). Median trullae sunken in pygidium, forming a distinct notch of an inverted V-shape at the apex of the latter.
2(3). Second and third trullae with both lobules well developed: *C. pogonantherae*.
3(2). Third trullae with lateral lobule represented by a serrate process.
4(5). Third trullae with mesal lobule well developed: *C. lithocarporum*.
5(4). Third trullae with both lobules represented by serrate processes.
6(9). Submedian macroducts present.
7(8). Median trullae with basal zygotic sclerosis slightly produced anteriorly beyond the bases of the trullae: *C. melastomatis*.
8(7). Median trullae with basal zygotic sclerosis well produced anteriorly beyond the bases of the trullae: *C. trigonobalani*.
9(6). Submedian macroducts absent.
10(11). Abd III with marginal macroduct: *C. quercea*.
11(10). Abd III without marginal macoduct: *C. oligocera*.
12(1). Median trullae robust, set close together, with apical parts distinctly produced beyond pygidial margin.
13(16). Dorsal macroducts occurring both submedially and submarginally.
14(15). Median trullae with basal zygotic sclerosis strongly produced anteriorly: *C. berincangensis*.
15(14). Median trullae with basal zygotic sclerosis a little produced anteriorly beyond the bases of the trullae: *C. glutae*.
16(13). Dorsal macroducts absent submedially or both submedially and submarginally.
17(22). Abd III with marginal macroduct.
18(21). Second trullae with both lobules small but distinct
19(20). Second trullae with both lobules sclerotized: *C. rhombifera*.
20(19). Second trullae with both lobules membranous: *C. samatana.*
21(18). Second and third trullae with both lobules replaced with serrate sections of pygidial margin: *C. kinabaluana*.
22(17). Abd III without marginal macroduct.
23(24). Second trullae with both lobules small but distinct: *C. rhombiphora*.
24(23). Second and third trullae represented by minute processes: *C*. TR*L*.

Local forms

C. lithocarporum as understood in the present study was collected at two widely separated localities in Malaya, Ulu Kali and the Cameron Highlands, and the samples are divisible into two local forms. The median trullae are somewhat shorter in the form from the Cameron Highlands (Fig. 20, C, D), and the main wax organs tend to be less numerous in the samples from this locality (*Wax-secreting organs in adult females* under *Chionaspis lithocarporum*, n.sp.). The two localities are about 135km distant from each other, with a range of mountains between them. Material from the intermediate area, when available, may indicate whether the local forms really belong to one and the same species.

C. rhombiphora was collected in Malaya on *Lithocarpus* and in Sabah on *Castanopsis* and *Quercus*. The allopatric forms show no obvious differences between them in their morphological characters in spite of the geographical segregation and the different host plants. This may partly be due to the wax-secreting organs which are reduced to form a simplified set in association with the burrowing habit.

Collection altitudes and host plants

Of the 13 species described in this paper, eight species were collected in montane localities at altitudes of about 1400–2000m in Malaya, five species (including one occurring in both Malaya and Sabah) were obtained also in montane forests at altitudes of about 1300–1900m in Sabah, and one species was taken on a hill not exceeding 555m in altitude but lying on a much higher mountain in Luzón.

Ten of these species including the one from Luzón (10/13 or ca. 77%) were collected from trees of Fagaceae (*Trigonobalanus*, *Lithocarpus*, *Quercus*, *Castanopsis*), another one from a plant of the family Anacardiaceae (*Gluta*), and the remaining two from plants of Melastomataceae (*Melastoma*, *Medinilla*, *Pogonanthera*).

Morphological comparisons

The 13 species were all collected from leaves of their host plants, no individuals of both sexes having been found on twigs or branches. Specimens were mounted from leaf blades except for Sample 2 of *C. pogonantherae*. In this sample, adult females were found not only on leaf blades but also on petioles, but there have been recognized no morphological differences between the specimens mounted from these subsamples. The comparisons made below, therefore, are not concerned with polyphenistic variation which takes place in association with different feeding sites on the host plant body in many species of *Chionaspis* occurring in the temperate region.

The 13 species are divisible into two groups on the basis of the median trullae in the adult females. In one of the groups, these trullae are deeply sunken into the apex of the pygidium and divergent, forming a distinct notch of an inverted V-shape in the latter. In the other group, these trullae are produced beyond the pygidial margin for about their posterior halves or certain apical parts, robust, set close together, leaving a slender space between their bases, and parallel or nearly so to each other.

The first group comprises *C. trigonobalani*, *C. lithocarporum*, *C. quercea*, and *C. oligocera*, species associated with fagaceous trees, and *C. melastomatis* and *C.*

pogonantherae, species feeding on melastomataceous plants. The second group consists of *C. rhombifera*, *C. rhombiphora*, *C.* sp.TR*L*, *C. berincangensis*, *C. kinabaluana*, and *C. samatana*, species occurring on fagaceous plants. *C. glutae*, which was collected from the anacardiaceous genus *Gluta* and has the median trullae largely sunken into the pygidium but robust and set close together, may be included in this group.

Three species from the first group, *C. trigonobalani*, *C. melastomatis*, and *C. pogonantherae*, are commonly characterized, and different from all the other species of the two groups, in having the median trullae slender and the lateral macroducts occurring through the meso- and metathorax and the first to third abdominal segments. They are provided with dorsal macroducts both submedially and submarginally. In all these characters they may represent relatively generalized or primitive forms among the 13 species. The second trullae are well represented in *C. trigonobalani* and *C. melastomatis*, and both the second trullae and the third trullae are well developed in *C. pogonantherae*.

The other three species of the first group have the median trullae somewhat elongated or broadened. Among them, *C. lithocarporum* is relatively generalized in having the lateral trullae well represented, the dorsal macroducts occurring both submedially and submarginally, and the lateral macroducts persisting on the metathorax and the first to third abdominal segments. The other two, *C. quercea* and *C. oligocera*, have the median trullae elongated or broadened, the third trullae practically obsolete, and the macroduct system (dorsal, lateral, and marginal macroducts) represented by a remarkably incomplete set, and thus are specialized especially in the last character. The females of these two species live under a thin upper epidermal layer on the lower surface of leaves, and their morphological specialization is undoubtedly associated with the burrowing habit.

The second group, in which the adult females are provided with robust and produced median trullae, also includes burrowing species: *C. rhombifera*, *C. rhombiphora*, and *C. kinabaluana*. These three species are similar to the burrowing species of the first group in having the lateral trullae reductive and the macroduct system noticeably incomplete. These features are also reductive or incomplete in *C. samatana* and remarkably so in *C.* sp.TR*L*. It is supposable, therefore, that these two species, too, burrow in the leaf epidermis. In my observations, however, no individuals on dry leaf material appeared to be burrowing in either species.

The other two species of the second group, *C. berincangensis* and *C. glutae*, have the lateral trullae and the macroduct system not particularly reductive or incomplete, and apparently do not burrow, occurring on the upper surface of leaves.

Supposed relations

C. trigonobalani and C. *melastomatis* from Sabah and *C. pogonantherae* from Malaya are similar to each other in spite of the host plants which are greatly different between the first and the latter two. It is possible that they are similar because they have generalized character patterns. It may also be possible that they are really closely related to each other. In the course of the present study, there has been found no substantial clue for proceeding with the question (see under *Northern connections* and *Second instar males*).

C. berincangensis from Malaya and *C. kinabaluana* from Sabah are very similar in the median trullae in spite of the fact that they have quite different modes of life on *Lithocarpus* leaves. They have the median trullae very robust and united by a prominent

zygotic sclerosis. On the other hand, they are remarkably different in the development of the lateral trullae and also of the macroduct system. It is possible to suppose that *C. berincangensis* represents or approaches a form ancestral to *C. kinabaluana*, which has greatly changed in association with the burrowing habit.

C. rhombifera and *C. rhombiphora*, both being leaf-burrowing species, are so closely similar to each other that they may be open to question as to their distinctness. They are distinguished almost exclusively by the presence (in *C. rhombifera*) and absence (in *C. rhombiphora*) of a marginal macroduct on each side of the third abdominal segment. The discrimination between the two species by the use of these characters has been made completely through all of the sympatric samples of these species from Mt. Kinabalu, Sabah, and the samples of *C. rhombiphora* from Gg. Hijau, Malaya. These characters are stable in all the samples examined irrespective of sympatry and allopatry. They are, therefore, not concerned with any of individual variation, local variation, and character displacement. The view is adopted that these species are well differentiated and distinct. It may reasonably be assumed that *C. rhombifera* is an immediate ancestor of *C. rhombiphora* and, in this connection, it should be emphasized that *C. rhombiphora* occurs not only in Sabah but also in Malaya.

The pair of *C. berincangensis* and *C. kinabaluana* and especially that of *C. rhombifera* and *C. rhombiphora* suggest that there have been interflows of montane forms between Malaya and Sabah. *C. samatana* from Luzón is very similar to *C. rhombifera* from Sabah. This similarity may simply due to convergence (see the paragraph below), but the possibility that there is a connection in some montane forms between these areas is not definitely excluded in the present state of study.

C. quercea and *C. oligocera*, the other burrowing species, find no particularly close species in the collection. *C.* sp.TR*L* and *C. samatana* have the macroduct system remarkably incomplete as in all the known burrowing species, and the possibility may not be excluded that they have also evolved in association with burrowing. Thus the *Chionaspis* fauna under study has an impressive proportion (5/13 or 7/13) of burrowing species. The pair of *C. berincangensis* and *C. kinabaluana* suggests the possibility that the other burrowing species, too, have evolved within the fauna. If the burrowing species except *C. kinabaluana* have a common ancestral form in the fauna, C. *lithocarporum* may be expected to represent or approach that form.

C. oligocera may be supposed to belong to *Aulacaspis*, having no lateral macroducts nor lateral gland spines anteriorly to the second abdominal segment except for rare cases where a single lateral macroduct occurs on the first segment (see the diagnostic description of *Aulacaspis* in Takagi, 1999). But these characters are undoubtedly due to a remarkable reduction of wax-secreting organs in association with the burrowing habit. *C. quercea* shows a tendency to the same state. These species have six-segmented antennae in the first instar. In *Aulacaspis* the antennae in this instar are five-segmented at least so far as the 'typical species' of the genus are concerned (Takagi, 2012).

Finally, *C. glutae* finds no particularly close relative among the other 12 species.

Northern connections

In the Himalayas, four species of *Chionaspis* are known to occur on fagaceous plants (Takagi, 1985). Three of them are especially similar to *C. lithocarporum* occurring in Malaya: *C. arkhola* Takagi, *C. castanopsidis* Takagi, and *C. himalaica* Takagi.

C. arkhola was collected in central Nepal at an altitude of about 2000m from

Lithocarpus elegans; the foliicolous form alone is known, occurring on the upper surface of leaves. In pygidial characters, it is distinguishable from *C. lithocarporum* in having the median trullae more divergent from each other and united by a much less prominent basal zygosis (Fig. 20). It is characterized in having the spiracular disc pores quadrilocular, whereas this type of disc pores is quite rare and extraordinary not only in the Diaspidini but also in the whole family. Generally speaking, when the occurrence of quadrilocular spiracular disc pores is only occasional among individuals, it is no more than an abnormal variation (see *Remarks* under *C. arkhola* and *C. himalaica* in Takagi, 1985), but if it is stable at the level of population, it is usable as a taxonomic character irrespective of its evolutionary significance. In the case of *C. arkhola*, the occurrence of quadrilocular spiracular disc pores is stable and may be useful for recognizing the species, but I do not think that it has further taxonomic value. The view is adopted that *C. arkhola* is a close relative of *C. lithocarporum* in spite of the unusual disc pores.

C. castanopsidis was collected in eastern Nepal at an altitude of about 2000m from *Castanopsis tribuloides*; the foliicolous form alone is known, occurring on the lower surface of leaves. It has the median trullae apparently larger than those in *C. arkhola* and *C. lithocarporum*, whereas it shows the third trullae reduced to serrate processes (Fig. 20).

C. himalaica was recorded from higher altitudes, about 2500–3000m, in association with *Quercus semecarpifolia*, and is probably broadly distributed along the Himalayan mountain range; it occurs on branches usually. In the adult female, it is especially similar to *C. arkhola*. Above all, it differs in the second instar female from both *C. arkhola* and *C. castanopsidis* and also from *C. lithocarporum* in having submarginal macroducts usually or normally.

I have little doubt that *C. lithocarporum* from Malaya is closely related to these three species from the Himalayas. I (Takagi, 1985) once supposed that these Himalayan species were related to *C. dryina* (=*Phenacaspis dryina* Ferris) occurring in Yunnan on *Quercus* and on leaves, and also to *C. saitamaensis* (=*Phenacaspis saitamaensis* Kuwana) occurring in Japan on various species of *Quercus* and usually on twigs and branches. In the present study, the speculation is made that *C. lithocarporum* represents a form ancestral to some leaf-burrowing species of *Chionaspis* occurring in Malaya and Sabah. If all these suppositions are correct, the montane fauna in the tropics under the present study is at least partly connectable with northern faunas occurring in the Himalayas and northeastern Asia.

Chen (1983) described three species of *Chionaspis* (one under *Phenacaspis*) as occurring on fagaceous plants in southern China. Among them, *C. agranulata* Chen and *C. obclavata* Chen are provided with robust and produced median trullae, which are similar to those in the Malayan species *C. berincangensis*. All these species agree in occurring on the upper surface of leaves and mainly on the midrib. The possibility, therefore, may not be excluded that the similarity among these species in the median trullae is due exclusively to convergence in association with the occurring site on the host leaves.

The discovery of *C. trigonobalani* from *Trigonobalanus verticillata* on Mt. Kinabalu is of special interest because of the host plant genus, which is a survival in the evolution and distribution of the Fagaceae. So far as I am aware, however, no species of *Chionaspis* are known in association with *T. verticillata* on Fraser's Hill, Malaya, and in Hainan Is. and with *Trigonobalanus doichangensis* in Chiang Rai, northern Thailand and Yunnan, southern China. Under these circumstances, there is no easy way to explain the occurrence of *C. trigonobalani* on Mt. Kinabalu in association with *T.*

verticillata. No close relations are easily detectable between *C. glutae*, *C. melastomatis*, and *C. pogonantherae* and species occurring in other parts of the world, where no species of *Chionaspis* have been recorded from plants of the families Anacardiaceae and Melastomataceae. It should be added here that *C. glutae* is very similar in the median and lateral trullae to *Chionaspis sozanica* Takahashi, which occurs on *Acer* (Aceraceae) in Taiwan and the Ryûkyû Islands.

Second instar males

In the present study, specimens of the second instar male have been available in eight species: *C. trigonobalani*, *C. lithocarporum*, *C. quercea*, *C. berincangensis*, *C. kinabaluana* (Fig. 21), *C. samatana*, *C. melastomatis* (Fig. 22), and *C. pogonantherae* (Fig. 23).

The second instar male of *C. kinabaluana* is provided with a continuous series of well-developed pectinate processes around the margin of, presumably, the fourth to eighth abdominal segments. *C. samatana* is very similar to *C. kinabaluana* in the development of the marginal processes. The other six species have the marginal processes less developed in various ways and rudimentary in general.

The eight species have peculiarly modified macroducts ('cup-like ducts' in authors) along the abdominal margin as in many other species of *Chionaspis*. In three of them, *C. trigonobalani*, *C. lithocarporum*, and *C. quercea*, there are four such ducts on each side of the abdomen. The anteriormost of these ducts is supposed to be situated on the second abdominal segment, the following two are set close together but presumed to belong to the third and fourth segments and, then, the posteriormost should be on the seventh segment. This pattern is seen in many *Chionaspis* species occurring in Japan and the Himalayan Region (Takagi, 1985).

Three other species, *C. berincangensis*, *C. kinabaluana*, and *C. samatana*, appear to differ from the above-mentioned three in having no modified macroduct on the second abdominal segment. There is a small duct at the position where the modified macroduct of the segment may be expected. The detailed structure of this small duct is hardly detectable owing to the size, but I am inclined now to believe that the duct does not belong to the usual two-barred type but represents a diminished type of the modified macroduct. (It should be added here that, among the species examined in the present study and provided with four modified macroducts on each side, *C. trigonobalani* has the duct occurring on the second abdominal segment sometimes becoming much smaller.) Similar small ducts occur on the fifth and sixth abdominal segments in all these six species, two or three ducts on the fifth segment and one on the sixth. They may also be diminished modified macroducts (see the case concerned in *C. melastomatis* mentioned below). When this supposition is adopted, it may reasonably be expected that more than one modified macroduct can occur at least on the fifth segment. In fact, this expectation is realized sufficiently enough in *C. pogonantherae* (see below).

C. melastomatis and *C. pogonantherae* are particular in the genus for their association with melastomataceous plants. They are noticeable especially for the occurring patterns of modified macroducts in their second instar males. *C. melastomatis* has six modified macroducts on each side of the abdomen, one on each of the second to seventh segments. It is noteworthy (in connection with the supposed occurrence of diminished modified macroducts on the fifth and sixth abdominal segments mentioned above) that in this species the modified macroducts occurring on the fifth and sixth

segments are sometimes remarkably reduced in size.

In *C. pogonantherae* (Sample 1, seven specimens examined), too, modified macroducts occur on all of the second to seventh abdominal segments but, in this species, more than one duct is seen on each of the third to sixth segments, and often also on the second, on either side of the abdomen. Nine patterns have been observed in their occurrence in number on the segments as formulated in the following lines, where the numbers are given in order of segment from the second to the seventh. Pattern I: 1–3–3–3–2–1 (13 ducts in total); II: 1–3–3–3–3–1 (14); III: 2–3–3–3–2–1 (14); IV: 1–3–3–4–3–1 (15); V: 2–3–3–3–3–1 (15); VI: 2–3–3–4–2–1 (15); VII: 2–3–4–3–2–1 (15); VIII: 2–3–3–3–4–1 (16); IX: 2–4–4–3–2–1 (16). These patterns occur in various combinations in individuals. The observed combinations are as follows: I+IV (28 ducts in total), II+VII (29), III+V (29), II+IX (30), V+VI (30), and V+VIII (31). After all, so far as observed, the second instar male of *C. pogonantherae* has modified macroducts variable in number from 13 to 16 on each side of the abdomen and from 28 to 31 in total for both sides. The patterns and their combinations observed in the present study with the limited number of specimens probably represent only part of the variation really occurring in the species.

C. melastomatis and *C. pogonantherae* are probably closely related to each other so far as based on their adult females and host plants. In morphological characters of the adult females, they are also very similar to *C. trigonobalani*, which is associated with the primitive fagaceous genus *Trigonobalanus*. In spite of the close similarities among the adult females, these three species exhibit three quite different types in the second instar males, thus affording another remarkable example of discrepancy between the stages of the adult female and the second instar male. Whether these three species are closely related or not, there should be, as a background for the discrepancy, much relaxed adaptive pressure on the phenotype in the stage of the second instar male in addition to the modular organization of genetic and developmental processes, a universal mechanism in organisms.

Number of the antennal segments in the first instar

In the present study, exuvial casts of the first instar, of the female or the male or of both, have been available except for *C.* sp.TR*L*. In these exuvial casts the antennae are six-segmented so far as based on specimens in good condition. In *C. glutae*, the examined exuvial casts are few and not good in condition, but I take the view that they also have six- segmented antennae.

References

Balachowsky, A.S., 1954. Les Cochenilles Paléarctiques de la Tribu des Diaspidini. Institut Pasteur.

Bodenheimer, F.S., 1951. Description of some new genera of Coccoidea. Entomologische Berichten, Amsterdam 13: 328–331.

Chen F.-G., 1983. The Chionaspidini (Diaspididae, Coccoidea, Homoptera) from China. [Sichuan Science and Technology Publishing House].

Liu, T.-X. and Kosztarab, M., 1987. Two new species of *Chionaspis* (Homoptera: Coccoidea: Diaspididae) from North America. Florida Entomologist 70: 512–520.

Liu, T.-X. and Kosztarab, M., 1989. Biosystematics of the adult females of the genus *Chionaspis* (Homoptera: Coccoidea: Diaspididae) of North America, with emphasis on polymorphism. Virginia Polytechnic Institute and State University Bulletin 88-2:

1–126.
Rao, V.P., 1953. Some New Diaspine Scale Insects from India. Proceedings of the Royal Entomological Society of London (B) 2: 61–68.
Takagi, S., 1985. The scale insect genus *Chionaspis*: A revised concept (Homoptera: Coccoidea: Diaspididae). Insecta Matsumurana New Series 33.
Takagi, S., 1999. For a better understanding of *Aulacaspis*: The *calcarata* species group (Homoptera: Coccoidea: Diaspididae). Insecta Matsumurana New Series 55: 133–180.
Takagi, S., 2012. Atypical species of *Aulacaspis* (Sternorrhyncha: Coccoidea: Diaspididae). Insecta Matsumurana New Series 68: 17-115.
Tang, F.-t., 1986. The Scale Insects of Horticulture and Forest of China, III. Shaanxi Agricultural University Press.
Vea, I.M., Gwiazdowski, R.A., and Normak, B.B., 2012. Corroborating molecular species diversity: Four new pine-feeding species of *Chionaspis* (Homoptera: Diaspididae). Zookeys 270: 37–58.
Williams, D.J. and Watson, G.W., 1988. The Scale Insects of the Tropical South Pacific Region, Part I. C·A·B International Institute of Entomology.

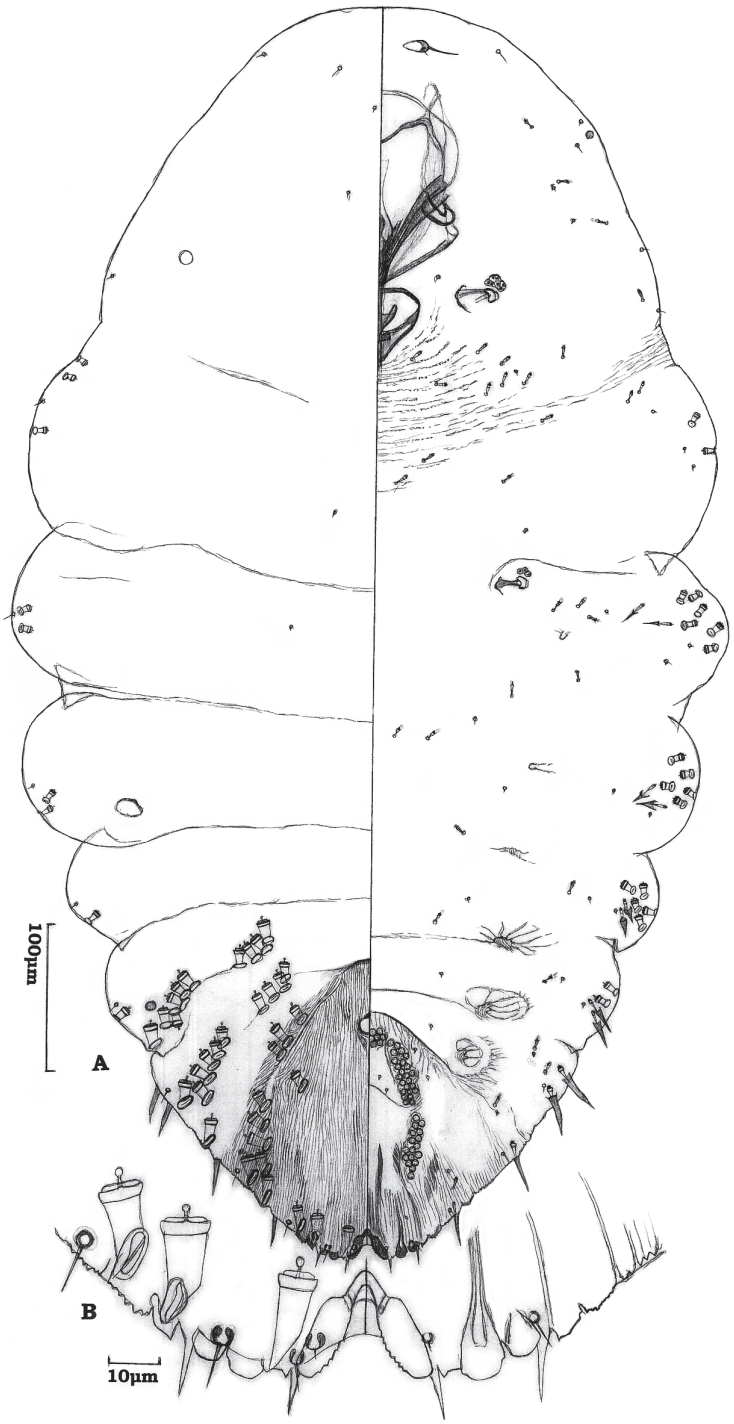

Fig. 1. *Chionaspis trigonobalani*, adult female. Sample 1: Mt. Kinabalu, Sabah, on *Trigonobalanus*. B, trullae.

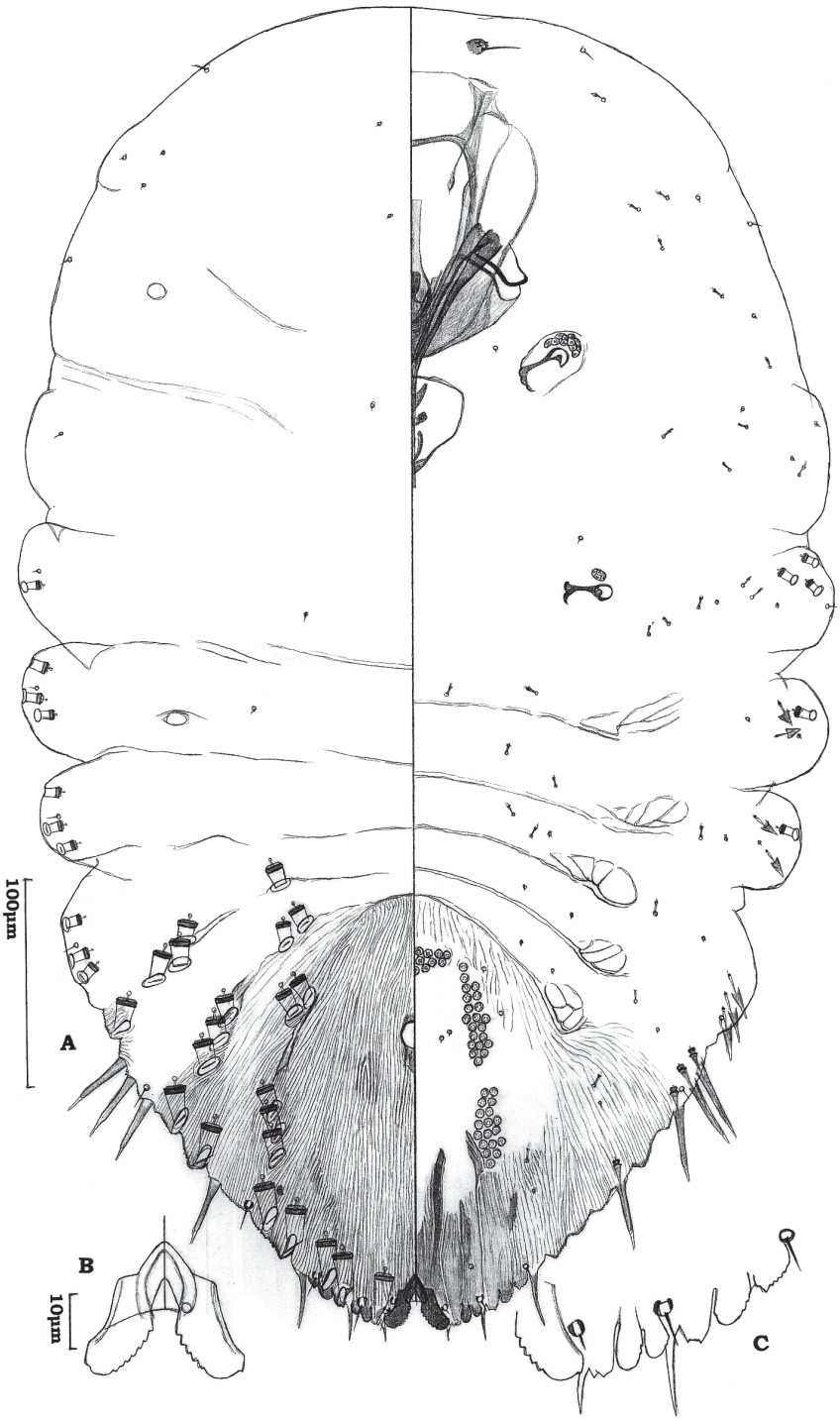

Fig. 2. *Chionaspis lithocarporum*, adult female. Sample 1: Ulu Kali, Malaya, on *Lithocarpus*. B, median trullae; C, lateral trullae. Scale bar: 10μm for B, C.

Fig. 3. *Chionaspis lithocarporum*, adult female. Sample 1: Ulu Kali, Malaya, on *Lithocarpus*. A, macroducts and microducts on dorsal surface of abdomen; B, dorsal microducts on abd III; C, pygidial margin; D, antenna; E, F, anterior and G, H, posterior spiracles on the same individual. Scale bar: 10µm for B–H.

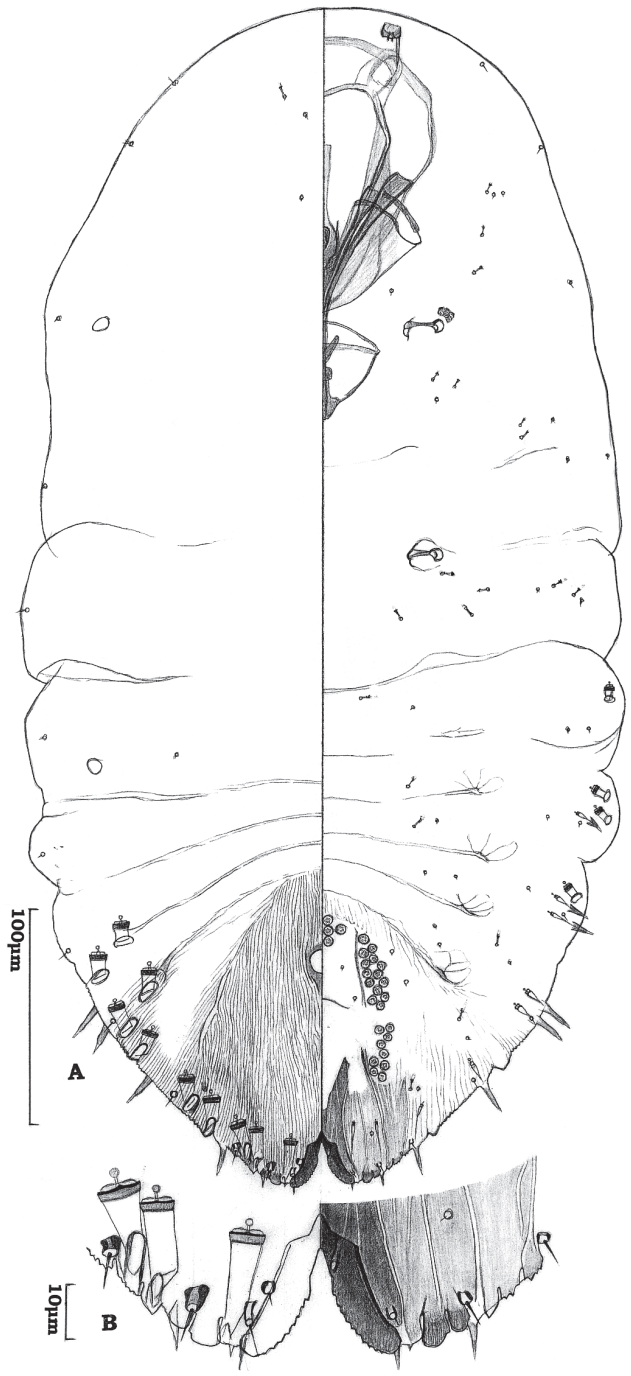

Fig. 4. *Chionaspis quercea*, adult female. Cameron Highlands, Malaya, on *Quercus*. B, trullae.

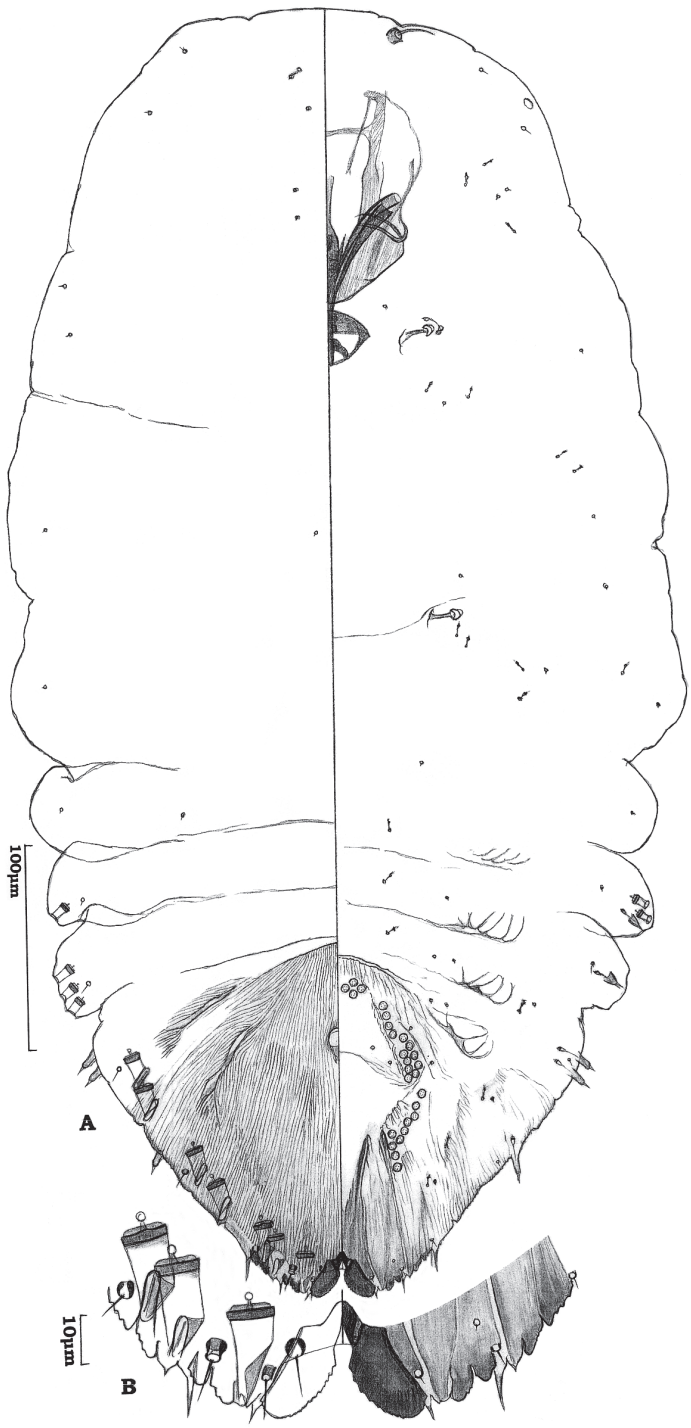

Fig. 5. *Chionaspis oligocera*, adult female. Cameron Highlands, Malaya, on *Lithocarpus*. B, trullae.

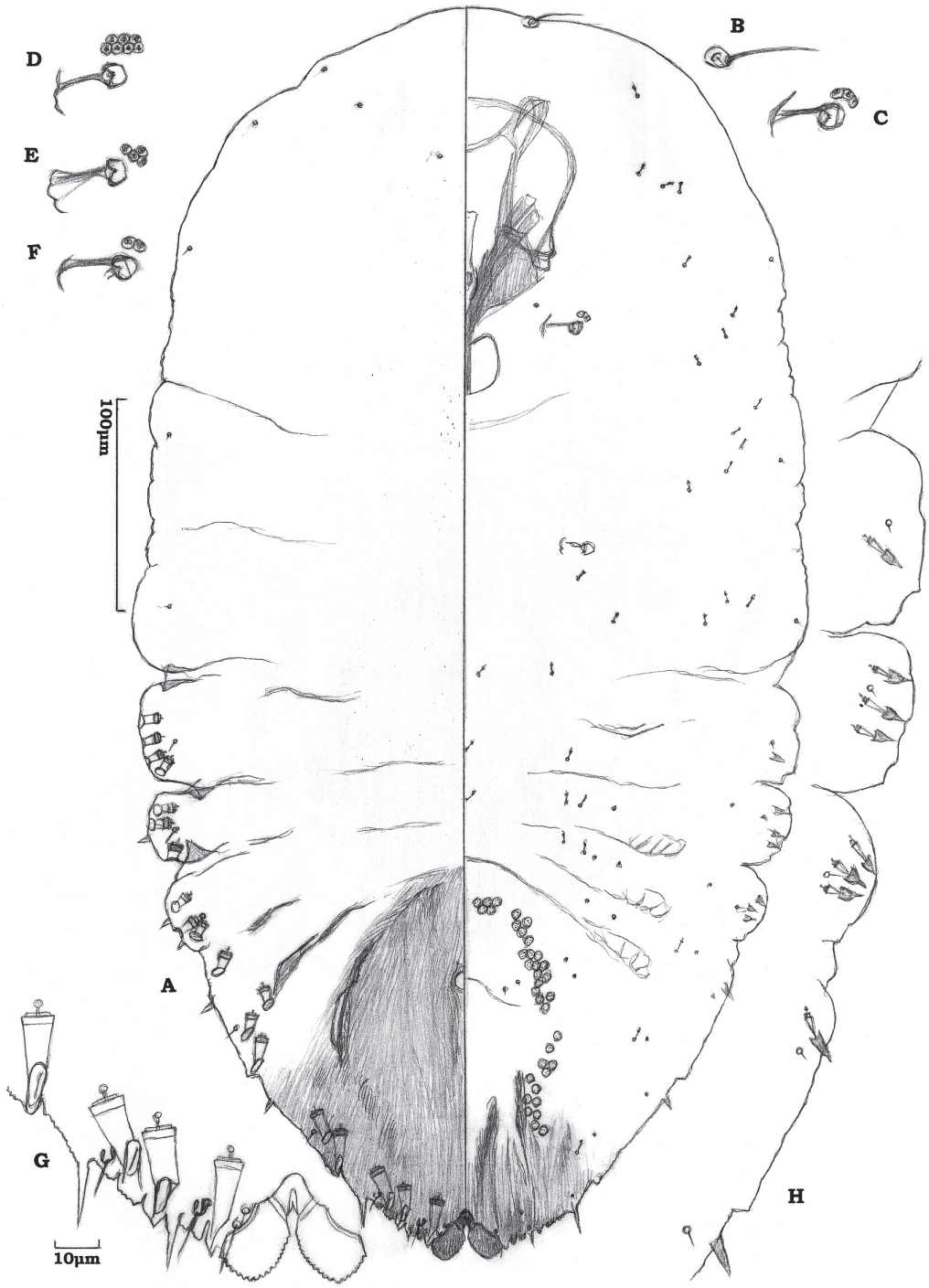

Fig. 6. *Chionaspis rhombifera*, adult female. Mt. Kinabalu, Sabah, on *Castanopsis*. B, antenna; C–F, anterior spiracles; G, trullae; H, gland spines on abd I–V. Scale bar: 10µm for B–H.

Fig. 7. *Chionaspis rhombifera*, adult female. Mt. Kinabalu, Sabah, on *Castanopsis*. A, abdomen; B–D, marginal and submarginal macroducts on abd III–V (B, D) or III–VII (C); E, trullae. Scale bar: 10µm for B–E.

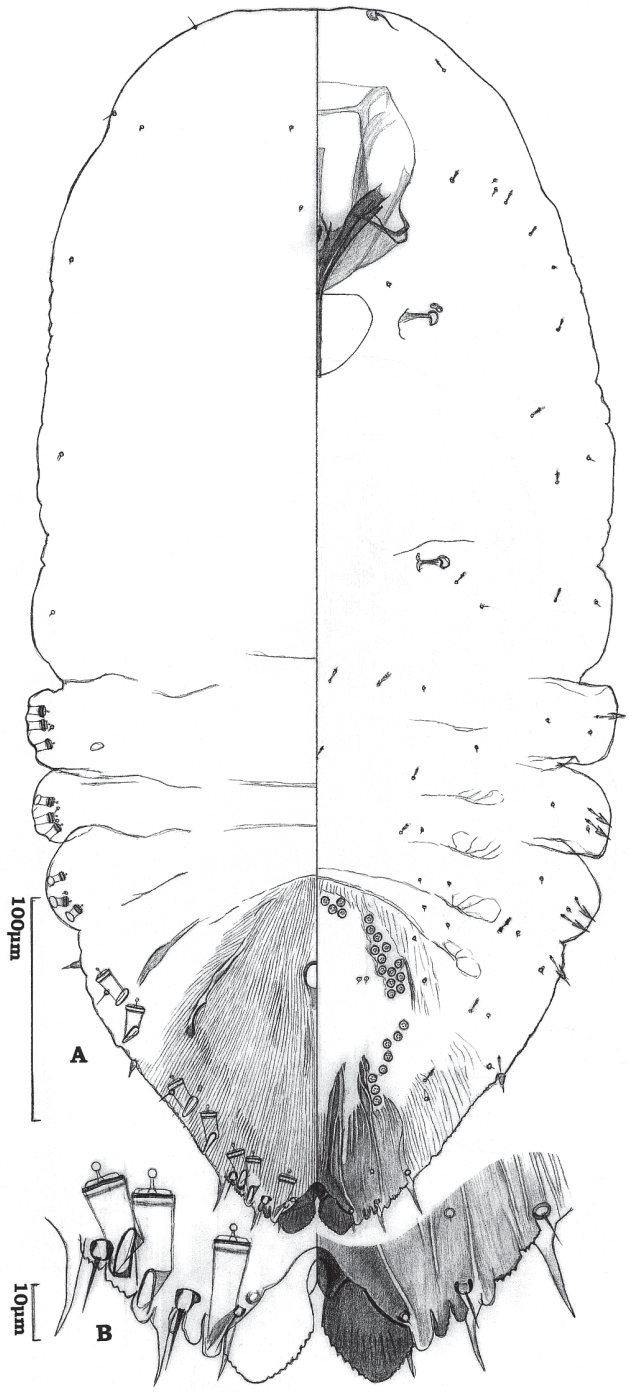

Fig. 8. *Chionaspis rhombiphora*, adult female. Gg. Hijau, Malaya, on *Lithocarpus*. B, trullae.

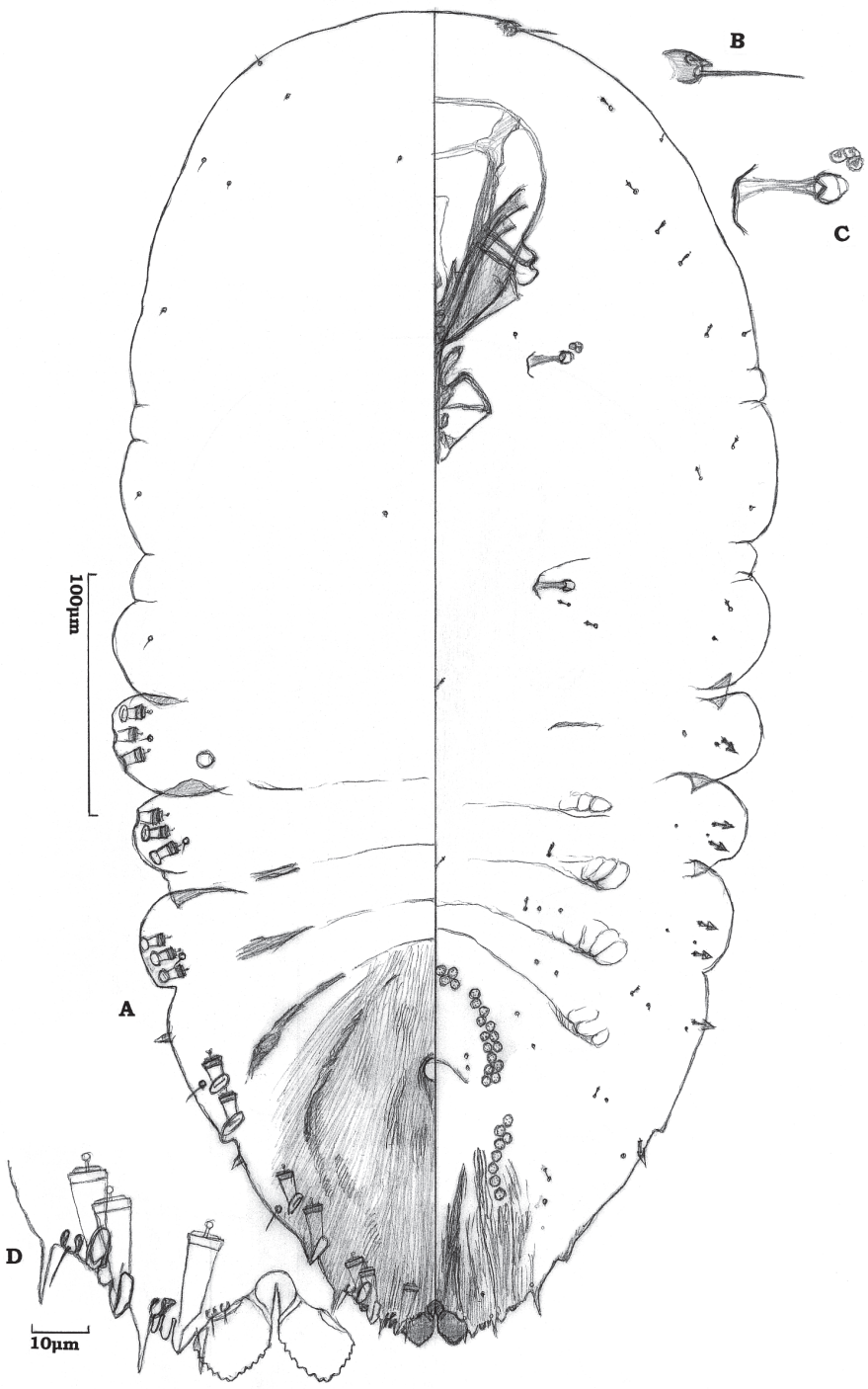

Fig. 9. *Chionaspis rhombiphora*, adult female. Mt. Kinabalu, Sabah, on *Quercus*. B, antenna; C, anterior spiracle; D, trullae. Scale bar: 10µm for B–D.

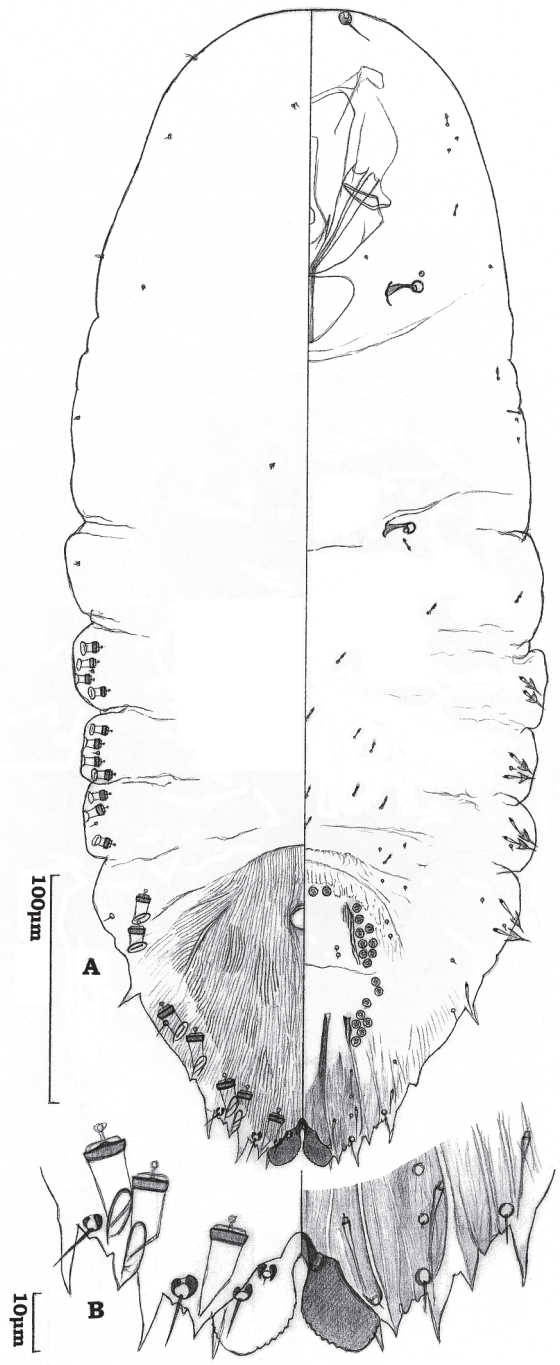

Fig. 10. *Chionaspis* sp.TR*L*, adult female. Cameron Highlands, Malaya, on *Lithocarpus*. B, trullae.

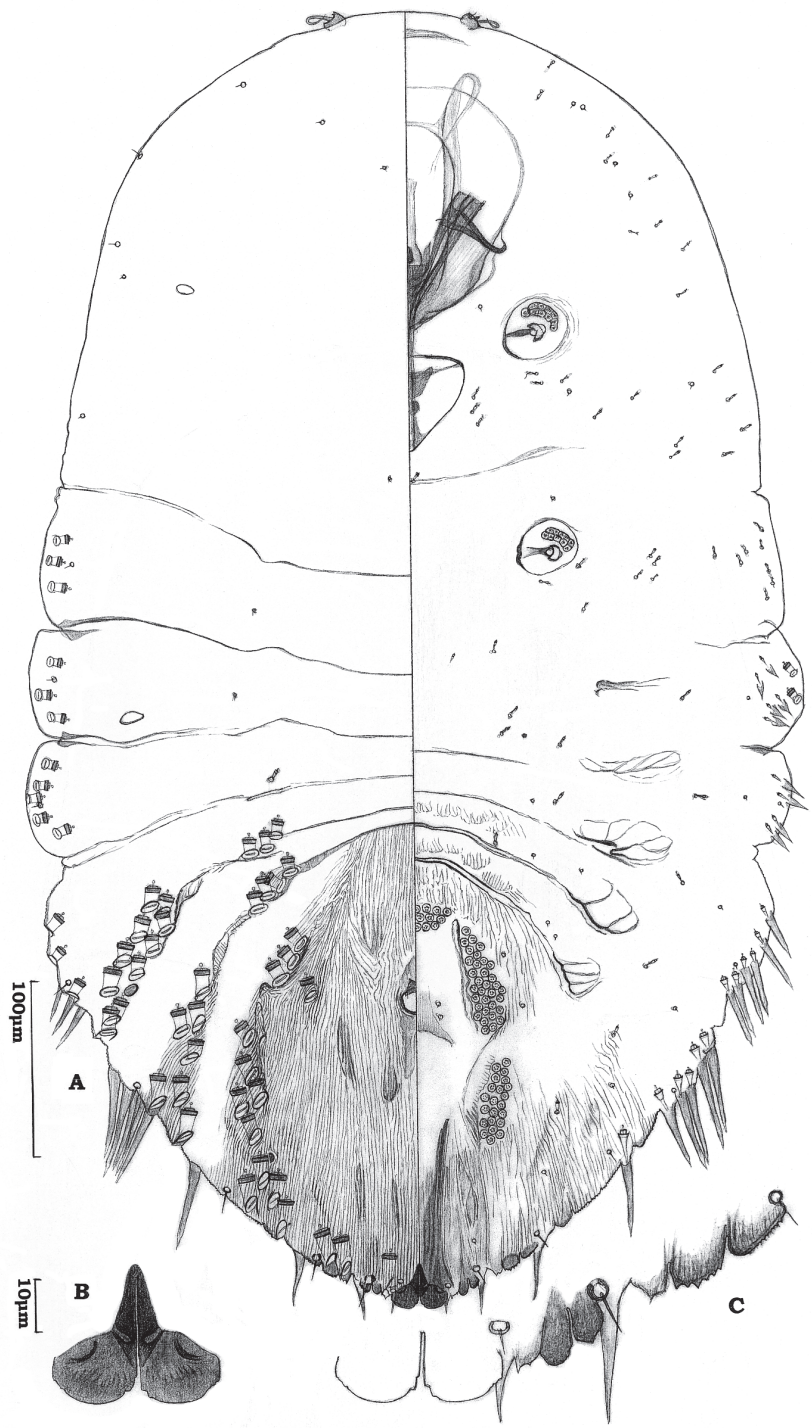

Fig. 11. *Chionaspis berincangensis*, adult female. Sample 1: Mt. Berincang, Cameron Highlands, Malaya, on *Lithocarpus*. B, median trullae; C, lateral trullae. Scale bar: 10μm for B, C.

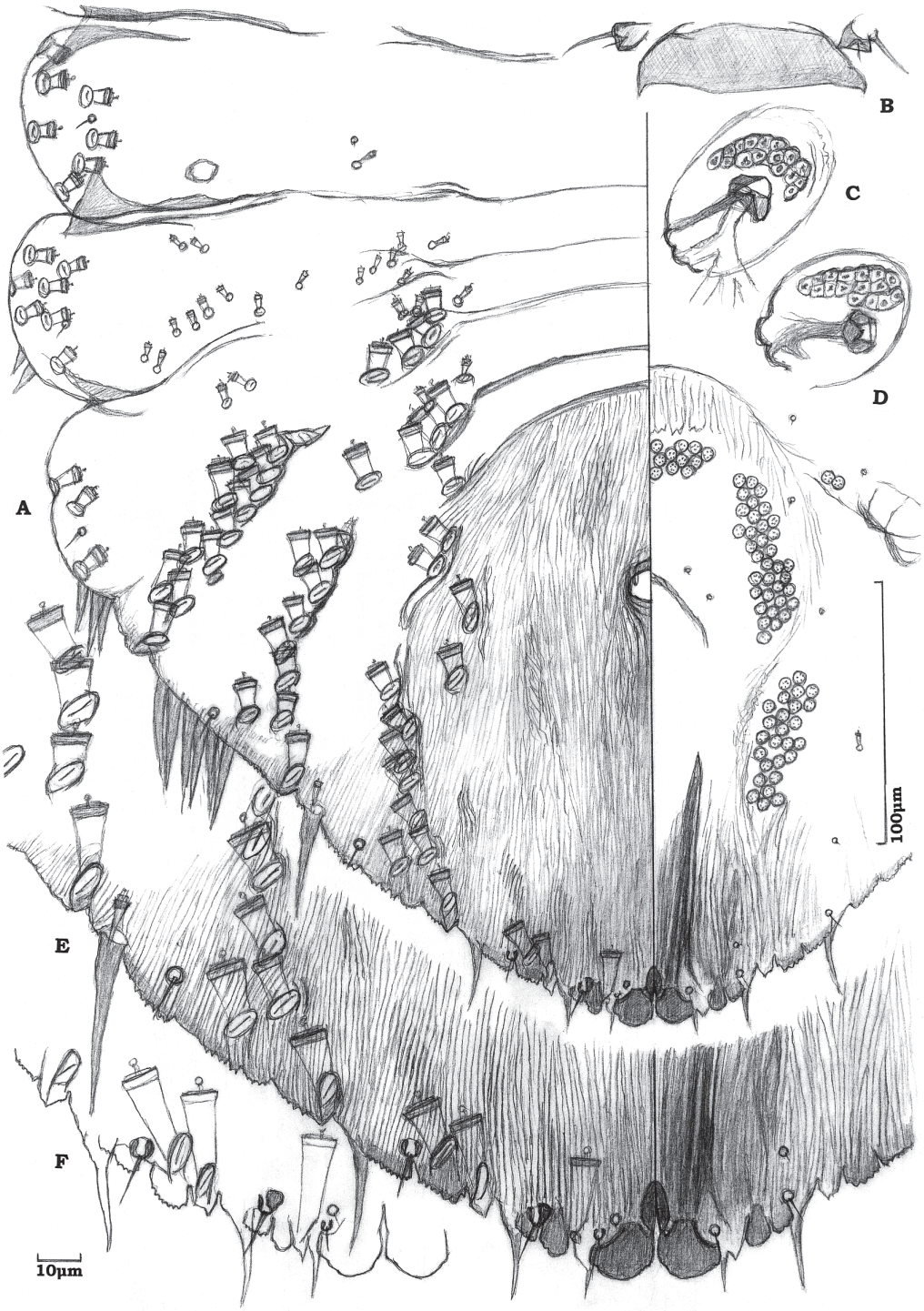

Fig. 12. *Chionaspis berincangensis*, adult female. Sample 1: Mt. Berincang, Cameron Highlands, Malaya, on *Lithocarpus*. A, abdomen; B, interantennal swelling; C, anterior spiracle; D, posterior spiracle; E, pygidial margin; F, trullae. Scale bar: 10µm for B–F.

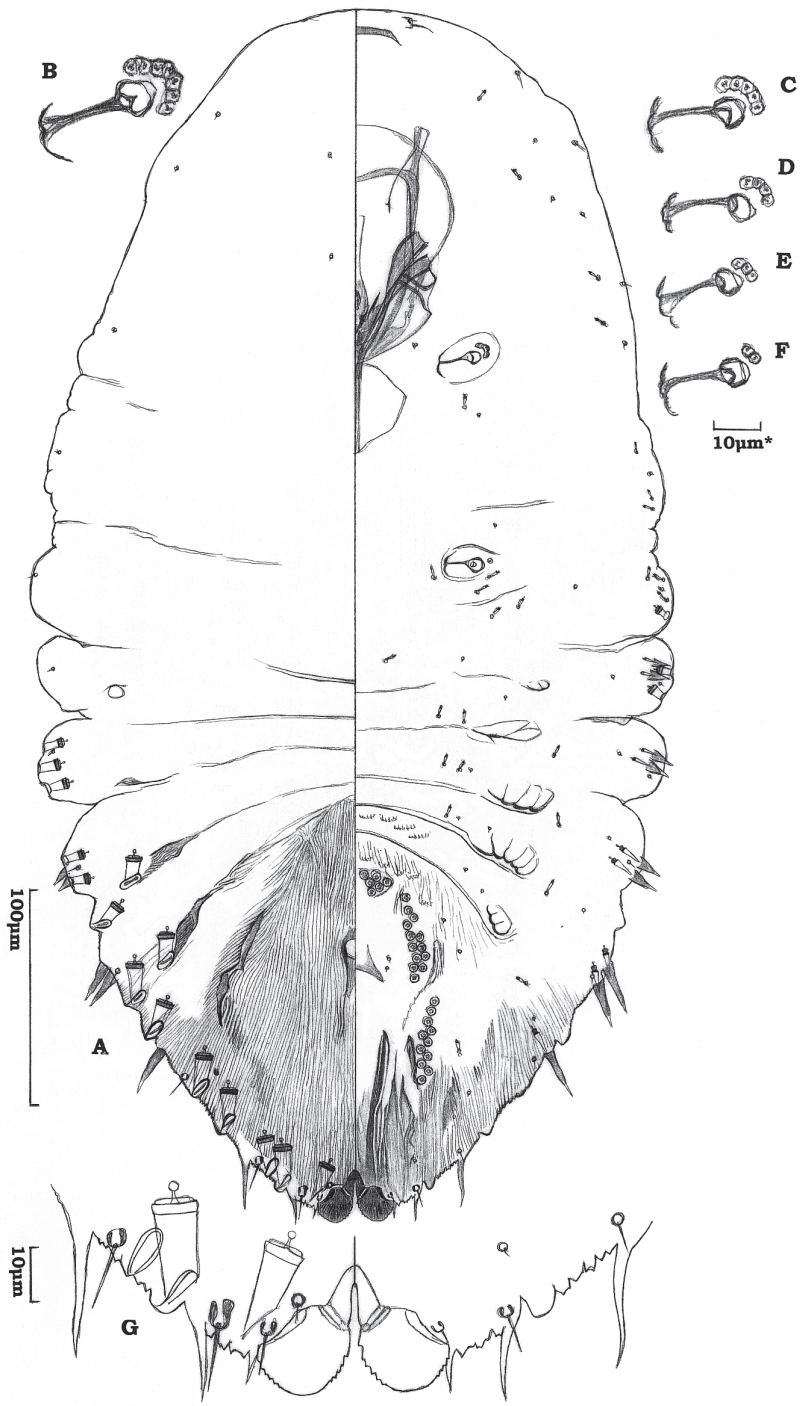

Fig. 13. *Chionaspis kinabaluana*, adult female. Mt. Kinabalu, Sabah, on *Lithocarpus*. B–F, anterior spiracle; G, trullae. Scale bars: 10µm for B, G; 10µm* for C–F.

Fig. 14. *Chionaspis samatana*, adult female. Samat Hill, Luzón, on *Lithocarpus*. B, antenna; C, anterior spiracle; D, posterior spiracle; E, trullae. Scale bar: 10µm for B–E.

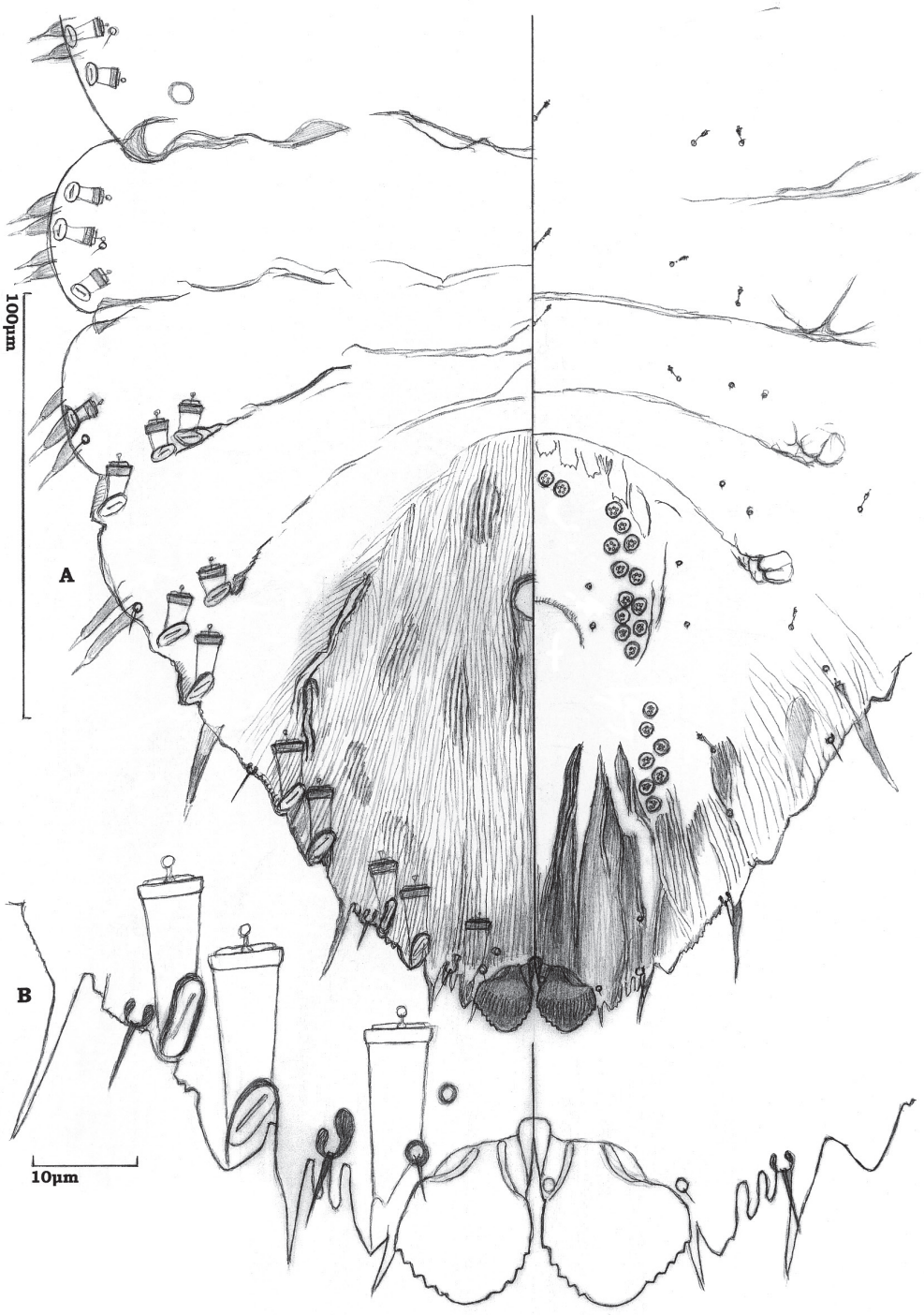

Fig. 15. *Chionaspis samatana*, adult female. Samat Hill, Luzón, on *Lithocarpus*. A, abdomen; B, trullae.

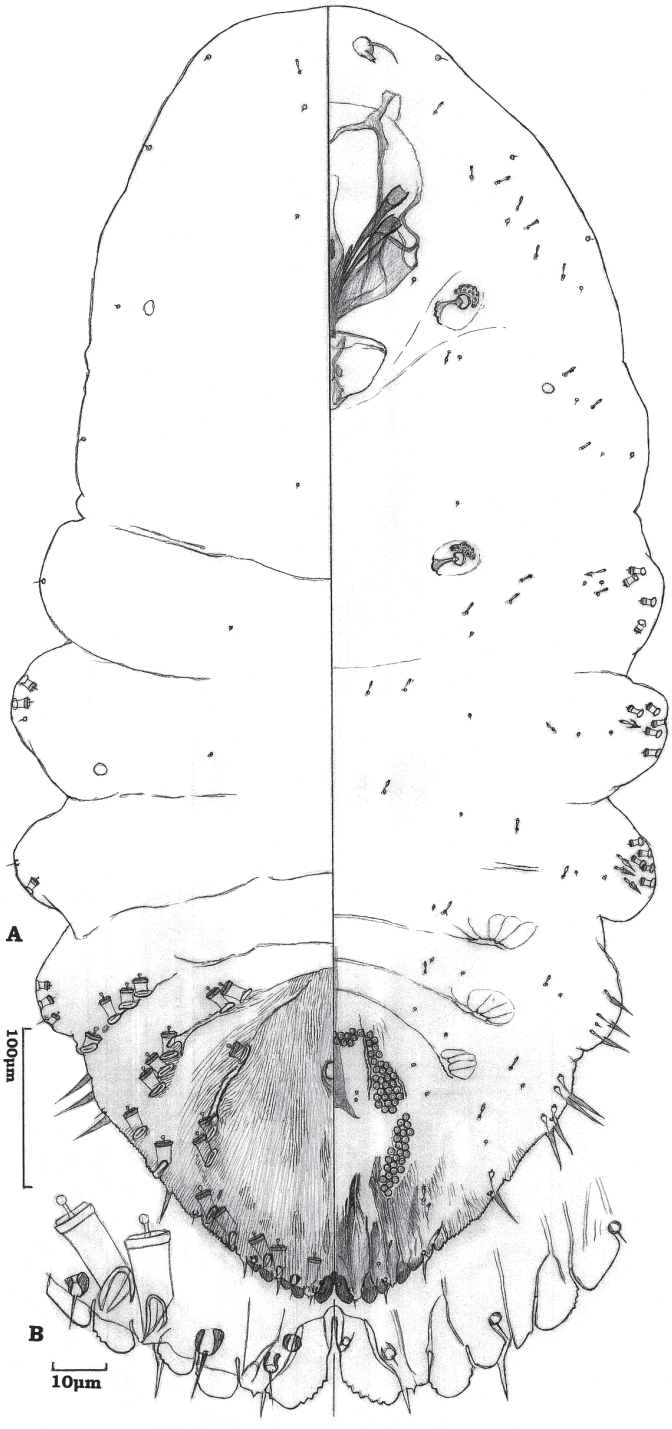

Fig. 16. *Chionaspis glutae*, adult female. Ulu Kali, Malaya, on *Gluta*. B, trullae.

Fig. 17. *Chionaspis melastomatis*, adult female. Mt. Kinabalu, Sabah, on *Melastoma*. B, eye spot; C, antenna; D–F, anterior spiracle; G, trullae. Scale bars: 10µm for B, C, G; 10µm* for D–F.

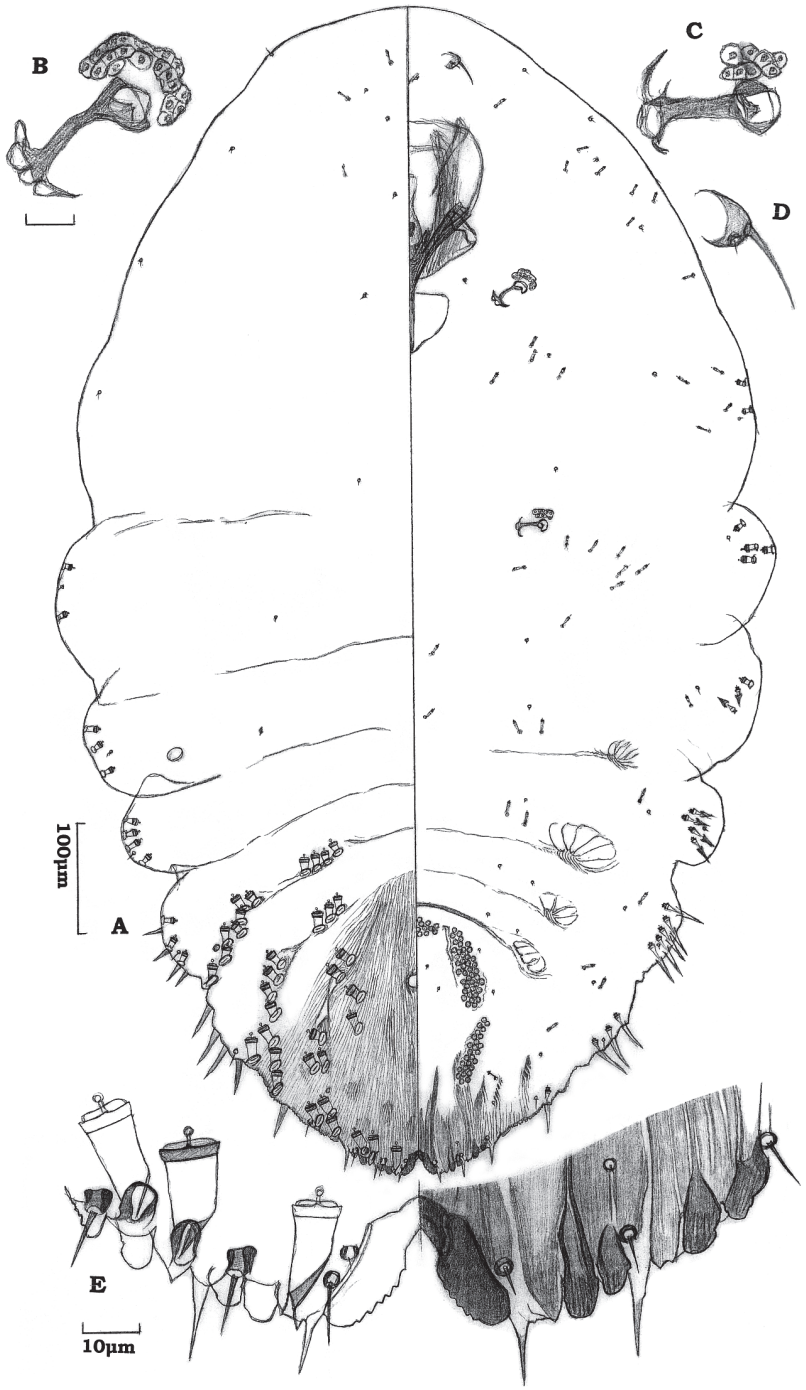

Fig. 18. *Chionaspis pogonantherae*, adult female. Sample 1: Mt. Berincang, Cameron Highlands, Malaya, on *Medinilla*. B, anterior spiracle; C, posterior spiracle; D, antenna; E, trullae. Scale bar: 10µm for B–E.

Fig. 19. *Chionaspis pogonantherae*, adult female. Sample 2: Cameron Highlands, Malaya, on *Pogonanthera*. B, antenna; C, anterior spiracle; D, posterior spiracle; E, F, trullae. Scale bar: 10µm for B–F.

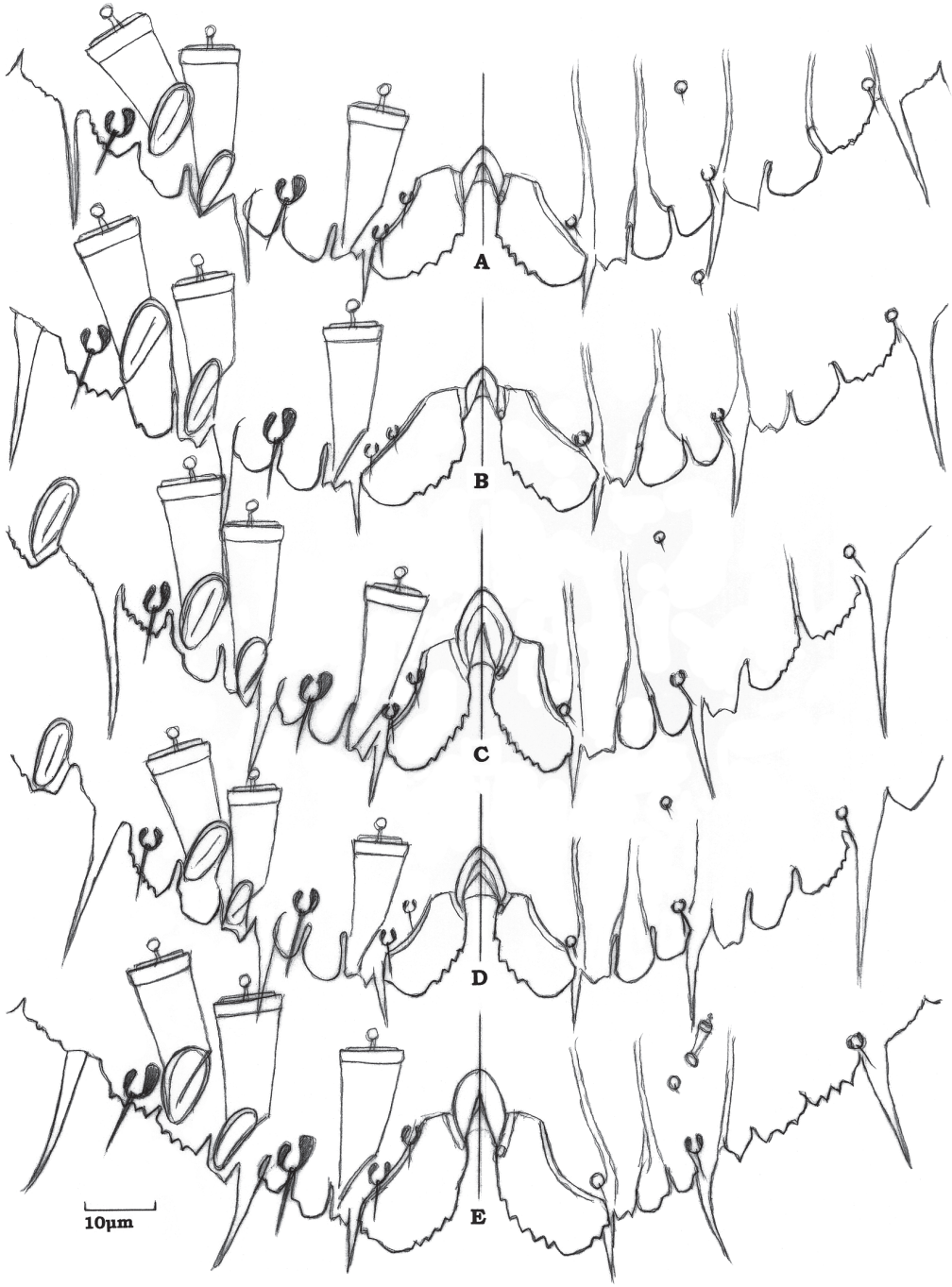

Fig. 20. Trullae in adult females. A, *Chionaspis arkhola*, Dunche, Nepal, on *Lithocarpus*. B, *C. arkhola*, Syabru, Nepal, on *Lithocarpus*. C, *Chionaspis lithocarporum*, Sample 1: Ulu Kali, Malaya, on *Lithocarpus*. D, *C. lithocarporum*, Sample 7: Cameron Highlands, Malaya, on *Lithocarpus*. E, *Chionaspis castanopsidis*, Sankranti, Nepal, on *Castanopsis*. Scale bar: 10µm for A–E.

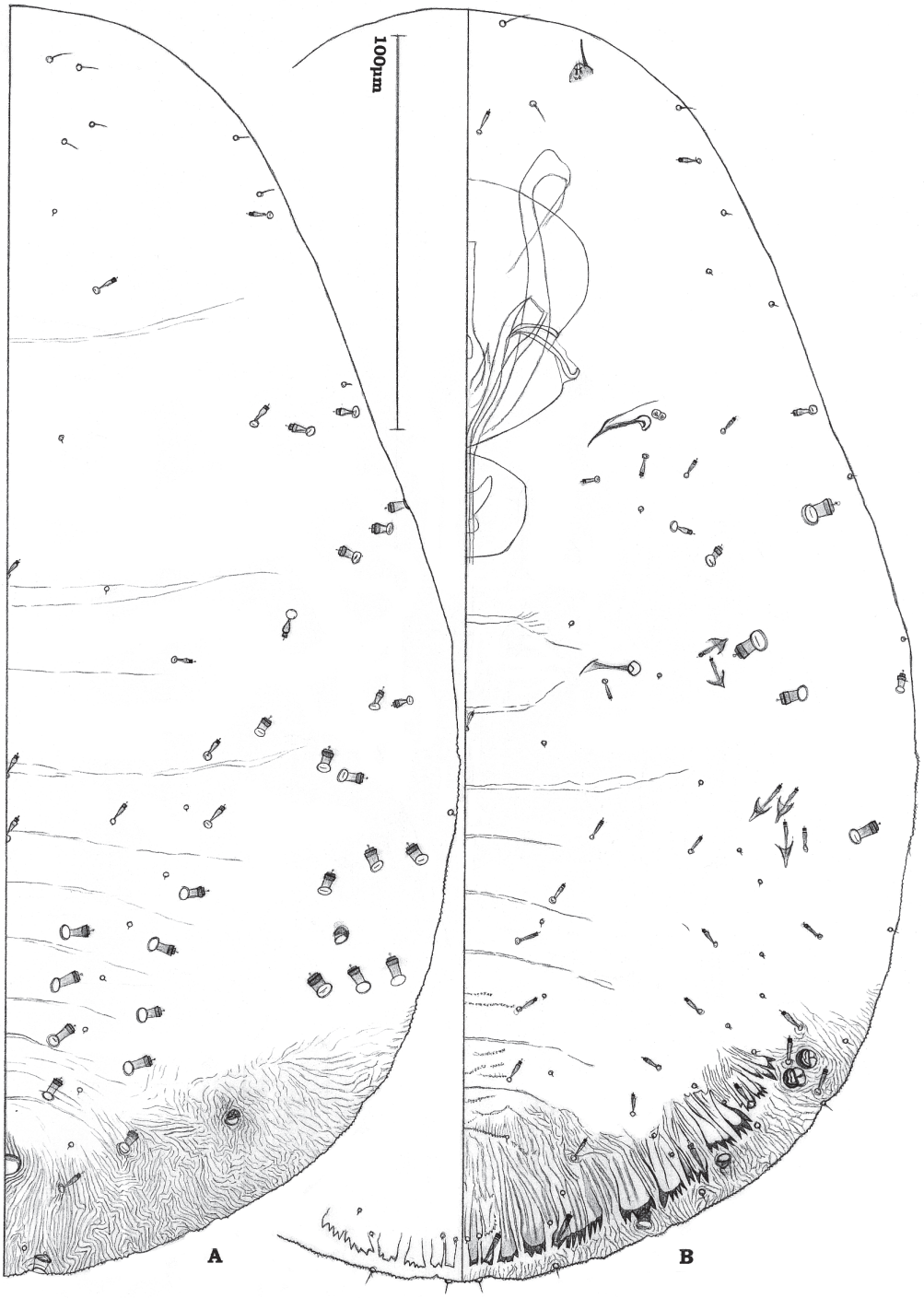

Fig. 21. *Chionaspis kinabaluana*, second instar male. Mt. Kinabalu, Sabah, on *Lithocarpus*. A, dorsal view; B, ventral view (dorsal surface of abdomen rolled onto ventral side marginally).

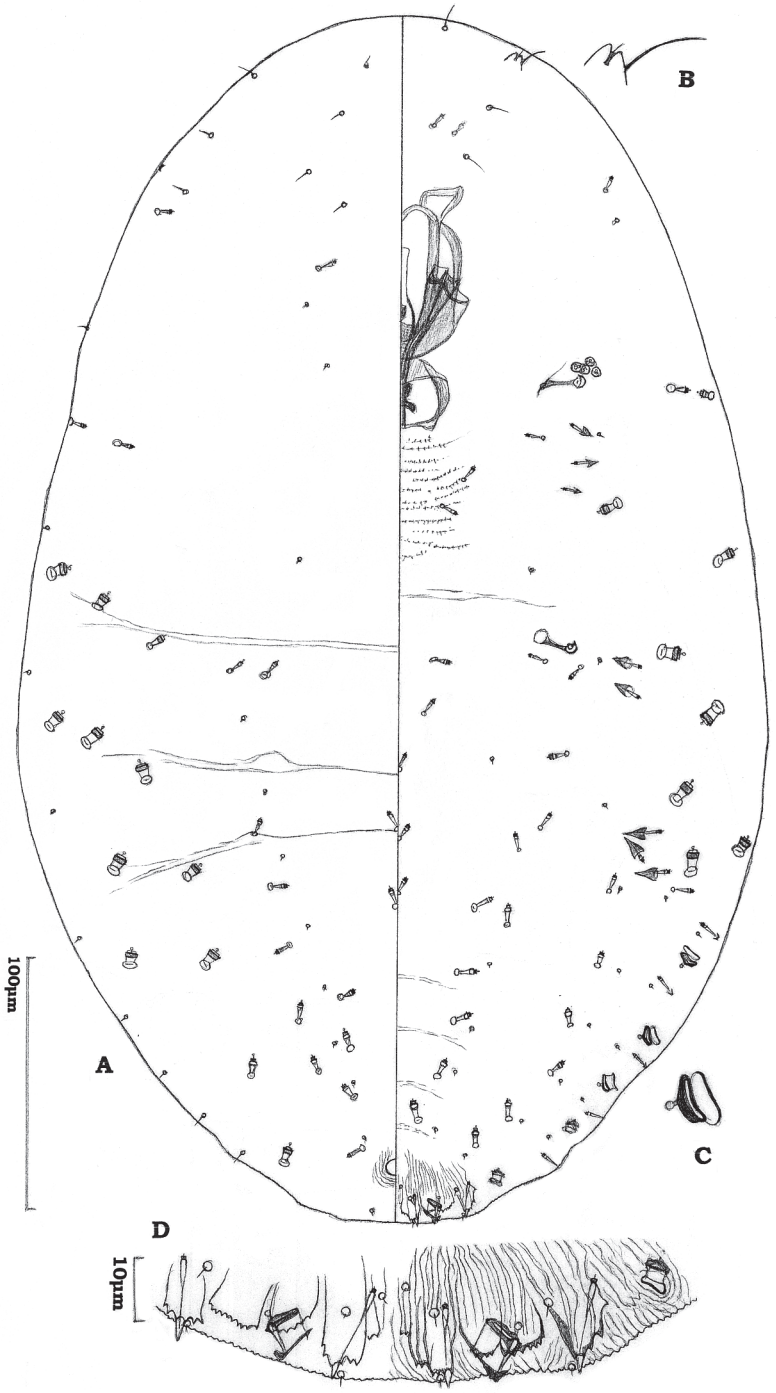

Fig. 22. *Chionaspis melastomatis*, second instar male. Crocker Range, Sabah, on *Melastoma*. B, antenna; C, modified macroduct on abd III; D, apical margin of pygidium. Scale bar: 10µm for B–D.

Fig. 23. *Chionaspis pogonantherae*, second instar male. Sample 1: Mt. Berincang, Cameron Highlands, Malaya, on *Medinilla*. A, ventral view; B, dorsal view (dorsal surface of abdomen rolled onto ventral side marginally); C, antenna; D, apex of abdomen, ventral view; E, modified macroducts on abd III and IV. Modified macroducts occurring in Pattern II (1–3–3–3–3–1 on abd II–VII). Scale bar: 10µm for C–E.