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THE ROSAE GROUP AND THE MEGALOBA GROUP
OF AULACASPI
(STERNORRHYNCHA: COCCOIDEA: DIASPIDIDAE)

By SADAO TAKAGI

Abstract

TAKAGI, S., 2017. The *rosae* group and the *megaloba* group of *Aulacaspis* (Sternorrhyncha: Coccoidea: Diaspididae). *Ins. matsum. n. s.* 73: 75–129, 4 tables, 27 figs.

Nine species of *Aulacaspis* recorded from plants of the family Rosaceae or the Ericaceae and another species from a supposedly ericaceous plant are mentioned in an annotated list. Five of them and four new species associated with plants of the mentioned families are lumped together under the *rosae* group, and two others, associated with plants of the rosaceous genus *Rubus*, under the *megaloba* group. The *rosae* group is divided into two subgroups: one of them is composed of *A. mali*, *A. ericacearum*, *A. sorbi*, n.sp., and the broadly distributed *A. rosae*, the former three species being restricted in distribution to northeastern Asia; the other subgroup contains *A. altiplagiae*, *A. langtangana*, n.sp., *A. pieridis*, n.sp., *A. lyoniae*, n.sp., and the broadly distributed *A. rosarum*, the former four species occurring in the Himalayan-Tibetan region. *A. megaloba* and *A. amamiana* represent the *megaloba* group, which, probably including unnamed forms, is distributed in southern areas in eastern Asia.

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Contents

Introduction

Terms; Numbers of wax organs; Depository of the holotypes

Annotated list: species of *Aulacaspis* recorded from Rosaceae or Ericaceae

Aulacaspis rosae (Bouché); *A. crawii* (Cockerell); *A. javanensis* Newstead; *A. mali* Borchsenius; *A. megaloba* Scott; *A. rosarum* Borchsenius; *A. amamiana* Takagi; *A. ericacearum* Takagi; *A. saigusai* Takagi; *A. altiplagae* Chen

List of new species

Species groups

The *rosae* group: northeastern Asian subgroup

Aulacaspis rosae (Bouché)

Aulacaspis ericacearum Takagi

Aulacaspis sorbi, n.sp.

Aulacaspis mali Borchsenius

The *rosae* group: Himalayan-Tibetan subgroup

Aulacaspis rosarum Borchsenius

Aulacaspis altiplagae Chen

Aulacaspis langtangana, n.sp.*

Aulacaspis pieridis, n.sp.*

Aulacaspis lyoniae, n.sp.*

The *megaloba* group

Aulacaspis megaloba Scott*

Aulacaspis amamiana Takagi

Concluding remarks

Table 1–4

Fig. 1–27

*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

The rose scale insect *Aulacaspis rosae*, a notorious pest of roses, has been known to occur broadly in the world and especially in the temperate regions including cold temperate areas. Another rose scale, *Aulacaspis rosarum*, occurs in China and some Pacific areas so far as based on reliable records, but it has probably settled more broadly in warmer parts of the world. These species should be native to eastern Asia, and have spread apparently in association with the world-wide introduction and cultivation of wild and horticultural roses especially since the nineteenth century.

Seven other species of *Aulacaspis* are similar to *A. rosae* and *A. rosarum* more or less closely, and may form together with the latter two a taxonomically significant group of species, the *rosae* group. This group is restricted in host association predominantly to plants of the families Rosaceae and Ericaceae. Three of these species, including one new, are limited in distribution to northeastern Asia. Another species was described from Tibet, and the other three, all new, occur in the Nepal Himalaya.

At least four other species of *Aulacaspis* have been recorded from rosaceous plants. They are not particularly closely related to the *rosae* group. Two of them are similar to each other and may represent another group, the *megaloba* group, which, probably including unnamed forms, is distributed in some southern areas of eastern Asia.

In the present paper, nine species of *Aulacaspis* which have been recorded from plants of the family Rosaceae or the Ericaceae are mentioned in an annotated list. Another species having the host plants not exactly identified is added to the list, because one of the plants was supposed to belong to the Ericaceae. These ten species are arranged in order of publication year. A list of the new species and an explanation of the two species groups follow the annotated list. Descriptions are given to the nine species of the *rosae* group (of which one species is known to me only through the original description and figure and is resketched on the basis of them) and to the two species of the *megaloba* group.

Terms. The term 'trullae' is used in place of 'pygidial lobes' in authors. The median trullae are 'horseshoed' basally when they have a pair of scleroses formed on their mesal bases and set close together and their bases are extended round the scleroses and united together to form the shape of a horseshoe. The abbreviations 'abd I', 'abd II', and so on stand for abdominal segments.

Numbers of wax organs (Table 1-4). The numbers of main wax-secreting organs (disc pores, macroducts, and gland spines) are given for each side of the body except for the total number of the dorsal macroducts (submedian and submarginal ones combined together) and that of the perivulvar disc pores. For each sample or ramicolous or foliicolous subsample, the lowest, mean, and highest values are given in the mentioned order; for smaller samples or subsamples the lowest and highest values in each of them or values in individuals are given.

Depository of the holotypes. The holotypes of the four new species described in this paper are deposited in the collection of the Systematic Entomology Laboratory, Hokkaidô University, Sapporo, Japan.

ANNOTATED LIST: SPECIES OF AULACASPI
RECORDED FROM ROSACEAE OR ERICACEAE

Aulacaspis rosae

=*Aspidiotus rosae* Bouché, 1833

The synonymy above has been accepted by authors, and I follow them. The scale insect recorded from roses under the names *Aspidiotus rosae*, *Chermes rosae*, and *Diaspis rosae* in Germany (where *Aspidiotus rosae* was named) and other areas of Europe should be identical, on circumstantial evidence, with the one which is understood to-day under the name *Aulacaspis rosae*. In warmer areas, however, records of *D. rosae* or *A. rosae* included another rose scale, *A. rosarum* (see notes under *Aulacaspis rosarum* in this list).

A. rosae occurs now broadly in the world on plants of the family Rosaceae, mainly of the genera *Rosa* and *Rubus*. It was recorded by authors also from plants of other families. According to Dekle (1965), *A. rosae* was recorded in Florida from *Rosa* and *Rubus* most frequently, and also from *Prunus* (peach, Rosaceae), *Geranium* (Geraniaceae), and *Chionanthus virginica* (Oleaceae). There should have been no possibility of misidentification in these records under *A. rosae*, because no species of *Aulacaspis* is native to the Americas (except for *Aulacaspis boisduvalii* var. *maculata* Cockerell, 1898, which, however, may be a *Diaspis* form native to Brazil), and also because two other species of *Aulacaspis* now known to occur in the U.S.A., *A. yasumatsui* Takagi and *A. tuberculatus* Newstead, were first detected in that country in 1996 and in 2002, respectively (Miller et al., 2005). The records of *A. rosae* from the diverse plants in Florida may mean the occurrence of host expansion under new ecological conditions (fauna of natural enemies, plant resistance, etc.) and, then, may suggest that *A. rosae* has a potential for expanding its host range to a considerable degree. This view is adopted in the present study, and several forms associated with non-rosaceous plants in Japan are identified with *A. rosae*.

Aulacaspis crawii

=*Diaspis crawii* Cockerell, 1898

This species occurs broadly in tropical to subtropical Asia and on diverse plants, and was introduced into Hawaii and South Africa. It was recorded from *Rubus* in China and from plants of *Rosa* and *Rubus* and only from these plants at four localities in Saint Helena Island. So far as I am aware, there has been published no further record of *A. crawii* from roses or other rosaceous plants (in this connection, see Takagi, 2013, Section 2.1.1b, 2.2.3b).

Aulacaspis javanensis Newstead, 1908 (Fig. 2)

This species was described from Java, with the host plants not exactly identified: ‘On Ericacea (?) and two undermentioned shrubs. Forest on the mount Smeroe, East Java, about 1800 m, ..., also on an aquifoliaceous shrub. ... in Bamboo-wood on the Smeroe, ...’ (Newstead, 1908). The interpretation may be adopted that the third host plant, which was not clearly mentioned by Newstead, was not a bamboo but an unidentified shrub in the bamboo grove. The original description with drawings has not been helpful in my attempt to find characters useful for recognizing the species.

A figure prepared by Dr D. J. Williams from ‘Type material’ of *A. javanensis* (but

without mention of the host plant) is available, and it is published in this paper with his approval (Fig. 2). So far as based on this figure, *A. javanensis* may be characterized by the following characters.

Adult female at full growth with prosoma well swollen and square rather than rounded in outline; peribuccal scleroses well developed. Anterior spiracles each with a loose cluster of disc pores. Dorsal macroducts numerous. Submedian macroducts on abd II to VI, divided into segmental and infrasegmental series on II to IV, 5 on VI. Submarginal macroducts on abd III to V, in nearly single rows. Lateral macroducts and lateral gland spines well represented on abd II and III, these gland spines much shorter than marginal gland spines of pygidium. Marginal gland spines 5 on abd IV. Median trullae moderate in size, situated in an apical recess of pygidium, with bases extending anteromesally into a pair of slender processes, which are set close together but separated from each other by a narrow space; mesal margins separated from each other by a good space subbasally, then divergent. Second and third trullae with both lobules well developed.

Aulacaspis mali Borchsenius, 1938

This species occurs in southern Primorskii Krai, Extreme Eastern Russia, on plants of the rosaceous genera *Malus*, *Crataegus*, and *Micromeles* (included in *Sorbus*, s.l.). A sample mounted from material collected in Ussuriysk on *Malus* sp. has been available for my study. Kawai (1980) recorded *A. mali* from Japan but, in the view adopted in the present study, what he identified with *A. mali* should represent another species (see Remarks under *A. sorbi*, n.sp.).

Balachowsky (1954) recognized *A. mali* as a form closely related to but distinct from *A. rosae*, and suggested their vicariant differentiation in Extreme Eastern Asia and Central Europe. However, no native species of *Aulacaspis* exists in Europe, where *A. rosae* is undoubtedly an introduced scale insect. In the present study, I have realized that there are closely similar forms of *Aulacaspis* in a corner of northeastern Asia, forming a compact group, which appears to be significant taxonomically and biogeographically. This group, so far as known, is composed of *A. mali*, *A. ericacearum*, and the new species *A. sorbi* in addition to *A. rosae*, the last species having spread broadly in the world in association with rose cultivation.

Aulacaspis megaloba Scott, 1952

This species was described from southern China and from plants of *Rubus*. Chen (1983) described *A. megaloba* from somewhere (Guizhou?) in China and from *Rubus*. His form, so far as described and figured and compared with Scott's figure, is somewhat peculiar in the shape of the median trullae, and thus appears to represent a form different from *A. megaloba*.

In the present study, some samples collected in Nepal on plants of *Rubus* are identified with *A. megaloba* and their variation is discussed.

Aulacaspis rosarum Borchsenius, 1958

This species was described from Chengdu, Sichuan, southern China, and from *Rosa* sp. Before that, however, it had been recorded from other areas under the name *Diaspis rosae* or *Aulacaspis rosae*. The oldest collection of *A. rosarum* in New Zealand was made in 1877 and recorded under the name *D. rosae* in 1879 (Archibald et al., 1979).

In Hawaii, *D. rosae* was first recorded in 1895 (Zimmerman, 1948), whereas ‘There is a possibility that all Hawaiian records of *A. rosae* are misidentifications’ (Nakahara, 1981) of *A. rosarum*. It is very probable that this species had been introduced into some other areas, too, of the world before the end of the nineteenth century. Confusions with *A. rosae* continued even after the species was formally described.

Williams and Watson (1988, fig 32) examined specimens of *A. rosarum* from the original material and also from Papua New Guinea and some South Pacific islands, and presented a description of the adult female accompanied with a figure of the whole body. They show that the prosoma is square rather than rounded in outline and the peribuccal scleroses are well developed, and also that submedian dorsal macroducts occur on the second abdominal segment. (The last character was shown also in the figure of the abdomen accompanying the original description.) I have observed these characters in some specimens mounted from the type material (Takagi, 2013, fig. 22, which shows a well-formed peribuccal sclerosis). (Needless to say, the shape of the prosoma and the development of the peribuccal scleroses are completed at the full growth of the body. In *A. rosae* the peribuccal scleroses are usually no more than slender sclerotic folds even when they are discernible at full growth.) *A. rosarum* is recognized now as a good species, being easily separable from *A. rosae* in having the characters mentioned above (which, however, are all prepygidial and may have been overlooked in hasty examinations). It is another pest of garden roses and cultivated berry plants of *Rubus*, and should have broadly spread in warm areas of the world.

Scott (1952) described *Aulacaspis thoracica* (=*Phenacaspis thoracica* Robinson, 1917) on the basis of the material used by the original author; at the same time he recorded it from China and from some various plants including rose. Chen (1983) described *A. thoracica* and *A. rosarum* from China and treated them as closely related but different species. Tang (1986) united them into the same species. In disagreement with these authors, I (Takagi, 2013) synonymized *A. thoracica* with *A. mischocarpi* (=*Phenacaspis mischocarpi* Cockerell and Robinson, 1914), these forms having originally been described from the same locality, Los Baños, Luzón Island. This synonymy leaves no room for the confusion of *A. thoracica* with *A. rosarum*, because *A. mischocarpi* is a well-characterized distinct species. Some records of *A. thoracica* from *Rosa* and *Rubus* may be misidentifications of *A. rosarum*, but all the records made under the name *A. thoracica* in China remain problematical, requiring critical re-examinations on the specimens concerned (in this connection, see Takagi, 2013, Section 2.2.3b).

Aulacaspis amamiana Takagi, 1961

This species was described from Amami-Ôshima, Ryûkyû Islands. In the present study, samples collected in three islands, all on *Rubus*, have been available.

Chen (1983) described under the name *A. amamiana* a scale insect collected in Xishuangbanna, Yunnan, on *Rubus* sp. and an unidentified tree, but his figure shows a form different from the type form occurring in the Ryûkyû Islands in some details. Tang (1986) described another scale under the name *A. amamiana* and as occurring in Guangdong and Yunnan on unidentified plants, but his figure shows a quite different species (see notes under *Aulacaspis saigusai* in this list).

Aulacaspis ericacearum Takagi, 1961

This species was described from Hokkaidô and from *Leucothoe* and *Vaccinium*. Kawai (1980) recorded *A. ericacearum* from northern Honshû. Danzig (1980, 1986, 1993) recorded it from Sakhalin and Kunashir and from *Vaccinium* and *Oxycoccus*. So far as recorded, *A. ericacearum* occurs in Hokkaidô and neighbouring islands, inhabiting mountainous environments in Hokkaidô and northern Honshû, and is associated with some plants of the family Ericaceae.

China was added to the distribution range of this species (Miller and Gimple, 2009), but I have failed to find any reliable record of the species from China. Danzig mentioned *Pseudaulacaspis ericacea* (=*Phenacaspis ericacea* Ferris), which occurs in China on *Vaccinium*, as a close relative of *A. ericacearum*. *Phenacaspis ericacea* in Ferris (1953, fig. 31) undoubtedly belongs to the genus *Pseudaulacaspis* (which belongs to the subtribe Fioriniina, whereas *Aulacaspis* to the Chionaspidina), and does not appear to be similar to *A. ericacearum*.

This species is closely similar to *A. rosae* in the stage of the adult female, in which it may sometimes be distinguished from the latter with difficulty. It was described and has been recognized as a form distinct from the latter on account of a certain character in the second instar female.

Aulacaspis saigusai Takagi, 1969

This species was described from Ali-Shan, Taiwan, and from a species of *Rubus*. Among the *Aulacaspis* species associated with rosaceous plants this species is characteristic in having the body cuneiform and the pygidium narrowed accordingly.

Chen (1983) states that *A. saigusai* occurs in Sichuan and Guizhou on a lauraceous tree (*Machilus*?) and *Elaeagnus*. I have some doubt about his identification because of the unexpected host plants. Tang's (1986) figure of *A. amamiana* shows a form similar to *A. saigusai* (see notes under *Aulacaspis amamiana* in this list).

Aulacaspis altiplagae Chen, 1983

This species was described from Tibet and from *Rosa* sp. I have tried in the present paper to resketch the species on the basis of Chen's study (see *Remarks* under *Aulacaspis altiplagae*).

LIST OF NEW SPECIES

Aulacaspis sorbi (=*Aulacaspis mali*: Kawai, 1980)

Occurring on *Sorbus* (Rosaceae) in Japan.

Aulacaspis langtangana

Occurring on *Rosa* (Rosaceae) in Nepal.

Aulacaspis pieridis

Occurring on *Pieris* (Ericaceae) in Nepal.

Aulacaspis lyoniae

Occurring on *Pieris* and *Lyonia* (Ericaceae) in Nepal.

SPECIES GROUPS

The rosae group

Aulacaspis rosae, *A. mali*, *A. rosarum*, *A. ericacearum*, *A. altiplagae* and the four new species may be grouped together not on account of their common possession of any peculiar character or characters but on the basis of their similarities in some or general characters. Some of them may easily be confused, and there have really been confusions (between *A. rosae* and *A. rosarum* and between *A. mali* and *A. sorbi*).

A. rosae, *A. mali*, *A. ericacearum*, and *A. sorbi* are especially similar to each other. These species except the first are restricted in distribution to northeastern Asia, being known from some spots which are scattered around the Sea of Japan and the Sea of Okhotsk and are cold temperate in climate; they may form the northeastern Asian subgroup. *A. altiplagae* was described from Tibet and *A. langtangana*, *A. pieridis*, and *A. lyoniae* occur in the Nepal Himalaya, the areas having a broad range of climates from subtropical to high-altitudinal; these species may be lumped together in the Himalayan-Tibetan subgroup. *A. rosae* and *A. rosarum* are now broadly distributed in the world, and their native lands are unknown; they may tentatively be referred to the northeastern Asian subgroup and the Himalayan-Tibetan subgroup, respectively.

The megaloba group

A. megaloba and *A. amamiana*, both associated with the rosaceous genus *Rubus*, are similar especially in having enormous median trullae. These species and certain other forms (see notes under *Aulacaspis megaloba* and *Aulacaspis amamiana* in Annotated List) may tentatively be grouped together in the *megaloba* group. In this understanding, this group is distributed in southern areas of eastern Asia ranging from the Ryûkyû Islands to the Nepal Himalaya.

The other species

A. cravii is similar to *A. rosarum*, through which it may have some connection with the *rosae* group. It seems that *A. javanensis* and *A. saigusai* are related neither with the *rosae* group nor with the *megaloba* group. No further mention is made of these three species in this paper.

THE ROSAE GROUP: NORTHEASTERN ASIAN SUBGROUP

Aulacaspis rosae (Figs 3-5)

Material examined

A great number of mounted specimens, all from Japan, have been available for the present study. Most samples were collected from plants of the family Rosaceae: garden roses; wild roses, *Rosa rugosa* in Hokkaidô and *Rosa multiflora* in Honsyû; *Rubus buergeri* and other wild species of *Rubus* in Honsyû, Sikoku, and Kyûsyû; the perennial herb *Agrimonia pilosa* var. *japonica* (=*A. eupatoria* var. *japonica*) in Honsyû (Mt. Rokkô, Hyôgo Pref., 3.XI.1956, M. Yamamoto).

Samples collected from the following non-rosaceous plants are referred to this species: *Aucuba japonica* var. *borealis* (Cornaceae), in Hokkaidô (Mt. Sengen, Osima Peninsula, 6.IX.1970); *Vaccinium smallii* (Ericaceae), in Honsyû (Mt. Hayatine, Iwate Pref., 4.VIII.1964); *Vaccinium*

vitis-idaea, in Honsyû (Dizô Pass [alt. 1733m at the highest point], Gunma Pref./Nagano Pref., 22.VIII.1959, S. Kanda); *Epigaea asiatica* (Ericaceae), in Honsyû (Mt. Mikawa, Hyôgo Pref., 4.X.1977). Each of these samples is represented by a few or several specimens except for the last-mentioned.

Among the collection localities of all these samples the northernmost is situated on the sea-coast of Isikari, Hokkaidô (host plant: *Rosa rugosa* in the littoral vegetation) and the southernmost is on Mt. Takakuma, Kagoshima Pref., Kyûsyû (*Rubus* sp.). The samples associated with the rosaceous plants were collected in lowlands, at littoral spots, on hillsides, or in urban environments, and only occasionally on mountains, whereas those from the non-rosaceous plants were collected exclusively in mountainous environments.

Three samples, which were collected from the following localities and plants, have been selected and examined for the numbers of wax-secreting organs (Table 1, 2): Sapporo, Hokkaidô, on a hybrid rose, 4.XI.1962 (32 adult females; the collection spot is in a cool temperate climate and under urban conditions); Mt. Takakuma, Kagoshima Pref., Kyûsyû, on *Rubus* sp., 24.V.1963 (32 adult females; the collection spot is on a hillside and in a warm temperate climate); Mt. Mikawa, Hyôgo Pref., Honsyû, on *Epigaea asiatica*, 4.X.1977 (30 adult females; the host plant belongs to the family Ericaceae).

Recognition characters

Adult female at full growth with prosoma swollen, distinctly broader than postsoma, and roundish along free margin; prosomatic tubercles indiscernible or indicated by slight prominences; postsoma robust, metathorax and basal 2 abdominal segments practically same in width, abd I a little narrower, abd II lobed posterolaterally; pygidium broad obdeltoïd, with a small recess apically; peribuccal scleroses usually not developed and represented by slender folds at most, rarely more developed. Anterior spiracles each with a compact group of disc pores; posterior spiracles each with a smaller and less compact group of disc pores. Perivulvar disc pores moderately numerous in 5 groups. Submedian dorsal macroducts on abd III–VI (rarely or abnormally absent on VI), in practically single rows, not distinctly separated into segmental and infrasegmental series; 1–5 on VI. Submarginal dorsal macroducts on abd III–V, forming a single or partly and irregularly double row on III and sometimes also on IV. Lateral macroducts and lateral gland spines usually well represented in number on abd II and III. Marginal gland spines 2–6 on abd IV. Median trullaæ moderate in size, sunk in apical recess of pygidium wholly or nearly so, basally with a pair of small sclerites set close together; not horseshoed; mesal margins separated from each other by a space and parallel or gently divergent subbasally, then strongly divergent and finely serrate; blunt or rounded apically. Second and third trullaæ with both lobules well developed, the lateral lobule smaller than the mesal, slanting on outer apical margin especially in third trulla. Marginal processes of abd IV and V not prominent.

Second instar female with single marginal macroducts on abd III–VII or IV–VII; no further macroducts.

Remarks

The examined material includes four samples collected from four non-rosaceous plants. I have failed to find any morphological difference sufficient to exclude them from the species. Among them, the samples collected from *Vaccinium smallii* and *V. vitis-idaea*, family Ericaceae, in northern Honsyû are especially noteworthy. They belong to *A.*

rosae and not to *A. ericacearum* so far as based on the morphological characters adopted as diagnostic in the present study for distinguishing the two species (for these characters, see *Remarks* under *Aulacaspis ericacearum*), but the host plants, the localities, and the environments of the collection spots may not exclude the possibility that the samples belong to *A. ericacearum* (in this connection, see notes under *Aulacaspis ericacearum* in Annotated List). Provided the samples associated with the *Vaccinium* species (and also the sample collected on *Epigaea asiatica*, another ericaceous plant, in western Honshū) are correctly identified with *A. rosae*, they put forward a possible evolutionary scenario for the relation between *A. rosae* and *A. ericacearum*. This scenario is composed of three events: the invasion of *A. rosae* into mountainous environments and onto rosaceous plants growing there; the occurrence of host expansion onto non-rosaceous plants including ericaceous ones in the new environments (in this connection, see notes under *Aulacaspis rosae* in Annotated List); the emergence of *A. ericacearum* from *A. rosae* settled on ericaceous plants. This scenario is based on the present distributions of *A. ericacearum* and the forms of *A. rosae* associated with ericaceous plants and, therefore, on the supposition that all these events took place in or around Japan.

It should be added that I have found in literature no records of *A. rosae* from ericaceous plants (the association of the species with ericaceous plants being recorded for the first time in the present paper) and that I have come across in my collection no specimens of *A. rosae* collected from ericaceous plants at lower altitudes (whereas, in general, some ericaceous shrubs are common and abundant in lowlands of Japan).

Aulacaspis ericacearum
(Figs 6–8)

Material examined

Collected in Hokkaidō, Japan, on shrubs of the family Ericaceae:

Aizan-Kei, alt. ca. 1000m, on *Leucothoe grayana*, *Vaccinium axillare* var. *coriaceum*, and *V. smallii*, 25.VII.1957 (type series). These three samples from the three plant species are small, each having a few or several specimens of the adult female; a total of 13 adult females and some exuvial casts of the second instar female, restained and remounted, have been examined in the present study.

Mt. Soranuma, near the city of Sapporo, alt. near 1000m, on *Vaccinium* sp., twig, 2.VIII.1967. Three adult females and 5 exuvial casts of the second instar female.

City of Sapporo, on a garden-cultivated plant of *Leucothoe grayana* var. *oblongifolia*, 30.VI, 24.VII, and 14.VIII, 1970. A good number of specimens mounted from twigs; 32 adult females from the sample collected on 24.VII were examined for the numbers of wax-secreting organs (Table 1, 2).

Recognition characters

Adult female at full growth with prosoma swollen, distinctly broader than postsoma, and rounded along free margin; prosomatic tubercles indiscernible; postsoma robust, gradually narrowing posteriorly on metathorax and basal 2 abdominal segments; pygidium broad obdeltoid, with a small recess apically; peribuccal scleroses represented by slender sclerotic folds at most. Anterior spiracles each with a compact group of disc pores; posterior spiracles each with a smaller group tending to be less compact. Perivulvar disc pores moderately numerous in 5 groups. Dorsal macroducts in single

rows; submedian macroducts on abd III–VI, sometimes with a slight suggestion of infrasegmental series on III and also on IV, 1–3 on VI. Submarginal macroducts on abd III–V. Lateral macroducts on abd II and III, usually not numerous; lateral gland spines on II and III, usually not numerous especially on II. Marginal gland spines 1–4 on IV. Median trullae moderate in size, sunk in apical recess of pygidium except for their apical parts, basally with a pair of sclerites set close together and a horseshoe round the sclerites, the horseshoe being various in thickness, sometimes very thin but often thickened medially to form a robust process produced into pygidium; mesal margins separated from each other by a space and parallel or nearly so subbasally, then divergent and finely serrate; rounded, blunt, or pointed apically. Second and third trullae well represented, lateral lobule in each trulla smaller than the mesal, with outer apical margin slanting. Marginal processes of abd IV and V not prominent.

Second instar female with single marginal macroducts on abd IV–VII and usually with a single submarginal macroduct on V.

Remarks

The specimens referred to *A. ericacearum* (see *Material examined*) have been compared with the specimens collected from rosaceous plants in Japan and referred to *A. rosae* (see *Material examined* under *Aulacaspis rosae*). In this comparison, *A. ericacearum* has been distinguished from *A. rosae* considerably successfully in having the median trullae horseshoed basally in the adult female and also in the second instar female. The horseshoe is variable in development and sometimes so thin that it may be barely visible. In the second instar female, *A. ericacearum* differs from *A. rosae* in having a submarginal macroduct on each side of the fifth abdominal segment except for rare cases of its absence, which are presumed to be merely abnormal. The combination of these characters in the adult and second instar females may be adopted as a good criterion for recognizing *A. ericacearum* in comparison with *A. rosae*. This criterion has been applied to three samples collected from ericaceous plants in Honshû; they have not met the criterion and have been referred to *A. rosae* in spite of the habitats and the host plants (see *Remarks* under *Aulacaspis rosae*).

A sample of *A. ericacearum* collected in Sapporo from *Leucothoe grayana* (see *Material examined*) and a sample of *A. rosae* collected in Sapporo from a hybrid rose (see *Material examined* under *Aulacaspis rosae*) have been compared in the numbers of wax-secreting organs. The collection spots of these samples are situated in the urban area and some 0.8km apart from each other. The results (Table 1, 2) should show what the two species exhibit under the same, or at least very similar, environmental conditions. (The host plant of the sample of *A. ericacearum* should have been transplanted from the wild. The urban conditions of the collection spot should be foreign to this scale insect. However, there were a few pieces of circumstantial evidence to support the assumption that both these samples were taken from populations which had been lasting on their host plants at the same sites for years.) These samples of the two species are not different in the numbers of the disc pores associated with the anterior and posterior spiracles and are similar in the total numbers of the perivulvar disc pores. They differ in the total numbers of the dorsal macroducts, the ranges and, accordingly, the mean values being distinctly different. In the numbers of the lateral organs (macroducts and gland spines) on the second and third abdominal segments and the marginal gland spines on the fourth, the two samples overlap or adjoin each other in the ranges and are statistically different in

the mean values, the differences being especially remarkable in those of the lateral gland spines.

The observed differences in the numbers of the macroducts and gland spines should reflect some eco-physiological differences between the populations from which the samples were obtained (because these organs and especially the macroducts are essentially associated with test formation), and may be sufficient to support the view that *A. ericacearum* is a taxonomic unit distinct from *A. rosae*.

Two more samples of *A. rosae* are brought here: one of these samples was collected from *Rubus* sp. on Mt. Takakuma, the southernmost locality in the material available for the present study, and the other sample from the ericaceous plant *Epigaea asiatica* on Mt. Mikawa (see *Material examined* under *Aulacaspis rosae*). These samples, together with the sample from Sapporo, are expected to afford examples of the local variation and possibly also examples of the variation due to host plants. The observations (Table 1, 2) suggest that the numbers of some wax organs are certainly variable among samples of *A. rosae*, but they also suggest the possibility that the lateral gland spines in this species are relatively stable in number and have a tendency to be more numerous than in *A. ericacearum*.

Aulacaspis sorbi, n.sp.
=*Aulacaspis mali*: Kawai, 1980
(Fig. 9)

Material examined

Collected on Ôdai-ga-Hara, alt. ca. 1500m, Nara Pref., Honsyû, Japan, on *Sorbus alnifolia* (Rosaceae), 28.VII.1967, S. Kawai. Fifteen specimens of the adult female were mounted from twigs, and 13 of them, one the holotype, were examined for the numbers of wax-secreting organs (Table 1, 2).

Recognition characters

Adult female at full growth with prosoma swollen, distinctly broader than postsoma, rounded along free margin; prosomatic tubercles indiscernible; postsoma robust, metathorax and basal 2 abdominal segments practically same in width, pygidium broad obdeltoid, with a small recess apically; peribuccal sclerosis formed well; anterior spiracles each with a compact group of disc pores, posterior spiracles each with a smaller, much less compact group of disc pores. Perivulvar disc pores moderately numerous in 5 groups. Dorsal macroducts in single rows. Submedian macroducts on abd III–VI, the rows often divided into segmental and infrasegmental series on III–V; 1–4, often 3, at times absent on VI. Submarginal macroducts on abd III–V. A few submedian dorsal microducts often present on abd I and II. Lateral macroducts and lateral gland spines usually well represented in number on abd II and III. Marginal gland spines 2–4 on abd IV. Median trulla moderate in size, with basal halves sunk in apical recess of pygidium; thickly sclerotized broadly along free margins in contrast with less strongly sclerotized inner parts; basally with a pair of small sclerites set close together and with a horseshoe enclosing the sclerites, not much thickened, flat on anterior margin; mesal margins separated from each other by a narrow space subbasally, then bent outwards, the divergent margins finely serrate; rounded apically. Second and third trulla with both lobules well developed; lateral lobule in each trulla smaller than the mesal, with outer

apical margin slanting. Marginal processes of abd IV and V not prominent.

Second instar female with single marginal macroducts on abd III–VII or IV–VII; no further macroducts.

Remarks

I have no doubt that this species is identical with the form recorded by Kawai (1980) from Japan under the name *A. mali*. According to him, this insect is known from several scattered mountainous spots in Honsyû and Sikoku and from ‘Nana-kamado’, *Sorbus commixta*. The material available to the present study was collected by him and probably included in his records of *A. mali* from Japan. However, the host plant of the material is another species of *Sorbus*.

This species is distinguishable from *A. mali* in the median trullae characterized as follows: their mesal margins are parallel and separated from each other by a space subbasally and then bent outwards and divergent (diverging from the very bases in *A. mali*); their blades are sclerotized broadly along the free margins in contrast with the inner parts, which are less sclerotized (uniformly sclerotized in *A. mali*); the horseshoe at their bases is broadly flat on the anterior margin (thickened medially to form a robust process in *A. mali*). Moreover, in the present study, it has been found that *A. mali* is variable in the occurrence of dorsal macroducts on abdominal segments. The examined specimens of *A. sorbi* are uniform in this feature, though they are not sufficiently abundant to show any possible variation in this species.

Aulacaspis mali

(Figs 10–12)

Material examined

Collected in Ussuriysk, southern Primorskii Krai, Extreme Eastern Russia, on *Malus* sp. (Rosaceae), 5.VIII.1949. The dry material was superscribed with ‘*Aulacaspis mali*’. About 30 adult females were mounted from branches; not all of them are in good condition, and 24 of them, full-grown, have been examined for the numbers of wax-secreting organs (Table 1, 2).

Recognition characters

Adult female at full growth with prosoma swollen, distinctly broader than metasoma, and roundish along free margin; prosomatic tubercles indiscernible; postsoma robust, metathorax and basal 2 abdominal segments nearly same in width; pygidium broad obdeltoid, with a small recess apically; peribuccal scleroses represented by slender folds at most. Anterior spiracles each with a compact group of disc pores; posterior spiracles each with a smaller and less compact group of disc pores. Perivulvar disc pores moderately numerous in 5 groups. Submedian dorsal macroducts on abd III–VI, often divided into segmental and infrasegmental series on abd III and on IV; 1–4, usually 2 or 3, or rarely absent on VI; 1 or 2 submedian dorsal microducts often present on abd I and also on II, rarely replaced with macroducts on II. Submarginal macroducts on abd III–V, in a single or at times partly irregular row on III; abd II sometimes with 2–9 macroducts or at times with a few microducts submarginally. Lateral macroducts and lateral gland spines usually well represented in number on abd II and III. Marginal gland spines 2–5 on abd IV. Median trullae sunk in apical recess of pygidium except for their apical parts, sclerotized uniformly, thickly horseshoed basally, median part of the horseshoe especially

thickened to form a robust process, which is produced into the pygidium and bicuspid on the anterior margin; mesal margins diverging from bases, serrate usually irregularly and obscurely. Second and third trullae well represented, the lateral lobule in each being smaller than the mesal and slanting on outer apical margin. Marginal process of abd IV and V not prominent.

Second instar female with single marginal macroducts on abd III-VII, rarely on IV-VII; no further macroducts.

Remarks

In the *rosae* group, this species is characterized well in having the mesal margins of the median trullae diverging from the very bases. In the specimens examined in the present study, the median trullae are thickly horseshoed basally and the median part of the horseshoe is especially thickened to form a robust process as is often the case with *A. ericacearum*. *A. mali* is distinguishable from *A. ericacearum* in the shape of the blades of the median trullae as mentioned above, and differs also in the second instar female, which has no submarginal macropoduct.

The examined specimens are sometimes provided with macroducts submarginally, and rarely also submedially, on the second abdominal segment. (These macroducts on the second segment are included in the total numbers of dorsal macroducts in Table 1 and 2.) These cases are not usual but, so far as the submarginal macroducts are concerned, they are not very infrequent (10/48, that is, ca. 21% in occurrence), either, so that they are not occasional nor abnormal. Balachowsky (1954) and Danzig (1980, 1986, 1993) revised the species, but did not mention the occurrence of dorsal macroducts on the second abdominal segment. Danzig in her figures showed extra submarginal macroducts forming a discrete infrasegmental series on the third abdominal segment instead. In the examined specimens, such a distinct series of infrasegmental macroducts has not been observed. Further samples, collected at various localities and on various plants, should be examined carefully for a better understanding of all these cases of variation.

Kawai (1980) recorded *A. mali* from Japan, but in the view adopted in the present study his records were based on another form, which should represent a new species, *A. sorbi*. These species are clearly distinguishable from each other in the characters of the median trullae and may not completely be the same in the occurrence of dorsal macroducts (see *Remarks* under *A. sorbi*).

THE ROSAE GROUP: HIMALAYAN-TIBETAN SUBGROUP

Aulacaspis rosarum (Fig. 13)

Material examined

Collected in the city of Sagamihara, Kanagawa Pref., Honshû, Japan, on garden roses (Rosaceae), 30.I.2000, 9.I.2006, G. Tokihiro.

Collected in 'Chengtu' [Chengdu], Sichuan, China, on *Rosa* sp. (Rosaceae), 5.XII.1954 (part of the type material). A figure of the adult female based on a specimen mounted from this material is given in Takagi (2013, fig. 22).

Sixteen adult females mounted from the sample collected in Sagamihara in 2006, and 19 from the sample collected in Chengdu, all from branches, have been examined for the numbers of

wax-secreting organs (Table 1, 2).

Recognition characters

Adult female at full growth with prosoma swollen, distinctly broader than postsoma, square rather than rounded; prosomatic tubercles prominent; postsoma robust, slightly narrowing posteriorly on metathorax and basal 2 abdominal segments, pygidium broad obdeltoid, with a small recess apically; peribuccal scleroses developed. Anterior spiracles each with a moderate group of disc pores, which form irregular clusters within the group; posterior spiracles each with a smaller loose group of disc pores. Perivulvar disc pores moderately numerous in 5 groups. Submedian macroducts on abd II–VI, usually distinctly divided into segmental and infrasegmental series on II–IV; 2–6 on VI. Submarginal macroducts on abd III–V; in a single or irregularly double or multiple row on III. Lateral macroducts and lateral gland spines on abd II and III, gland spines often few on II. Marginal gland spines 1–6 on IV. Median trullae sunk in apical recess of pygidium, moderate in size, basally with a pair of sclerites set close together; mesal margins separated from each other by a narrow space subbasally, then curved and divergent, minutely serrate; roundish apically. Second and third trullae well developed, mesal and lateral lobules similar in shape but the latter smaller. Marginal processes of abd IV and V not prominent.

Second instar female with single marginal macroducts on abd IV–VII.

Remarks

This species is very similar to *A. rosae* in pygidial characters, but is easily distinguishable from the latter, irrespective of the growth of the body, in having submedian macroducts on the second abdominal segment in addition to those occurring on the third to sixth. In spite of this clear difference, *A. rosarum* had been confused with *A. rosae* and recorded under the name of that species probably in not a few warmer parts of the world before it was described from Chengdu (see under *Aulacaspis rosarum* in Annotated List). Under these circumstances, Chengdu or Sichuan may not necessarily be taken for the native land of the species.

In the present paper this species may be recorded from Japan for the first time at least formally. It may have been introduced only recently into Japan, but the possibility should not be excluded that it settled earlier and has been overlooked for a long time in this country, too.

Aulacaspis altiplagae

Remarks

This species was described from material collected at ‘Linzhi’ [Nyngchi], Tibet, at an altitude of 3400m, on *Rosa* sp. (Rosaceae). Recognition characters of this species may be given as follows on the basis of the description and figure in Chen (1983, fig. 24).

Adult female at full growth with prosoma swollen, a little broader than metathorax, rounded along free margin; prosomatic tubercles indiscernible. Anterior spiracles each with 20–25 disc pores; posterior spiracles each with 10–16. Perivulvar disc pores numerous in 5 groups. Submedian macroducts on abd II–VI, arranged along posterior margins of segments, those on III being divided into a segmental series and a slightly displaced infrasegmental one; 4–7, usually 6 or 7, on VI. Submarginal macroducts on abd

III–VI; 1–3, usually 2, on VI anteriorly to marginal macroducts. No lateral macroducts on abd II and III. Lateral gland spines 3–6 on abd II, 8–10 on III. Marginal gland spines 5–7 on abd IV, 2 or 3 on V, 1 or 2 on VI. Median trullae sunk in apical recess of pygidium for a greater part, large, surpassing marginal macroducts of abd VII in height; basally with a pair of sclerites set close together, not horseshoed; mesal margins strongly divergent, serrate. Second trullae with lobules rounded apically, the lateral lobule smaller; third trullae similar to the second but smaller.

Chen's description makes no mention of lateral macroducts, and his figure shows none of them. It is not easily understandable that this species has no lateral macroducts, because in his description and figure the species is provided with many dorsal macroducts. The figure includes the pygidial margin of the second instar female exuvial cast, which shows five single marginal macroducts occurring on the third to seventh abdominal segments.

Aulacaspis langtangana, n.sp.
(Figs 14–16)

Material examined

Collected near Ghora Tobela, Langtang Valley, Bagmati Zone, Nepal, on *Rosa sericea* (Rosaceae), 23.IX.1975, alt. ca.3200m (Sample 1) and ca.3000m (Sample 2). In the present study, 19 (Sample 1) and 32 (Samples 2) adult females, all mounted from branches, have been examined for the numbers of wax-secreting organs (Table 1, 2). Holotype: adult female from Sample 1.

Recognition characters

Adult female at full growth with prosoma swollen, broader than postsoma but not much, roundish along free margin; prosomatic tubercles indiscernible; postsoma robust, metathorax and basal 2 abdominal segments same in width, gently lobed laterally; pygidium broad obdeltoid, with a recess apically; peribuccal scleroses usually slender. Anterior spiracles each with a compact group of disc pores; posterior spiracles each with a smaller group. Perivulvar disc pores moderately numerous in 5 groups. Submedian macroducts on abd II–VI; at times (6–9%) 5–10 macroducts on I, usually 1–10 microducts occurring submedially on this segment instead; macroducts on II and also on III arranged in a row along posterior margin of segment; macroducts on IV and also on V divided into a segmental series and an infrasegmental one, which is distinctly displaced anteriorly from the segmental one; 4–11 macroducts on VI in a row often extending posteriorly. Submarginal macroducts on abd III–V in segmental rows; often 1 or a few infrasegmental macroducts occurring on IV and also on V, distinctly displaced laterally from the row, those on IV being at times more numerous, up to 7; in addition, often (45–47%) 1–4 on II, reduced in size, and usually 1 or 2 on VI anteriorly to marginal macroducts. Lateral macroducts and lateral gland spines usually well represented in number on abd II and III. Marginal gland spines 1–6 on abd IV, 1 or 2, rarely 3, on V, 1 or at times 2 on VI, 1 or rarely 2 on VII. Submarginal dorsal bosses on abd I and III often rudimentary or indiscernible. Median trullae sunk in apical recess of pygidium for a greater part; large, as high as marginal macroducts of abd VII; basally with a pair of sclerites set close together and horseshoed round the sclerites; mesal margins separated from each other by a broad space subbasally, then strongly divergent and finely serrate; rounded apically. Second and third trullae bilobulate in many cases as usual in the genus,

but unilobed in not a few cases; mesal lobule rounded, lateral lobule less produced, with outer apical margin slanting. Marginal processes on abd IV and V distinct but not prominent.

Second instar female with single macroducts marginally on abd III–VII, submarginally on IV–VI, submedially on IV–VII (the one on VII being situated laterally to anal opening), and medially on VI (anterolaterally to anal opening), but seldom in a complete set; at times with single small macroducts marginally on abd II and submedially on I–III.

Remarks

This species is probably closely related to *A. altiplagiae*, another high-altitudinal scale insect, which was described from Nyngchi, Tibetan Plateau, the localities of these species being some 850km distant from each other. My understanding of *A. altiplagiae* is based exclusively on Chen (1983, fig. 24) (see *Remarks* under *Aulacaspis altiplagiae*).

This species is similar to *A. altiplagiae* in the body shape and especially in the prosoma, which is swollen only weakly and rounded, in the marginal gland spines not always single on the fifth to seventh abdominal segments, in the median trullae large and strongly divergent, and in having one or a few submarginal macroducts on each side of the sixth abdominal segment.

This species has infrasegmental macroducts occurring submedially and submarginally on the fourth and fifth abdominal segments and distinctly displaced from the segmental rows of macroducts, whereas in the figure of *A. altiplagiae* all the macroducts are arranged along the posterior margins of the segments on which they occur. *A. langtangana* has lateral macroducts on the second and third abdominal segments, but this feature is not mentioned in the description, and not shown in the figure, of *A. altiplagiae*. The specimens of *A. langtangana* have submedian macroducts, which are often replaced with microducts, on the first abdominal segment, whereas the occurrence of such ducts is not mentioned in *A. altiplagiae*. The median trullae are horseshoed basally in *A. langtangana*, but the figure of *A. altiplagiae* shows no trace of the horseshoe. The second instar female of *A. langtangana* is provided not only with marginal macroducts but also with median, submedian and submarginal ones; what the figure of *A. altiplagiae* shows is limited to the occurrence of marginal macroducts.

Provided several if not all of these presumed differences are real, they may be sufficient to show that *A. langtangana* is distinct from *A. altiplagiae*. Above all, the occurrence of median, submedian, and submarginal dorsal macroducts in the second instar female may be adopted as a useful diagnostic character of *A. langtangana*.

In the examined adult females, the second and third trullae are often unilobed, with the lateral lobule lacking or with the mesal and lateral lobules fused together: 47% and 39% of the second trullae and 13% and 16% of the third trullae in Sample 1 and 2, respectively, are unilobed. In the examined exuvial casts of the second instar female 29% of the second trullae in Sample 1 and 2 combined are unilobed. These percentages show that this variation was far from occasional in the populations from which the samples were obtained. The biological significance of the variation is not knowable at present. However, the possibility may not be excluded that the variation takes place as an effect of some high-altitudinal environmental conditions on the course of morphogenesis in the stages of the adult and second instar females. If this assumption is correct, it represents no more than deformation under the particular conditions.

Aulacaspis pieridis, n.sp.
(Fig. 17, 18)

Material examined

Collected near Ghora Tobela, Langtang Valley, Bagmati Zone, Nepal, alt. 2750m, on *Pieris formosa* (Ericaceae), 29.IX.1975. Occurring on branches and leaves; 18 adult females mounted from the ramicolous subsample and 3 from the foliicolous subsample have been examined for the numbers of wax-secreting organs (Table 1, 2); the description below is based on both subsamples. Holotype: adult female from the ramicolous subsample.

Recognition characters

Adult female at full growth with prosoma swollen, broader than postsoma but not much, tending to be ovate in outline of free margin; prosomatic tubercles indiscernible; metathorax and basal 2 abdominal segments nearly same in width; pygidium slightly roundish along free margin, with a small recess apically; peribuccal scleroses usually not developed. Anterior spiracles each with a group of many disc pores, which are small and make some irregular and narrow blank spaces within the group; posterior spiracles each with a smaller group of disc pores, which also are small and irregularly clustered within the group. Perivulvar disc pores moderately numerous in 5 groups. Submedian and submarginal macroducts on abd III–V, in single or partly irregular rows along posterior margins of segments; abd VI usually with no submedian macroduct, at times with 1. Lateral macroducts and lateral gland spines well represented on abd II and III; lateral gland spines on III well developed in size, as large as marginal gland spines occurring on IV and V. Marginal gland spines 4–9 on abd IV, 1–4, usually 2, on V. Median trullae moderate in size, sunk in apical recess of pygidium for a greater part; basally united through a disk-like sclerite, horseshoe round the sclerite; mesal margins separated from each other by a good space subbasally, then divergent and obscurely serrate; blunt or narrowly rounded apically. Second and third trullae with both lobules well developed. Marginal processes of abd IV and V low.

Second instar female usually with single marginal macroducts on abd III–VII and a submarginal macroduct on V; at times no marginal one on III; at times no submarginal one on V; at times a submarginal one also on III or IV.

Remarks

This species agrees with *A. ericacearum* in having, usually, a submarginal macroduct on each side of the fifth abdominal segment in the second instar female. In the adult female, it differs from the latter in the body less robust, the prosoma tending to be ovate and the postsoma being not much broadened, in the spiracular disc pores small unusually for a member of the genus, and in the lateral gland spines on the third abdominal segment enlarged also unusually. In consideration of all these characters the view may be adopted that *A. pieridis* is not particularly closely related to *A. ericacearum* and that the agreement in the second instar female is attributable to parallelism.

Aulacaspis lyoniae, n.sp.
(Figs 19–22)

Material examined

Collected in Bagmati Zone, Nepal, on *Lyonia ovalifolia* and *Pieris formosa* (both these plants belonging to the family Ericaceae).

On trekking from Kulumsang to Pati Bhanjyang, alt. ca.2400m, on *Lyonia ovalifolia*, 12.X.1975 (Sample 1); Syabru, alt. 2260m, on *Pieris formosa*, 21.IX.1975 (Sample 2); Ramche, alt. ca.1700m, on *Lyonia ovalifolia*, 15.IX.1975 (Sample 3); Ramche, alt. ca.1600m, on *Lyonia ovalifolia*, 15.IX.1975 (Sample 4). Females and males occurring on branches; 32 adult females from Sample 1, 32 from Sample 2, 11 from Sample 3, and 7 from Sample 4 have been examined for the numbers of wax-secreting organs (Table 1, 2). Holotype: adult female from Sample 1.

Recognition characters

Adult female at full growth with prosoma swollen, much broader than postsoma, rounded along free margin; prosomatic tubercles indiscernible; metathorax and basal 2 abdominal segments nearly same in width, well lobed laterally; pygidium obdeltoid, apically with a recess; peribuccal scleroses usually not developed. Anterior spiracles each with a loose group of disc pores; posterior spiracles each with a longitudinally arciform fold of derm laterally, some disc pores being arranged along the crease of the fold and others scattered mesally to the fold and around spiracular orifice. Perivulvar disc pores numerous in 5 groups. Submedian macroducts on abd III–V, 0–5, usually 1 or 2, on VI; when numerous, usually divided into segmental and infrasegmental series on III–V, the infrasegmental series on IV distinctly displaced anteriorly from the segmental one. Submarginal macroducts on abd III–V. Submedian dorsal microducts present or absent; when present, usually 1 or a few on abd I and II, at times more numerous, up to 7 on I and to 9 on II; sometimes 1 or a few on metathorax and abd III. Lateral macroducts and lateral gland spines well represented in number on abd II and III, these gland spines being much shortened. Marginal gland spines 1–5 on abd IV. Median trullae sunk in apical recess of pygidium, moderate in size, rather narrow, strongly sclerotized broadly along free margins; basally with a pair of small sclerites usually set close together, not horseshoed; mesal margins separated by a space from each other subbasally, then divergent and serrate; rounded apically. Second and third trullae well developed, with lateral lobule smaller than the mesal. Marginal processes flattish on abd IV and V.

Second instar female with single marginal macroducts on abd IV–VII, at times also on III.

Remarks

This species is sympatric with *A. pieridis*, but has been collected at lower altitudes, and shares one of the host plants, *Pieris formosa*, with the latter. In morphological characters it does not appear to be related to the latter particularly closely. Among the species of the *rosae* group, this species is easily recognizable in the posterior spiracles each provided with a well-developed dermal fold laterally, which bears a row of disc pores along the crease, and in having much shortened gland spines on the lateral lobes of the second and third abdominal segments.

The four examined samples, collected at four different altitudes, exhibit decreases in the numbers of wax-secreting organs apparently in accordance with the decreasing

altitudes of the collection spots (Table 1, 2). Obvious gaps in the observed values are found between Sample 2 and 3, which were collected at spots different by 560m in altitude. In addition to the decreases of the disc pores, macroducts, and gland spines, the submedian dorsal microducts which usually occur in Sample 1 and 2 disappear from Sample 3 and 4 usually completely.

I have failed to find any significant difference among the samples in other features. In the present state of my study, I adopt the view that the four samples all belong to the same species and that the gaps will be bridged by material to be obtained from the blank altitudes.

THE MEGALOBA GROUP

Aulacaspis megaloba (Figs 23–25)

Material examined

Collected in three Zones of Nepal on plants of *Rubus* (Rosaceae): Kosi Zone, eastern Nepal, 14–19.XI.1983 (Sample 1–7); Kathmandu Valley, Bagmati Zone, central Nepal, 6.IX.1975 (Sample 8); Pokhara District, Gandaki Zone, central Nepal, 10.XII.1983 (Sample 9). The samples are numbered in order of collection altitude.

Sample 1–4, on *Rubus paniculatus*: on trekking from Sankranti to Sikkama, alt. ca.2500m (Sample 1); from Sikkama to Madi Mulkharka, alt. ca.2400m (Sample 2); from Basantpur to Hile, alt. ca.2300m (Sample 3); from Sikkama to Madi Mulkharka, alt. 2250m (Sample 4).

Sample 5–7, on *Rubus ellipticus*: near Sankranti, alt. ca.2000m (Sample 5), alt. 1950m (Sample 6), alt. ca.1900m (Sample 7).

Sample 8, on *Rubus* sp., Balaju, Nagarjun, alt. ca.1400m.

Sample 9, on *Rubus ellipticus*, Chotepatan, alt. 980m.

Females and males occurring on twigs and branches; females burrowing under the bark in Sample 2 and 3; 183 adult females in total have been examined for the numbers of wax-secreting organs (Table 3, 4).

Recognition characters

Adult female at full growth with prosoma swollen, distinctly broader than metasoma, roundish along free margin; prosomatic tubercles indiscernible or indicated by slight prominences; postsoma gradually narrowing posteriorly, pygidium obdeltoid, with a large recess apically; peribuccal scleroses sometimes developed well. Anterior spiracles each with a group of small disc pores crowded together; posterior spiracles each with a group of disc pores irregularly clustered. Perivulvar disc pores numerous in 5 groups. Submedian macroducts on abd II–VI, often divided into segmental and infrasegmental series, but not always clearly, on II–V; variable in number, abd VI at times with no submedian macroduct. Submarginal macroducts on abd III–V. Lateral macroducts and lateral gland spines usually well represented in number on abd II and III. Marginal gland spines 2–7 on abd IV. Median trullae large, deeply sunk in apical recess of pygidium, much exceeding marginal macroducts of abd VII in height; basally with a pair of small sclerites set close together, thickly horseshoed round the sclerites; elongate, with mesal margins diverging from bases and finely serrate; rounded apically. Second and third trullae well represented, each with lateral lobule smaller than the mesal.

Marginal processes on abd IV and V not prominent.

Second instar female with 5 marginal macroducts on abd III–VII or 4 on IV–VII; at times with a small submarginal macroduct occurring on V in association with 5 marginal macroducts.

Remarks

This species was described from Kunming (type locality) and Hong Kong, southern China, and from plants of *Rubus*. The adult females examined in the present study agree well with the original description (Scott, 1952, fig. 26) in the very large median trullae, in the arrangement of the dorsal macroducts, and in other features. Adult females at full growth do not exactly agree in body shape with Scott's figure, which may represent a growing adult female.

The examined samples are divisible into two groups: Group I is composed of Sample 1–4 and Group II contains Sample 5–9. The samples of Group I occur at higher altitudes, the collection spot of Sample 4 being 250m higher than that of Sample 5, and generally have more numerous wax organs. This pattern is clearly shown by the correlation between the mean total numbers of the dorsal macroducts and those of the perivulvar disc pores, as is visualized in Fig. 1. In this chart the two groups are plotted unexpectedly distantly from each other in comparison with the narrow extent of the blank altitudes separating them. It is noteworthy that there is within each group no obvious correlation between the numbers of these wax organs in spite of the apparent correlation at the level of the groups. This indicates that in either group the dorsal macroducts and also the perivulvar disc pores do not vary in number in accordance with the altitudes of the collection spots. Moreover, I have failed to detect in the variation any tendency or regularity which is common to both groups and, thus, may connect them. Furthermore, Sample 8 is isolated in the numbers of the wax organs, but it is not extraordinary in other features.

Sample 1–4 were collected only from *Rubus paniculatus* and Sample 5–9 (except Sample 8, of which the host plant species was not identified) from *Rubus ellipticus*, whereas these plant species broadly overlap in distribution in the Midlands of Nepal.

On the basis of the observations above, the two groups of samples may be supposed to represent different morphological units, which are different also in habitat altitude and host association. If they represent two species, the name *A. megaloba* should be applied to Group II (see Fig. 1).

In spite of all this, I have failed to find any stable morphological characters usable as diagnostic ones for distinguishing between the two groups. The prosoma and basal two abdominal segments become sclerotized at full growth in the adult females of Group I, whereas usually not so much sclerotized in Group II. However, the dermal sclerotization is a growth phenomenon, and does not always afford stable taxonomic characters. In the second instar female, Group II has the marginal macroducts tending to be decreased to four pairs. However, the number of this feature in this instar is not always stable in a species of *Aulacaspis*. Under these circumstances, there is no good reason for separating these groups into different species. Interpretations are attempted below from this viewpoint for the observations adopted above as grounds for the possibility that the samples represent more than one species.

First, not only altitude but other topographical factors should change environmental conditions. In trekking on Himalayan mountains, especially at higher altitudes, I noticed

that opposite slopes sometimes exhibited a remarkable difference in vegetation. It is easily conceivable that the northern (south-facing) and southern (north-facing) slopes of a valley, for example, will produce significant differences in some abiotic conditions between them. It is reasonable therefore to think that, especially at higher altitudes, the numerical variation of wax organs should reflect not only the change of altitude but also the configuration of mountains.

Secondly, the narrow extent (250m) of the blank altitudes between Group I and II, therefore, does not necessarily mean correspondingly small gaps in the numbers of wax organs. It is very probable that the blank altitudes are simply due to an occasional failure to collect material at those altitudes, having no further meaning.

Thirdly, *Rubus paniculatus* usually grows at altitudes of 1500 to 3200m, whereas *Rubus ellipticus* is mainly tropical to subtropical in distribution. It is possible, therefore, that the association of Group I with *R. paniculatus* and that of Group II with *R. ellipticus* simply reflect the relative frequencies in appearance of these plants in different environmental conditions (altitude and mountain configuration). If this assumption is correct, the combinations in host association should have no particular significance. Syntopic samples occurring on *R. paniculatus* and *R. ellipticus*, if available, will be helpful for deciding the question about the relation between the two groups.

Aulacaspis amamiana
(Fig. 26, 27)

Material examined

Collected in three islands of the Ryûkyû Islands, Japan, on *Rubus sieboldii* (Rosaceae).

Sumiyô, Amami-Ôshima, 15.V.1957 (type material) (Sample 1; specimens newly mounted from the material); Tate, Tokuno-Sima, 8.XI.1989 (Sample 2); Oppa-dake, Nakizin, Okinawa, 21.III.1989 (Sample 3). Females occurring on branches and leaves; males on branches (Sample 1). Ramicolous and foliicolous adult females from Sample 1 and 3 and ramicolous ones from Sample 2, 103 in total, have been examined for the numbers of wax-secreting organs (Table 3, 4).

Recognition characters

Adult female at full growth with prosoma swollen but not much, scarcely or a little broader than postsoma, roundish along free margin; prosomatic tubercles indiscernible; postsoma robust, basal 3 segments nearly same in width, abd II tending to be produced laterally; pygidium obdeltoid, with a large recess apically; peribuccal scleroses represented by slender folds at most. Anterior spiracles each with a compact group of disc pores; posterior spiracles each with a smaller group of disc pores. Perivulvar disc pores moderately numerous in 5 groups. Submedian macroducts on abd III–VI, at times divided into segmental and infrasegmental series on III and IV; 1–7, usually 2 or 3, on VI. Submarginal macroducts on abd III–V. Lateral macroducts and lateral gland spines moderate in number on abd II and III; marginal gland spines 1–4, usually 2, on IV. Median trullae sunk in apical recess of pygidium, very large, much surpassing marginal macroducts of abd VII in height, basally with a thick connecting yoke; divergent and finely serrate on mesal margins; blunt or rounded apically. Second and third trullae small, each with lateral lobule much smaller than the mesal; third trullae with mesal lobule not produced beyond apex of pore prominence situated just mesally. Marginal processes on abd IV and V low.

Second instar female with single marginal macroducts on abd IV–VII.

Remarks

This species is similar to *A. megaloba* in having very large median trullae, and both these species occur on plants of *Rubus*. They may be grouped together, and certain other forms described from *Rubus* may also be referred to the group (see *Aulacaspis megaloba* and *Aulacaspis amamiana* in Annotated list).

This species differs from *A. megaloba*, above all, in body shape and in having no submedian macroducts on the second abdominal segment. The median trullae are connected together basally by a thick yoke, which appears to be sclerotized almost uniformly, showing no distinct parts (mesobasal sclerites and horseshoe). The lateral trullae are smaller, and especially the third trullae are much less developed, than in *A. megaloba*.

The reliable records of *A. amamiana* are restricted to the Ryûkyû Islands. The three samples examined in the present study are very similar to each other, suggesting no clear differentiation among the island populations, which should be isolated from each other.

CONCLUDING REMARKS

If the concept and composition of the *rosae* group adopted in this study are correct, and if the wide disjunction in distribution between the northeastern Asian subgroup and the Himalayan-Tibetan subgroup reflects the reality, the evolution of this group should have been closely associated with the glacial-interglacial change of climate in eastern Asia. The origin of this group was probably in tropical-subtropical eastern Asia, where the genus is abundant in species. In fact, *A. rosarium*, which is referred to the Himalayan-Tibetan subgroup, has spread broadly in tropical and subtropical areas in the world. However, the group is predominantly boreomontane, and should have further species occurring at high altitudes, whereas surveys for scale insects in such environments have been attempted in very limited areas in eastern Asia as well as in other regions of the world.

The examined samples of *A. lyoniae* and *A. megaloba* are available from broad ranges of altitudes on the Himalayas. In the Malay Peninsula, *A. ferrisi* Scott was collected at various altitudes including a mountain ridge 1700m high and a spot by the seaside (Takagi, 2014). These species are variable in the numbers of wax-secreting organs so broadly that it may well be questioned whether they are recognized correctly. If they are recognized really correctly, they show how broadly one species can vary in the numbers of wax organs in accordance with environmental conditions varying within a limited geographical extent.

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Table 1. Numbers of disc pores and dorsal macroducts in eight species of the *rosae* group of *Aulacaspis*.

Species Sample Host plant	Anterior spiracular disc pores	Posterior spiracular disc pores	Perivulvar disc pores total	Dorsal macroducts total	Submedian macroducts on abd VI
<i>rosae</i> <i>Sapporo</i> <i>Rosa</i> r	21-27.8-35 [64]	6-10.7-20 [64]	116-132.8-155 [32]	85-100.8-123 [32]	1-5 1 [1] 2 [8] 3 [50] 4 [3] 5 [2]
<i>rosae</i> <i>Mt.Takakuma</i> <i>Rubus</i> r	22-33.1-47 [56]	7-12.4-22 [62]	100-124.7-144 [32]	70-82.2-103 [32]	1-4 1 [1] 2 [24] 3 [36] 4 [3]
<i>Rosae</i> <i>Mt.Mikawa</i> <i>Epigaea</i> r	ca.(20-30)	9-11 [5]	78 103 113	50 63 67	1-3 1 [3] 2 [2] 3 [1]
<i>rosae</i> <i>Mt.Mikawa</i> <i>Epigaea</i> f	20-26.3-35 [33]	7-9.9-14 [60]	82-104.9- 127 [30]	46-61.0-72 [30]	0-2 0 [1] 1 [43] 2 [16]
<i>ericacearum</i> <i>Sapporo</i> <i>Leucothoe</i> r	21-27.3-40 [64]	6-11.4-18 [64]	86-120.4- 155 [32]	42-60.3-75 [32]	1-3 1 [24] 2 [37] 3 [3]
<i>sorbi</i> Odai- ga-Hara <i>Sorbus</i> r	22-30.3-36 [25]	6-9.1-19 [22]	100-112.4- 129 [13]	68-74.9-84 [13]	0-4 0 [3] 1 [4] 2 [4] 3 [14] 4 [1]
<i>mali</i> <i>Ussuriysk</i> <i>Malus</i> r	16-27.0-37 [20]	6-8.4-12 [42]	81-100.3- 132 [24]	68-78.0-92 [24]	0-4 0 [1] 1 [3] 2 [27] 3 [15] 4 [2]
<i>rosarum</i> <i>Sagamihara</i> <i>Rosa</i> r	23-31.7-40 [31]	10-14.3-18 [31]	130-135.8-145 [11]	83-108.0-123 [14]	2-4 2 [7] 3 [17] 4 [5]
<i>rosarum</i> <i>Chengdu</i> <i>Rosa</i> r	20-24.3-33 [20]	8-11.6-17 [30]	116-146.9-186 [17]	102-141.9-169 [19]	2-6 2 [1] 3 [7] 4 [18] 5 [8] 6 [4]
<i>langtangana</i> Sample 1 <i>Rosa</i> r	20-26.9-35 [28]	13-17.1-23 [37]	125-138.9-154 [19]	94-120.8-150 [19]	4-7.4-11 [38]
<i>langtangana</i> Sample 2 <i>Rosa</i> r	25-29.3-45 [37]	11-18.3-25 [58]	126-154.2-192 [29]	110-139.9-176 [29]	4-7.9-11 [58]
<i>pieridis</i> <i>Ghora Tobela</i> <i>Pieris</i> r	ca.(52-95)	13-19.0-32 [36]	120-148.5-190 [18]	55-78.2-100 [17]	0 [38] 1 [4]
<i>pieridis</i> <i>Ghora Tobela</i> <i>Pieris</i> f	ca.(25-68)	12-17 [6]	90, 121, 130	35, 62, 68	0 [6]
<i>Iyoniae</i> Sample 1 <i>Lyonia</i> r	13-21.6-28 [64]	8-14.3-22 [64]	142-176.5-204 [32]	68-91.3-113 [32]	1-5 1 [21] 2 [39] 3 [3] 4 [0] 5 [1]
<i>Iyoniae</i> Sample 2 <i>Pieris</i> r	13-19.2-30 [64]	8-13.6-18 [64]	136-162.2-220 [32]	62-78.9-96 [32]	0-2 0 [1] 1 [35] 2 [28]
<i>Iyoniae</i> Sample 3 <i>Lyonia</i> r	9-14.2-17 [22]	6-7.5-9 [22]	105-118.8-133 [11]	33-41.8-55 [11]	0 [3] 1 [19]
<i>Iyoniae</i> Sample 4 <i>Lyonia</i> r	10-13.7-19 [13]	5-7.2-10 [14]	94-108.9-141 [7]	25-33.4-38 [7]	0 [5] 1 [9]

r: ramicolous sample or subsample; f: foliicolous subsample. 21-27.8-36 [64]: lowest, mean, and highest values in the mentioned order, followed by sample or subsample size in brackets. ca.(20-30): range based on approximate values for crowded pores. 9-11 [5]: range followed by subsample size in brackets. 78 103 113: individual values. 1-5: range. 1 [1]: value followed by frequency in brackets.

Table 2. Numbers of lateral macroducts, lateral gland spines, and marginal gland spines in eight species of the *rosae* group of *Aulacaspis*.

Species Sample Host plant	Lateral macroducts on abd II	Lateral macroducts on abd III	Lateral gland spines on abd II	Lateral gland spines on abd III	Marginal gland spines on abd IV
<i>rosae</i> Sapporo <i>Rosa</i> r	5-7.2-12 [64]	3-5.4-8 [64]	7-10.0-14 [64]	7-11.4-15 [64]	3-4.2-6 [64]
<i>rosae</i> Mt.Takakuma <i>Rubus</i> r	1-5.3-8 [64]	2-4.8-7 [64]	5-8.8-12 [64]	7-10.1-13 [64]	2-3.7-5 [64]
<i>rosae</i> Mt.Mikawa <i>Epigaea</i> r	2-6 [6]	2-4 [6]	3-7 [6]	8-10 [6]	2-4 [6]
<i>rosae</i> Mt.Mikawa <i>Epigaea</i> f	3-5.0-8 [60]	2-4.3-7 [60]	3-6.1-9 [60]	6-9.6-12 [60]	2-3.6-6 [60]
<i>ericacearum</i> Sapporo <i>Leucothoe</i> r	2-4.3-7 [64]	2-3.3-6 [64]	1-3.7-6 [64]	2-5.6-9 [64]	1-2.4-4 [64]
<i>sorbi</i> Odai- ga-Hara <i>Sorbus</i> r	5-6.4-8 [25]	3-5.3-7 [25]	2-4.8-6 [24]	2-5.7-8 [26]	2-3.0-4 [26]
<i>mali</i> Ussuriysk <i>Malus</i> r	5-6.8-9 [37]	4-5.0-8 [44]	4-4.9-7 [35]	2-5.9-8 [44]	2-3.2-5 [47]
<i>rosarum</i> Sagamihara <i>Rosa</i> r	3-5.4-8 [29]	2-4.5-6 [28]	1-1.6-3 [28]	5-7.6-12 [28]	1-3.0-5 [28]
<i>rosarum</i> Chengdu <i>Rosa</i> r	4-7.2-10 [37]	3-6.3-9 [37]	1-3.9-7 [32]	6-10.3-15 [33]	2-4.1-6 [36]
<i>langtangana</i> Sample 1 <i>Rosa</i> r	3-5.7-10 [38]	1-4.0-7 [38]	3-5.0-7 [38]	3-6.7-10 [38]	2-3.4-6 [38]
<i>langtangana</i> Sample 2 <i>Rosa</i> r	4-6.6-13 [58]	3-5.2-10 [58]	3-5.5-9 [58]	6-8.2-11 [58]	1-3.2-5 [58]
<i>pieridis</i> Ghora Tobela <i>Pieris</i> r	3-7.7-11 [35]	4-6.7-10 [36]	4-7.8-11 [35]	8-10.9-15 [36]	4-6.9-9 [36]
<i>pieridis</i> Ghora Tobela <i>Pieris</i> f	3-9 [6]	3-8 [6]	4-7 [6]	6-10 [6]	4-6 [6]
<i>lyoniae</i> Sample 1 <i>Lyonia</i> r	9-13.4-17 [64]	6-10.5-13 [64]	9-12.7-18 [64]	13-16.9-22 [64]	2-5 2 [4] 3 [40] 4 [17] 5 [3]
<i>lyoniae</i> Sample 2 <i>Pieris</i> r	9-12.0-16 [64]	6-9.8-12 [64]	9-13.2-18 [64]	10-16.6-23 [64]	1-5 2 [7] 3 [35] 4 [19] 5 [2]
<i>lyoniae</i> Sample 3 <i>Lyonia</i> r	6-8.2-11 [22]	6-7.4-9 [22]	4-6.6-9 [22]	6-9.1-13 [22]	1-3 1 [1] 2 [13] 3 [8]
<i>lyoniae</i> Sample 4 <i>Lyonia</i> r	6-7.8-9 [14]	4-6.7-8 [14]	4-4.9-6 [14]	6-7.7-9 [14]	1-3 1 [1] 2 [11] 3 [2]

r: ramicolous sample or subsample; f: foliicolous subsample. 5-7.2-12 [64]: lowest, mean, and highest values in the mentioned order, followed by sample or subsample size in brackets. 2-6 [6]: range followed by subsample size in brackets. 2-5: range. 2 [4]: value followed by frequency in brackets.

Table 3. Numbers of disc pores and dorsal macroducts in two species of the *megaloba* group of *Aulacaspis*.

Species Sample Host plant	Anterior spiracular disc pores	Posterior spiracular disc pores	Perivulvar disc pores total	Dorsal macroducts total	Submedian macroducts on abd VI
<i>megaloba</i> Sample 1 <i>Rubus r</i>	ca.(46-66)	24-30.4-37 [28]	219-258.3--302 [15]	104-125.1-144 [15]	3-7 3 [1] 4 [16] 5 [9] 6 [3] 7 [1]
<i>megaloba</i> Sample 2 <i>Rubus r</i>	ca.(55-80)	22-32.1-45 [55]	227-264.5-309 [30]	80-115.9-152 [30]	3-7 3 [5] 4 [23] 5 [18] 6 [10] 7 [4]
<i>megaloba</i> Sample 3 <i>Rubus r</i>	ca.(50-70)	23-30.6-40 [14]	229-263.3- 295 [7]	100-133.4-148 [7]	4-7 4 [4] 5 [5] 6 [4] 7 [1]
<i>megaloba</i> Sample 4 <i>Rubus r</i>	ca.(50-80)	11-26.8-38 [24]	201-252.4- 299 [13]	106-128.9-169 [13]	4-8 4 [7] 5 [7] 6 [7] 7 [4] 8 [1]
<i>megaloba</i> Sample 5 <i>Rubus r</i>	ca.(45-91)	18-33.5-57 [35]	149-169.9- 197 [18]	52-76.3-99 [18]	1-4 1 [1] 2 [10] 3 [22] 4 [3]
<i>megaloba</i> Sample 6 <i>Rubus r</i>	ca.(40-80)	ca.(20-50)	161-185.3- 220 [10]	63-75.1-86 [10]	1-4 1 [3] 2 [10] 3 [6] 4 [1]
<i>megaloba</i> Sample 7 <i>Rubus r</i>	ca.(28-44)	18-25.6-37 [58]	138-160.6-182 [30]	72-90.1-108 [30]	2-4 2 [17] 3 [30] 4 [13]
<i>megaloba</i> Sample 8 <i>Rubus r</i>	ca.(20-53)	9-18.6-32 [59]	112-126.4-146 [30]	46-53.4-70 [30]	0-3 0 [5] 1 [28] 2 [26] 3 [1]
<i>megaloba</i> Sample 9 <i>Rubus r</i>	ca.(28-46)	15-23.2-34 [59]	122-162.6-191 [30]	56-77.3-100 [30]	0-4 0 [10] 1 [23] 2 [20] 3 [4] 4 [3]
<i>amamiana</i> Sample 1 <i>Rubus r</i>	21-29.1-39 [33]	10-14.5-20 [31]	86-97.2-114 [19]	55-64.3-77 [19]	1-4 1 [1] 2 [24] 3 [12] 4 [1]
<i>amamiana</i> Sample 1 <i>Rubus f</i>	22-27.8-35 [28]	5-11.9-18 [38]	65-93.7-124 [26]	45-60.8-74 [26]	2-4 2 [35] 3 [16] 4 [1]
<i>amamiana</i> Sample 2 <i>Rubus r</i>	23-28.3-37 [27]	5-11.5-19 [47]	71-85.2-105 [27]	43-58.4-72 [27]	2-4 2 [42] 3 [11] 4 [1]
<i>amamiana</i> Sample 3 <i>Rubus r</i>	18-29.1-39 [23]	6-12.8-24 [26]	79-93.2-115 [14]	51-64.4-77 [14]	3-7 3 [8] 4 [17] 5 [2] 6 [0] 7 [1]
<i>amamiana</i> Sample 3 <i>Rubus f</i>	22-28.0-35 [33]	5-12.8-21 [34]	67-91.6-104 [17]	48-61.3-71 [17]	2-4 2 [18] 3 [15] 4 [1]

r: ramicolous sample or subsample; f: foliicolous subsample. ca.(46-66): range based on approximate values for crowded pores. 24-30.4-37 [28]: lowest, mean, and highest values in the mentioned order, followed by sample or subsample size in brackets. 3-7: range. 3 [1]: value followed by frequency in brackets.

Table 4. Numbers of lateral macroducts, lateral gland spines, and marginal gland spines in two species of the *megaloba* group of *Aulacaspis*.

Species Sample Host plant	Lateral macroducts on abd II	Lateral macroducts on abd III	Lateral gland spines on abd II	Lateral gland spines on abd III	Marginal gland spines on abd IV
<i>megaloba</i> Sample 1 <i>Rubus r</i>	4-10.1-14 [29]	8-11.5-16 [29]	6-9.8-15 [29]	11-15.5-20 [29]	4-5.3-7 [30]
<i>megaloba</i> Sample 2 <i>Rubus r</i>	1-7.7-14 [56]	3-9.4-15 [56]	1-6.2-11 [54]	3-13.0-17 [56]	3-4.8-6 [59]
<i>megaloba</i> Sample 3 <i>Rubus r</i>	4-10.1-13 [14]	7-12.5-16 [14]	3-7.1-10 [14]	10-14.9-17 [14]	4-5.4-7 [14]
<i>megaloba</i> Sample 4 <i>Rubus r</i>	6-8.6-11 [25]	7-10.7-14 [26]	4-8.4-16 [25]	11-15.3-20 [26]	4-5.0-7 [26]
<i>megaloba</i> Sample 5 <i>Rubus r</i>	3-5.3-9 [36]	3-5.4-8 [36]	2-4.7-9 [36]	6-8.1-14 [36]	2-3.2-5 [36]
<i>megaloba</i> Sample 6 <i>Rubus r</i>	1-5.1-8 [20]	3-4.8-7 [20]	3-5.7-7 [20]	7-8.6-11 [20]	2-3.2-5 [20]
<i>megaloba</i> Sample 7 <i>Rubus r</i>	1-6.7-11 [60]	2-6.2-9 [60]	3-7.8-12 [60]	7-10.8-16 [60]	2-4.2-7 [60]
<i>megaloba</i> Sample 8 <i>Rubus r</i>	3-5.0-7 [60]	3-4.7-7 [60]	2-3.7-6 [60]	4-6.4-9 [60]	2-2.5-3 [60]
<i>megaloba</i> Sample 9 <i>Rubus r</i>	5-7.5-10 [60]	5-6.9-9 [60]	3-6.1-10 [60]	5-9.5-14 [59]	2-4.1-7 [60]
<i>amamiana</i> Sample 1 <i>Rubus r</i>	2-4.4-7 [38]	2-3.7-5 [38]	2-2.9-4 [38]	2-4.1-6 [38]	1-3 1 [1] 2 [31] 3 [4]
<i>amamiana</i> Sample 1 <i>Rubus f</i>	2-4.6-6 [51]	2-3.9-6 [52]	2-3.1-5 [51]	2-4.0-6 [52]	1-4 1 [3] 2 [41] 3 [6] 4 [1]
<i>amamiana</i> Sample 2 <i>Rubus r</i>	1-4.8-7 [51]	2-3.3-6 [51]	1-3.5-5 [51]	2-4.1-6 [51]	1-3 1 [3] 2 [45] 3 [1]
<i>amamiana</i> Sample 3 <i>Rubus r</i>	2-4.8-8 [28]	2-3.2-5 [28]	1-3.1-5 [28]	2-3.6-5 [28]	1-3 1 [1] 2 [21] 3 [5]
<i>amamiana</i> Sample 3 <i>Rubus f</i>	3-4.6-6 [34]	2-3.7-6 [34]	2-3.3-4 [34]	2-3.7-5 [34]	1-3 1 [1] 2 [27] 3 [6]

r: ramicolous sample or subsample; f: foliicolous subsample. 4-10.1-14 [29]: lowest, mean, and highest values in the mentioned order, followed by sample or subsample size in brackets. 1-3: range. 1 [1]: value followed by frequency in brackets.

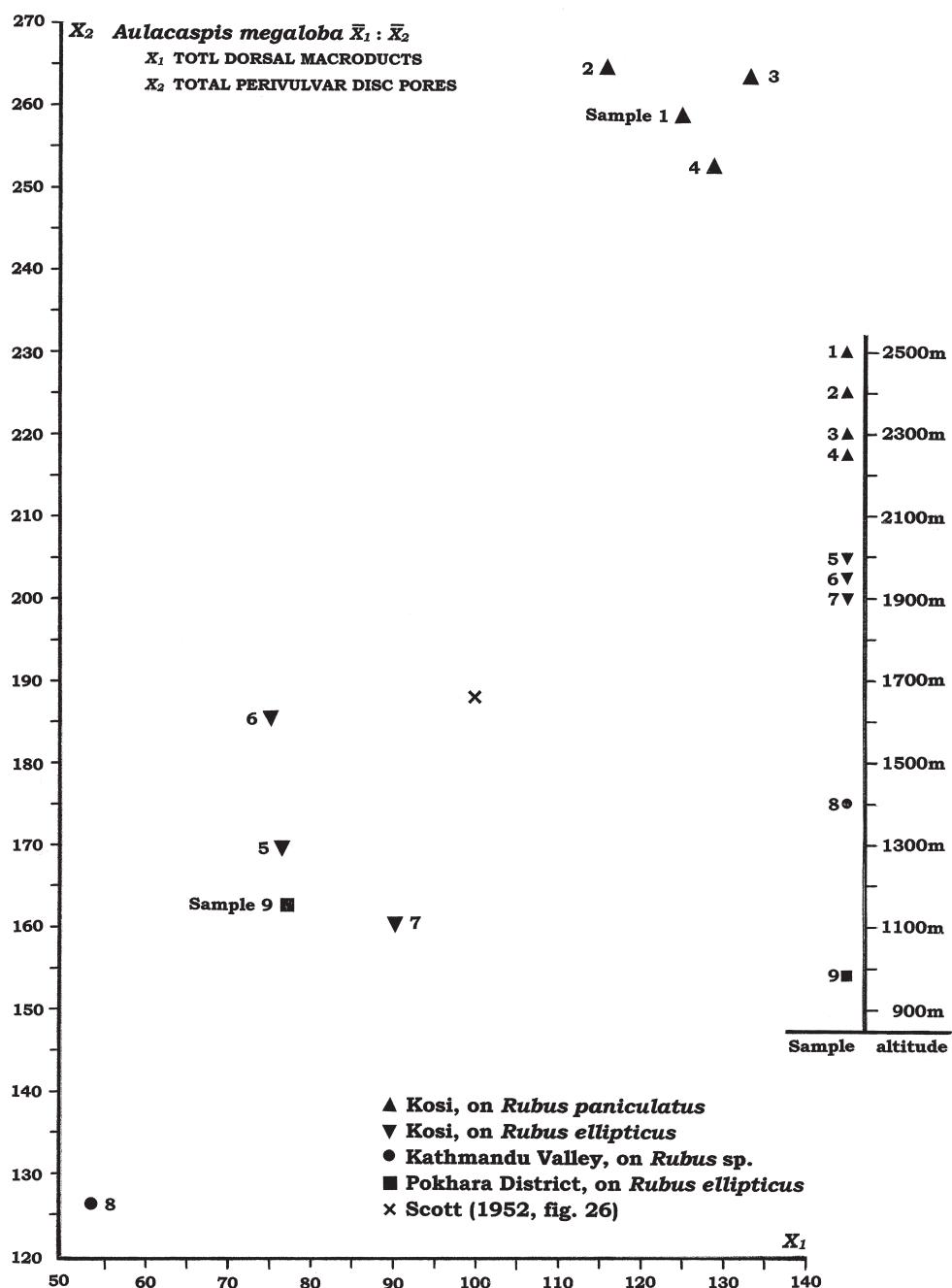


Fig. 1. *Aulacaspis megaloba*, adult females. Scatter diagram for mean total numbers of perivulvar disc pores against mean total numbers of dorsal macrodants. The collection altitudes of the samples are shown on the right side of the diagram. The specimen drawn by Scott (1952, fig. 26) is plotted on the chart on the basis of presumed numbers.

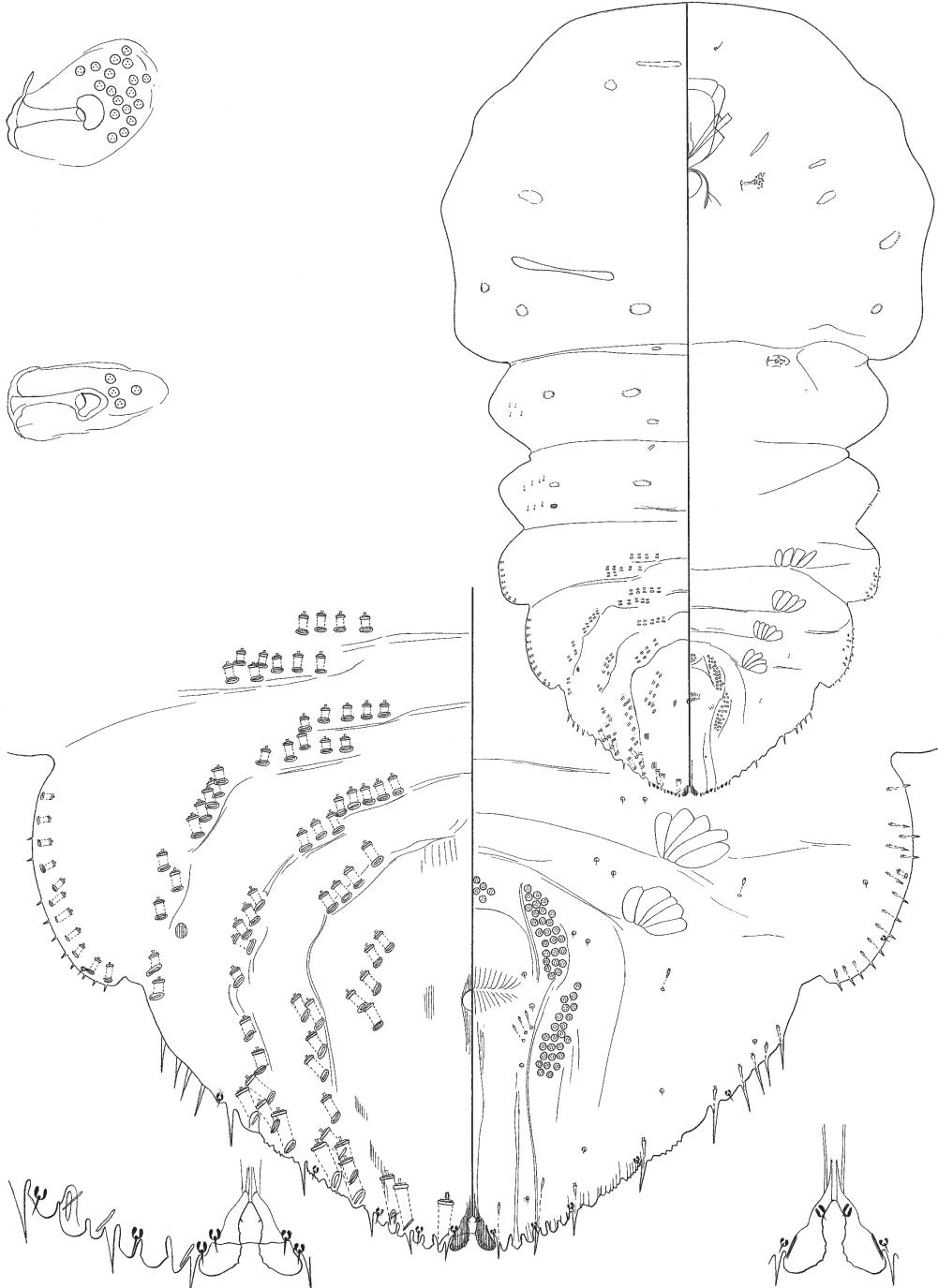


Fig. 2. '*Aulacaspis javanensis* Newstead, Java, ex coll. Busse, Type material' (D. J. Williams).

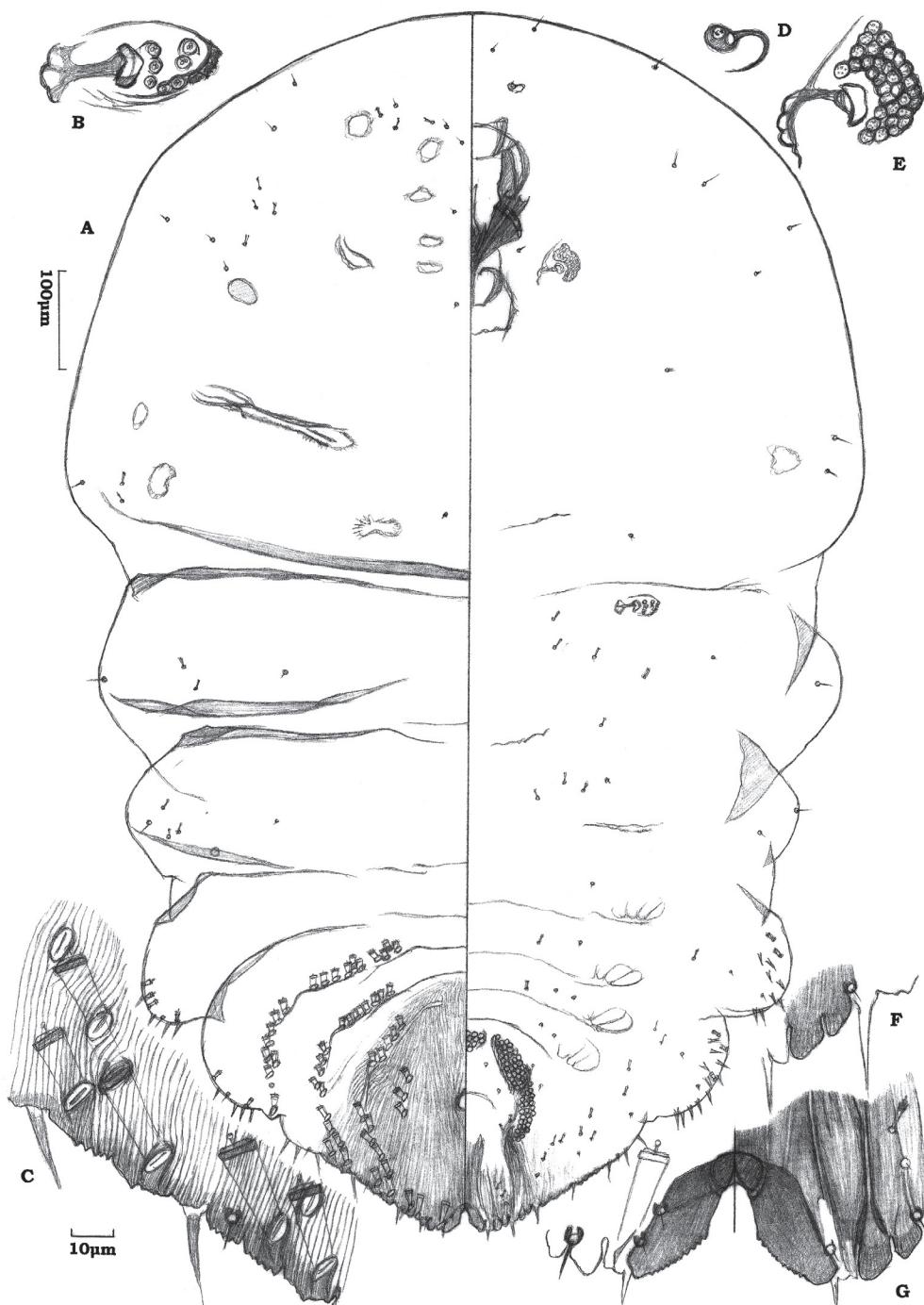


Fig. 3. *Aulacaspis rosae*, adult female, full-grown. Sapporo, Hokkaidō, on garden rose. B, posterior spiracle; C, marginal processes on abd IV and V; D, antenna; E, anterior spiracle; F, G, trullae. Scale bar, 100μm for A; 10μm for B–G.

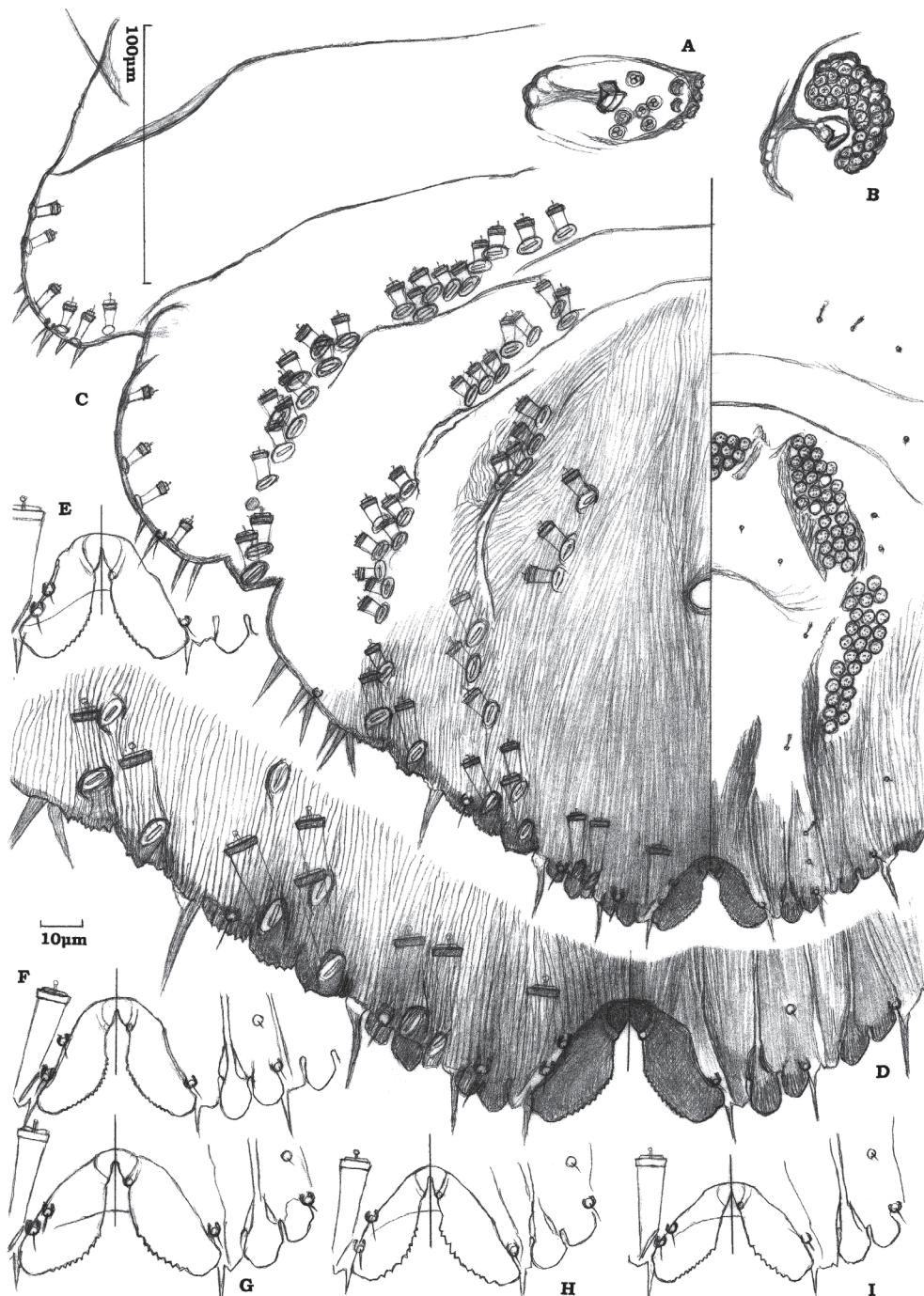


Fig. 4. *Aulacaspis rosae*, adult females on *Vaccinium*. A–F, Mt. Hayatine, Iwate Pref., on *V. smallii*; G–I, Dizô Pass, Gunma Pref./Nagano Pref., on *V. vitis-idaea*. A, posterior spiracle; B, anterior spiracle; C, pygidium; D, pygidial margin; E, F, median trullae (other specimens); G–I, median trullae. Scale bar, 100μm for C; 10μm for A, B, D–I.

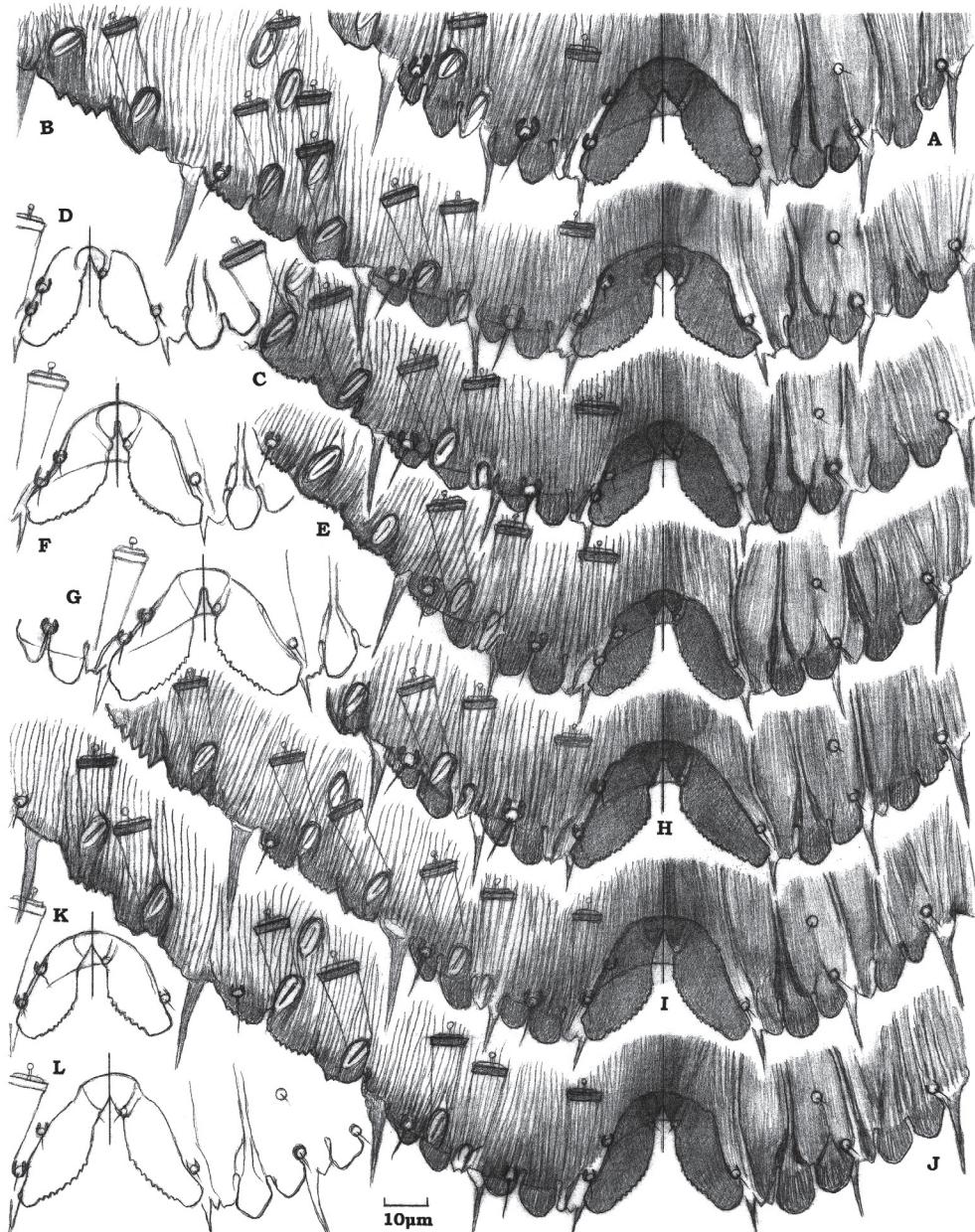


Fig. 5. *Aulacaspis rosae*, adult females, pygidial margins or trullae. A, B, Mt. Apoi, Hokkaidō, on *Rosa rugosa* bark; C, D, Mt. Sengen, Hokkaidō, on *Aucuba japonica* var. *borealis* leaf; E–G, Mt. Mikawa, Hyōgo Pref., on *Epigaea asiatica* leaf; H, Mt. Rokkō, Hyōgo Pref., on *Agrimonia pilosa* var. *japonica* leaf; I, Kozagawa, Wakayama Pref., on *Rubus buergeri* leaf; J–L, Omogo-Kei, Ehime Pref., on *Rubus* sp. stem. Scale bar, 10µm for A–L.

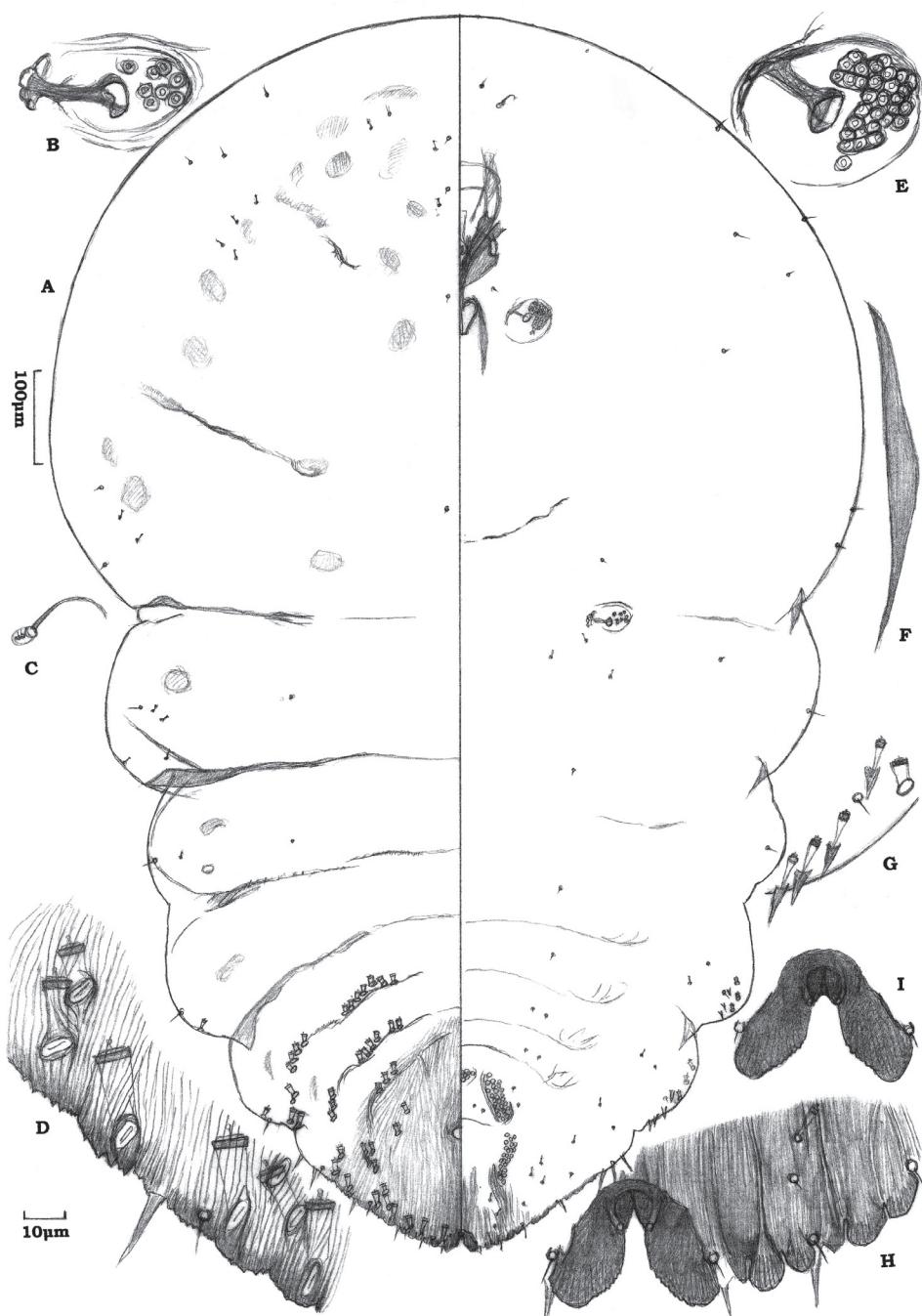


Fig. 6. *Aulacaspis ericacearum*, adult females. Aizan-Kei, Hokkaidō, on *Vaccinium axillare* var. *coriaceum*. A, body, full-grown; B, posterior spiracle; C, antenna; D, marginal processes on abd IV and V; E, anterior spiracle; F, peribuccal sclerosis; G, part of lateral lobe of abd III; H, trullae; I, median trullae (another specimen). Scale bar, 100µm for A; 10µm for B–I.



Fig. 7. *Aulacaspis ericacearum*, adult females (A–H) and second instar female exuvial casts (I, J). Mt. Soranuma, Hokkaidō, on *Vaccinium* sp. twig. A, anterior spiracle; B, posterior spiracle; C, lateral lobe of abd II; D, lateral lobe of abd III; E, pygidium; F, pygidial margin; G, pygidial margin, H, median trullae (other specimens); I, J, second instar female exuvial casts, pygidial margin (I) and trullae (J). Scale bar, 100µm for C–E; 10µm for A, B, F–J.



Fig. 8. *Aulacaspis ericacearum*, adult females. Sapporo, Hokkaidō, on *Leucothoe grayana* var. *oblongifolia*, twig. A, body, full-grown; B, posterior spiracle; C, posterior spiracle, disc pores (another specimen); D, marginal processes on abd IV and V; E, antenna; F, anterior spiracle; G, trullae; H–J, median trullae (other specimens). Scale bar, 100µm for A; 10µm for B–J.

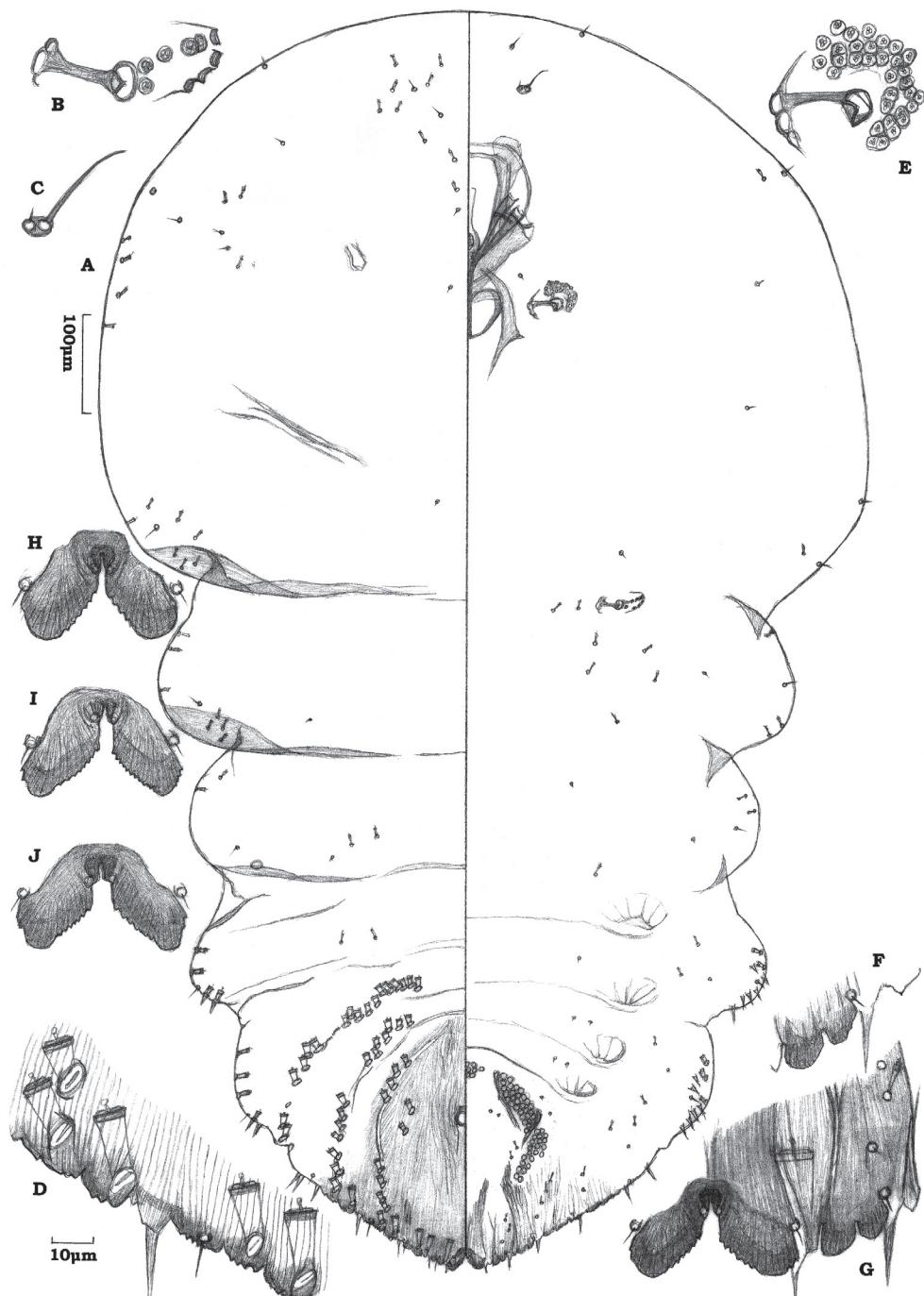


Fig. 9. *Aulacaspis sorbi*, adult females. Ôdai-ga-Hara, Nara Pref., on *Sorbus alnifolia* twig. A, body, full-grown; B, posterior spiracle; C, antenna; D, marginal processes on abd IV and V; E, anterior spiracle; F, G, trullae; H–J, median trullae (other specimens). Scale bar, 100 μ m for A; 10 μ m for B–J.



Fig. 10. *Aulacaspis mali*, adult female, full-grown. Ussuriysk, Primorskii Krai, on *Malus* sp. branch. B, posterior spiracle; C, antenna; D, marginal processes of abd IV and V; E, anterior spiracle; F, trullae. Scale bar, 100 μ m for A; 10 μ m for B-F.



Fig. 11. *Aulacaspis mali*, adult females. Ussuriysk, Primorskii Krai, on *Malus* sp. branch. A, C, pygidia; B, E, trullae for A and C; D, submedian macroducts on abd II for C. Scale bar, 100µm for A, C; 10µm for B, D, E.

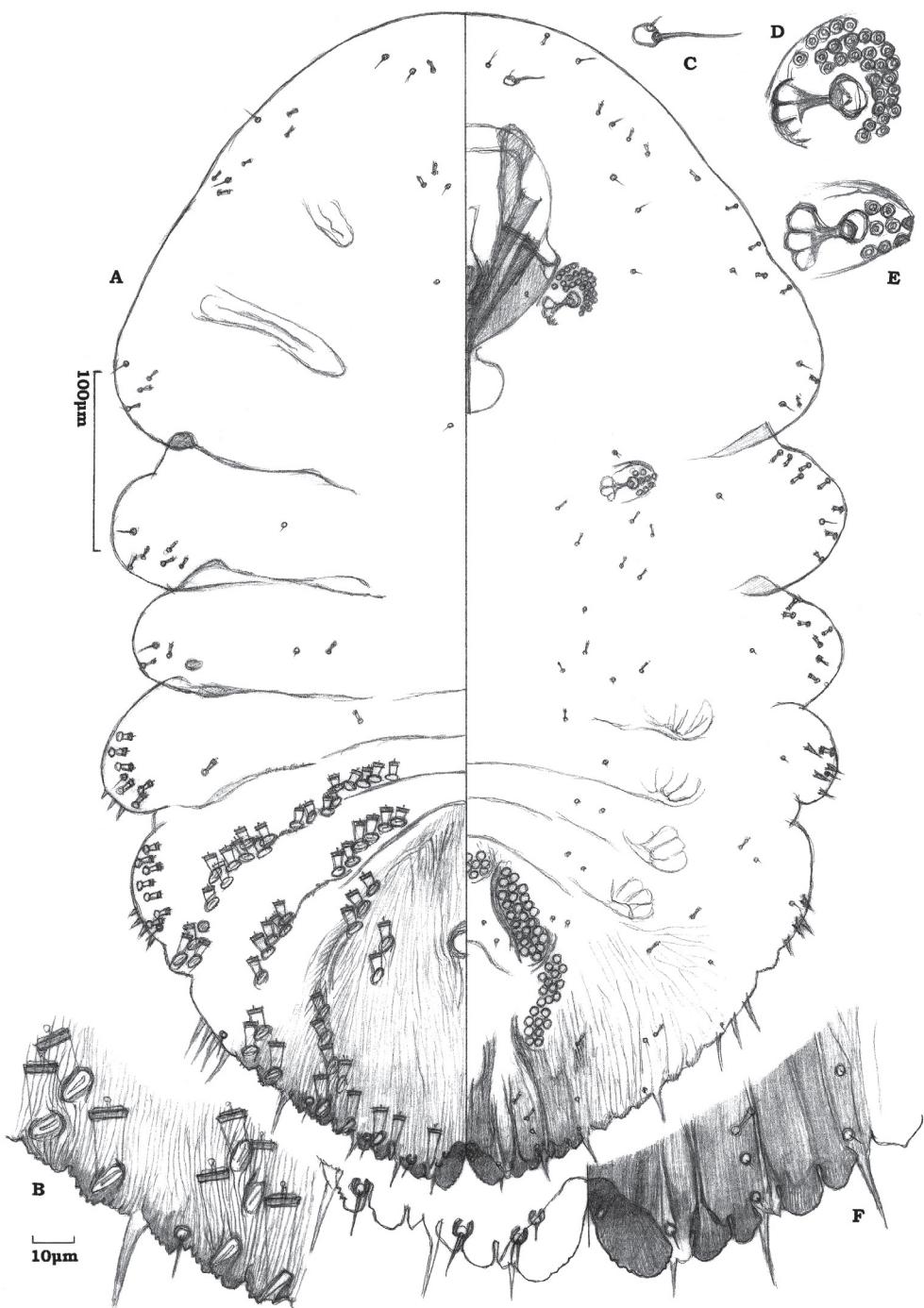


Fig. 12. *Aulacaspis mali*, adult female, teneral. Ussuriysk, Primorskii Krai, on *Malus* sp. branch. B, marginal processes on abd IV and V; C, antenna; D, anterior spiracle; E, posterior spiracle; F, trullae. Scale bar, 100 μ m for A; 10 μ m for B–F.



Fig. 13. *Aulacaspis rosarum*, adult females. Sagamihara, Kanagawa Pref., on garden rose. A, body, full-grown; B, posterior spiracle; C, antenna; D, marginal processes on abd IV and V; E, anterior spiracle; F, peribuccal sclerosis; G, lateral lobe of abd III; H, trullae; I, median trullae (another specimen). Scale bar, 100µm for A; 10µm for B–I.

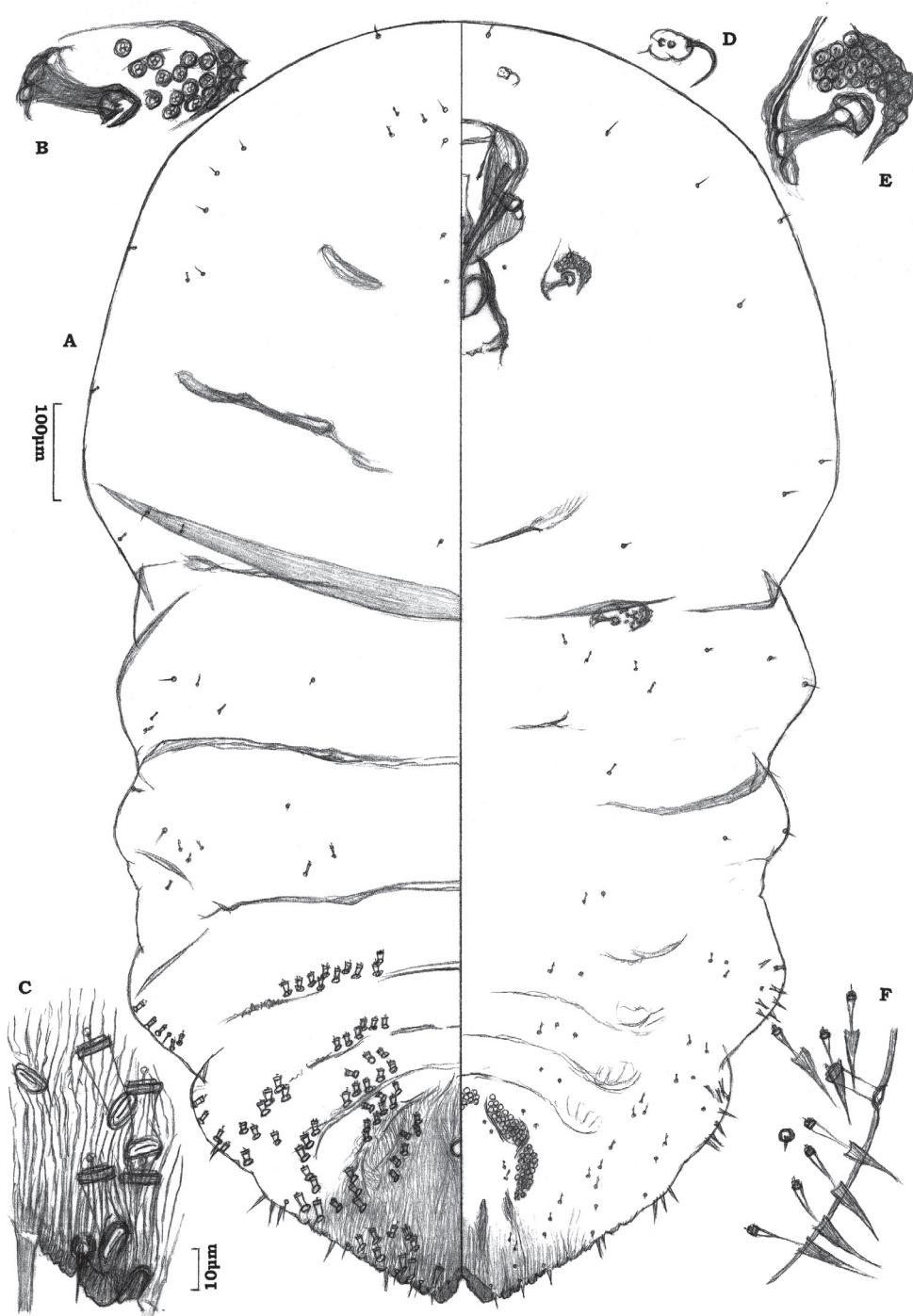


Fig. 14. *Aulacaspis langtangana*, adult female, full-grown. Sample 1. Langtang Valley, Bagmati, on *Rosa sericea* branch. B, posterior spiracle; C, marginal and submarginal macroducts on abd VI; D, antenna; E, anterior spiracle; F, lateral lobe of abd III. Scale bar, 100µm for A; 10µm for B-F.



Fig. 15. *Aulacaspis langtangana*, adult female. Sample 2. Langtang Valley, Bagmati, on *Rosa sericea* branch. A, abdomen; B, pygidial margin. Scale bar, 100µm for A; 10µm for B.

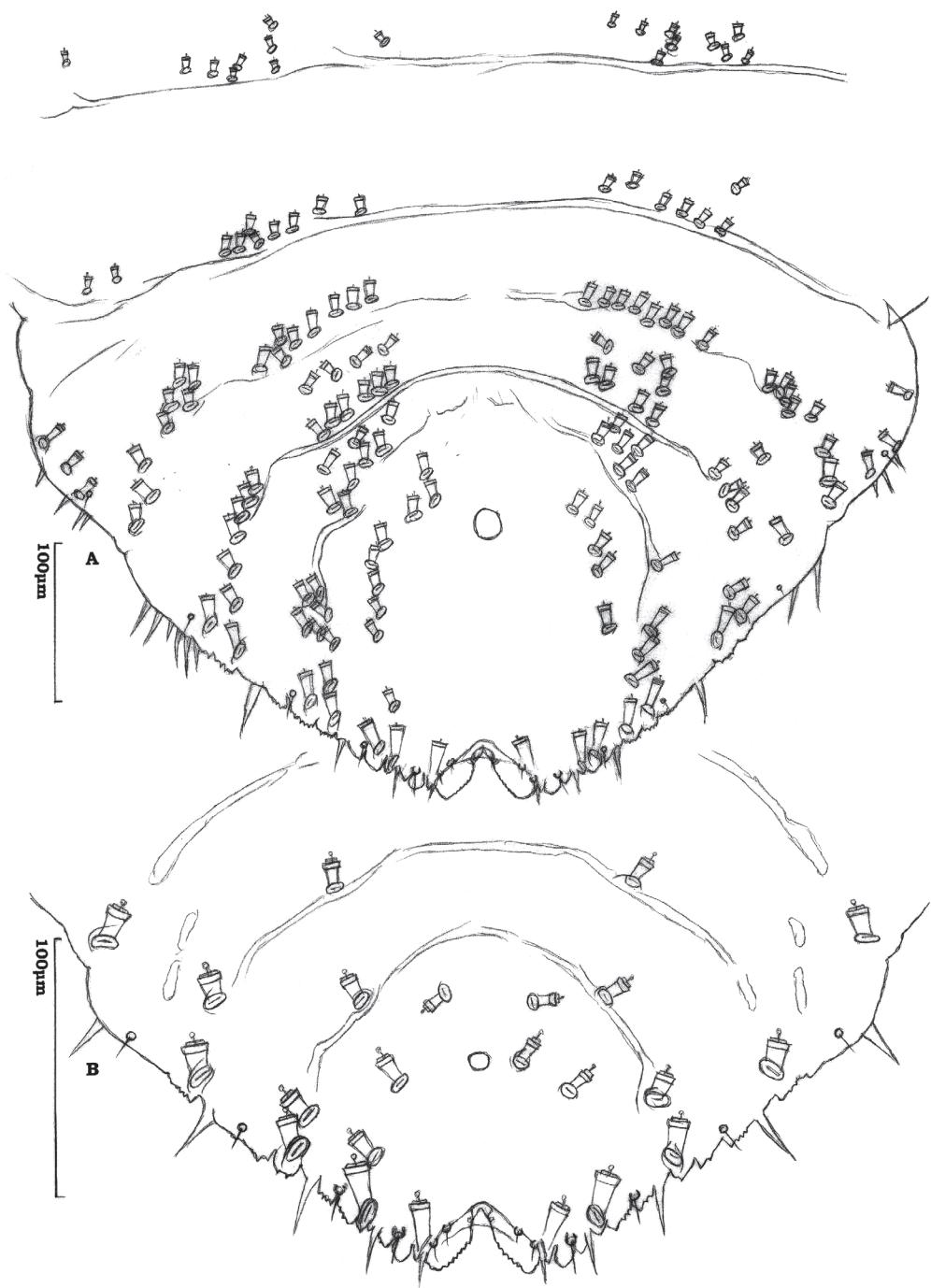


Fig. 16. *Aulacaspis langtangana*, adult female (A) and second instar female exuvial cast (B). Sample 1. Langtang Valley, Bagmati, on *Rosa sericea* branch. A, B, dorsal macroducts. Scale bars, 100 μ m for A and B, respectively.

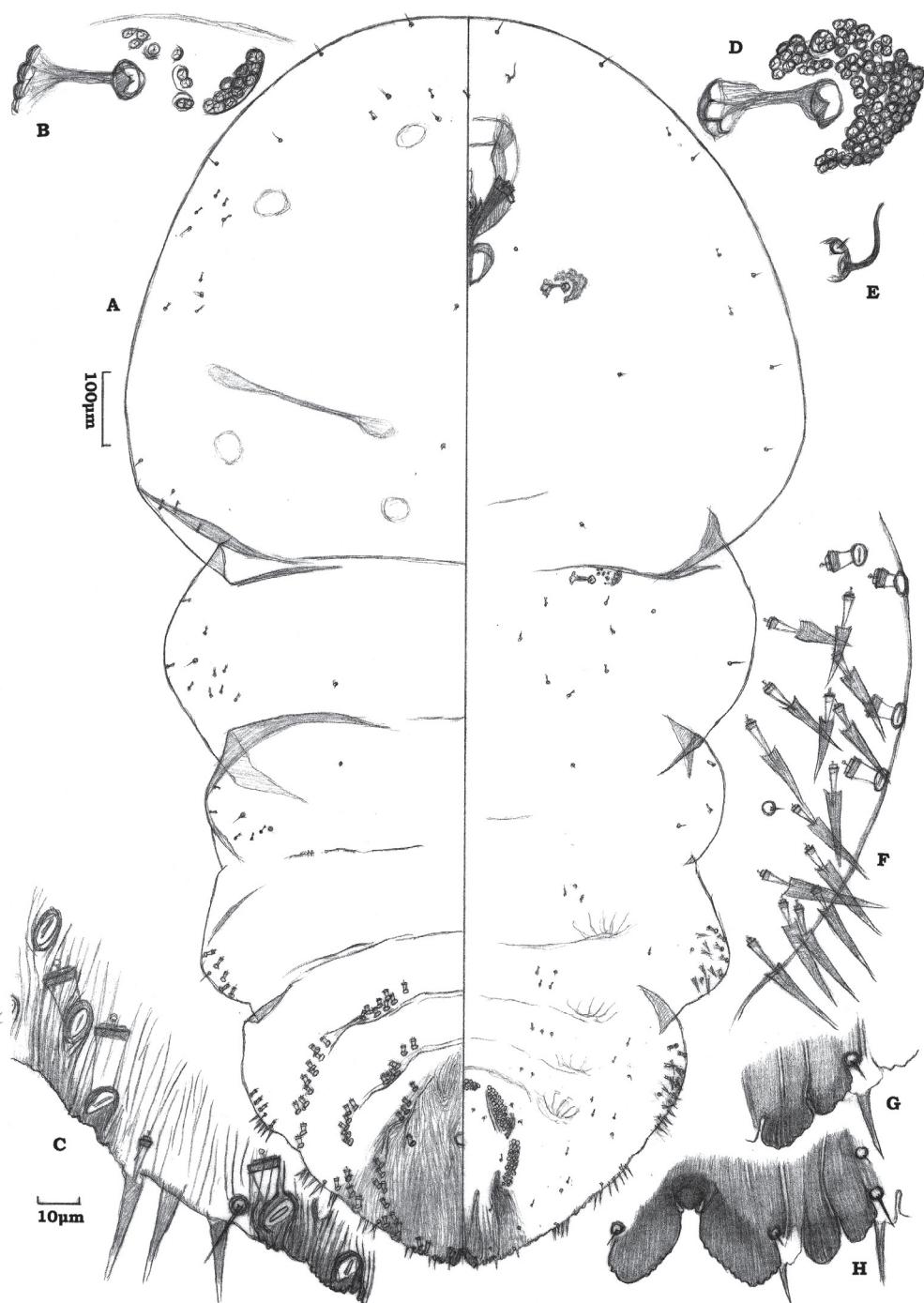


Fig. 17. *Aulacaspis pieridis*, adult female, full-grown. Langtang Valley, Bagmati, on *Pieris formosa* branch. B, posterior spiracle; C, marginal processes on abd IV and V; D, anterior spiracle; E, antenna; F, lateral lobe of abd III; G, H, trullae. Scale bar, 100 μ m for A; 10 μ m for B–H.



Fig. 18. *Aulacaspis pieridis*, adult females (A–E) and second instar female exuvial cast (F). Langtang Valley, Bagmati, on *Pieris formosa* branch. A, pygidium; B, pygidial margin; C, anterior spiracle; D, posterior spiracle; E, median trullae (another specimen); F, second instar female exuvial cast, pygidial margin. Scale bar, 100 μ m for A; 10 μ m for B–F.



Fig. 19. *Aulacaspis lyoniae*, adult female, full-grown. Sample 1. Bagmati, on *Lyonia ovalifolia* branch. B, lateral trullae; C, anterior spiracle; D, marginal processes on abd V; E, antenna; F, lateral lobe of abd III; G, median trullae; H, posterior spiracle. Scale bar, 100 μ m for A; 10 μ m for B–H.



Fig. 20. *Aulacaspis lyonae*, adult females. Sample 1. Bagmati, on *Lyonia ovalifolia* branch. A, pygidium; B, pygidial margin; C, anterior spiracle; D, lateral lobe of abd III; E, posterior spiracle; F, median trullae (another specimen); G, H, posterior spiracles (other specimens). Scale bar, 100µm for A, D; 10µm for B, C, E-H.

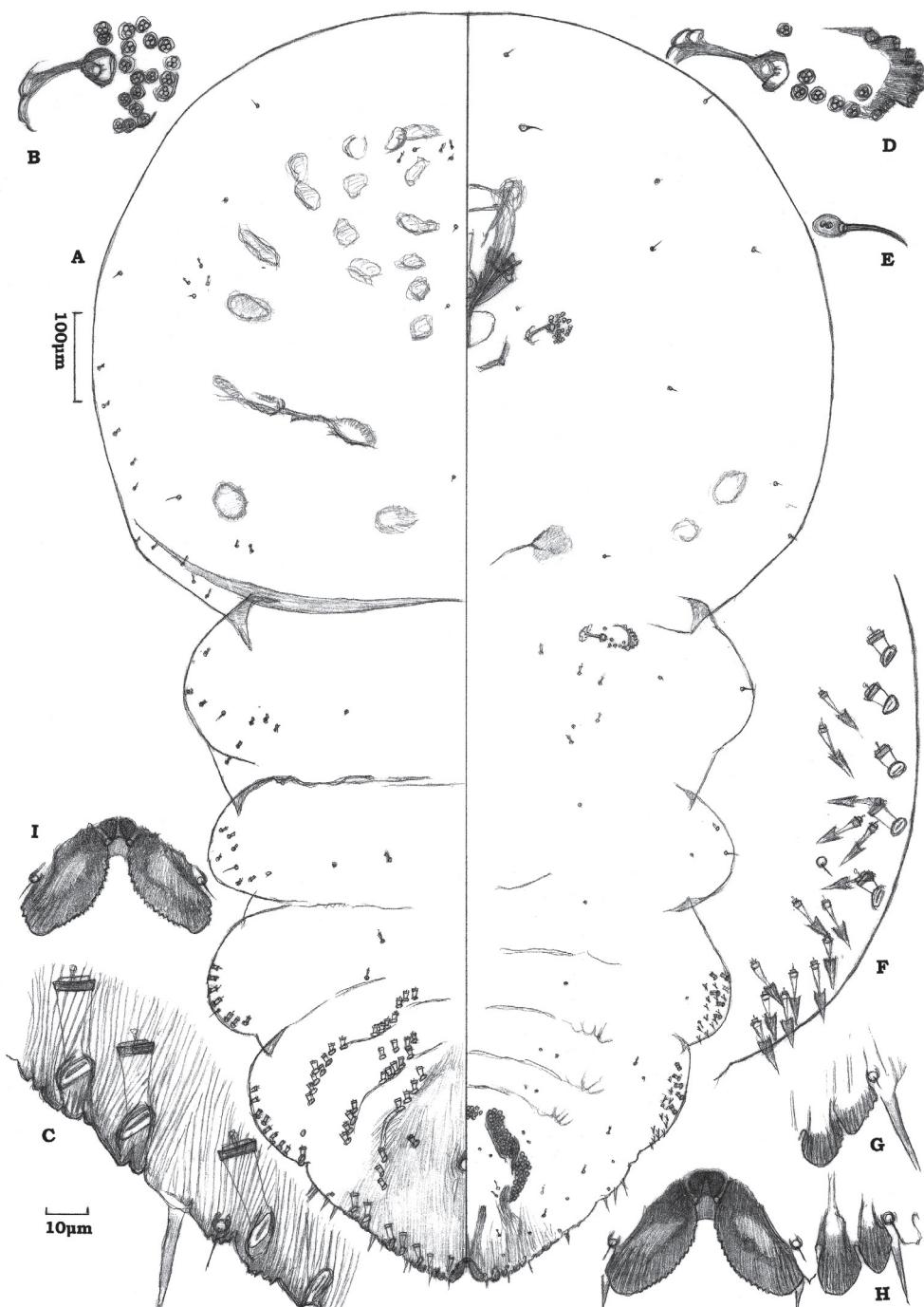


Fig. 21. *Aulacaspis lyoniae*, adult females. Sample 2. Bagmati, on *Pieris formosa* branch. A, body, full-grown; B, anterior spiracle; C, marginal processes on abd IV and V; D, posterior spiracle; E, antenna; F, lateral lobe of abd III; G, H, trullae; I, median trullae (another specimen). Scale bar, 100µm for A; 10µm for B–I.

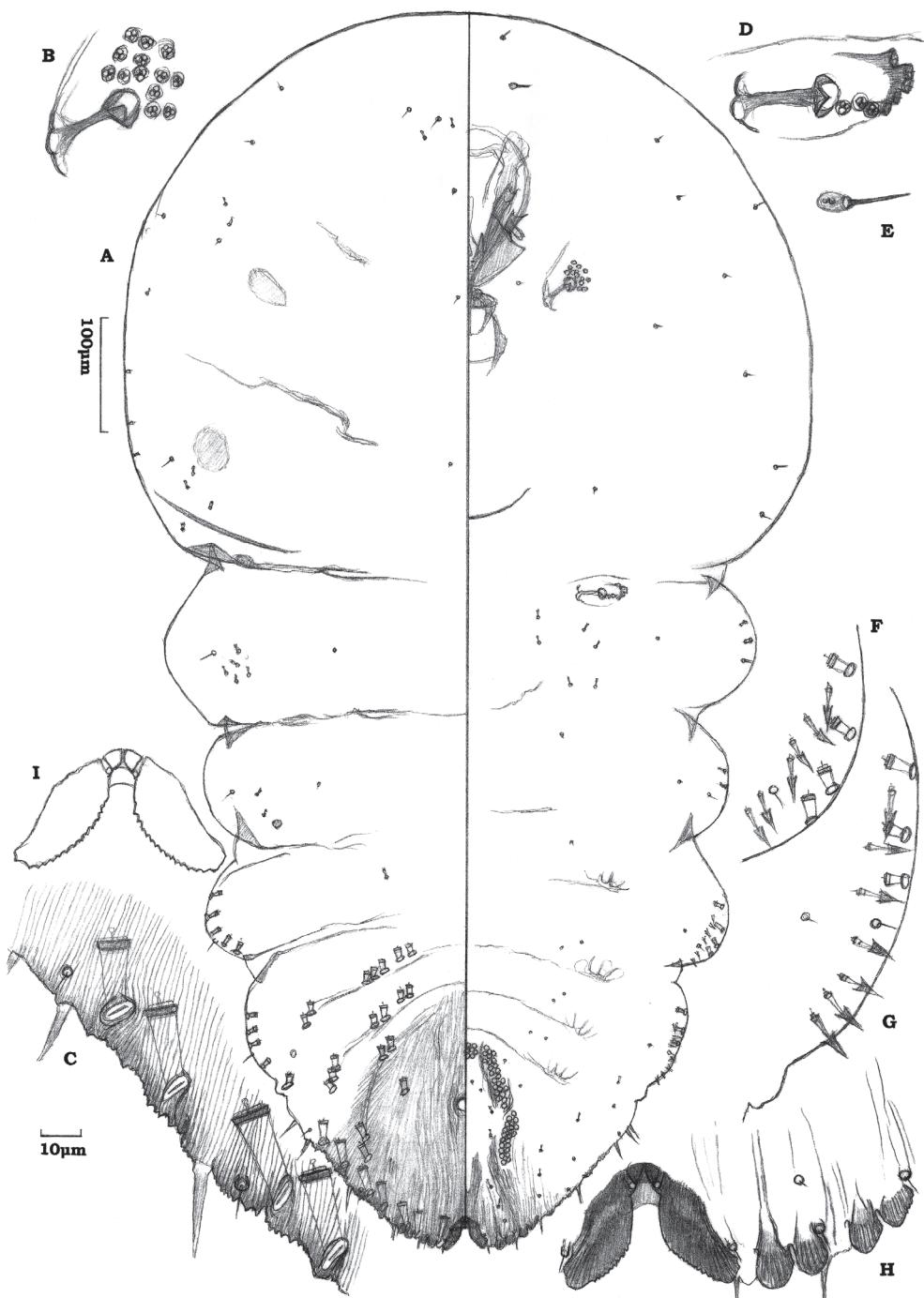


Fig. 22. *Aulacaspis lyoniae*, adult females. Sample 4. Bagmati, on *Lyonia ovalifolia* branch. A, body, full-grown; B, anterior spiracle; C, marginal processes on abd IV and V; D, posterior spiracle; E, antenna; F, lateral lobe of abd II; G, lateral lobe of abd III; H, trullae; I, median trullae (another specimen). Scale bar, 100µm for A; 10µm for B–I.

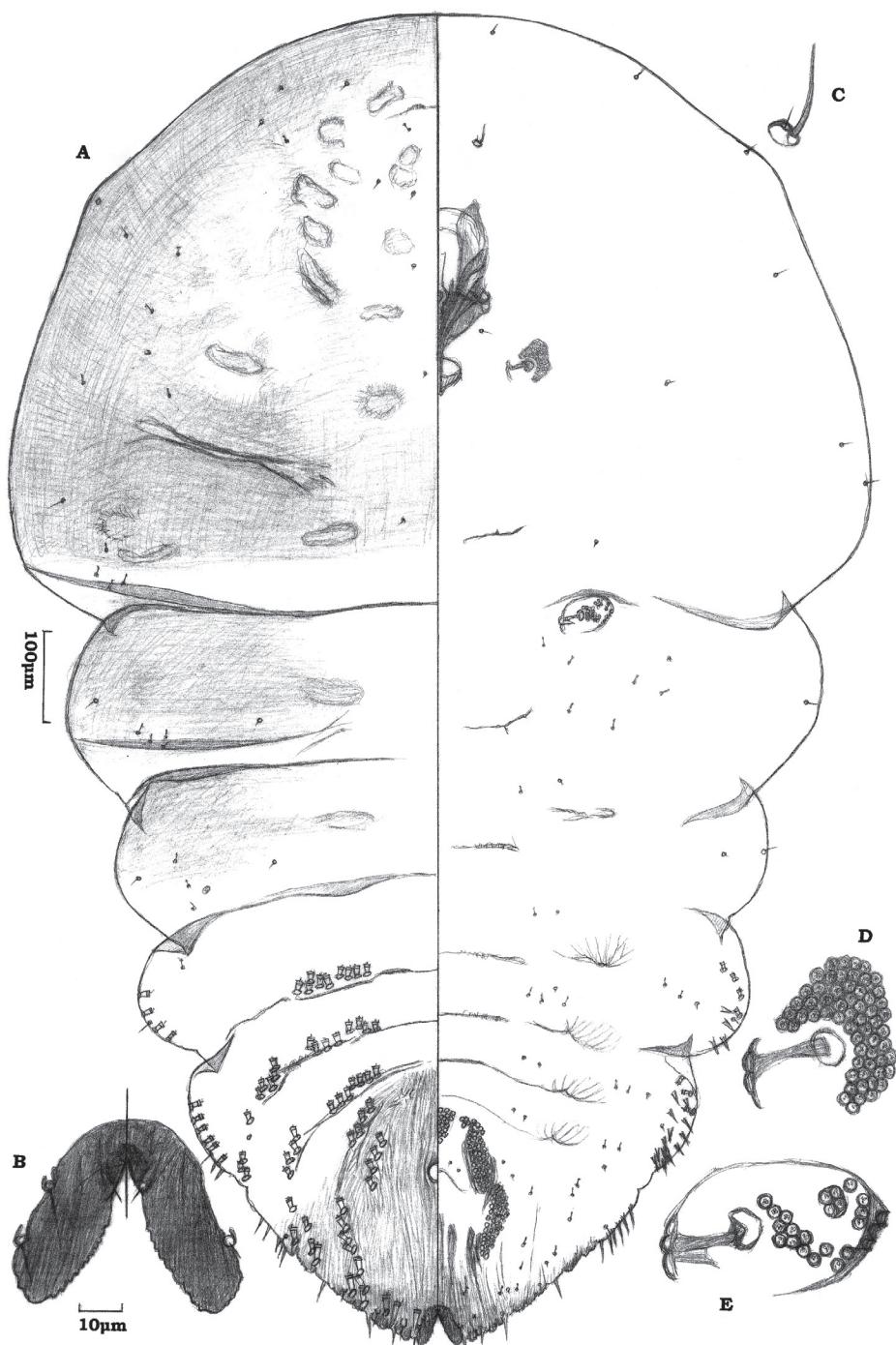


Fig. 23. *Aulacaspis megaloba*, adult female, full-grown. Sample 2. Kosi, on *Rubus paniculatus* branch. B, median trullae; C, antenna; D, anterior spiracle; E, posterior spiracle. Scale bar, 100 μ m for A; 10 μ m for B-E.



Fig. 24. *Aulacaspis megaloba*, adult female. Sample 1. Kosi, on *Rubus paniculatus* branch. A, pygidium; B, lateral lobe on abd III; C, pygidial margin; D, marginal processes on abd IV. Scale bar, 100µm for A, B; 10µm for C, D.

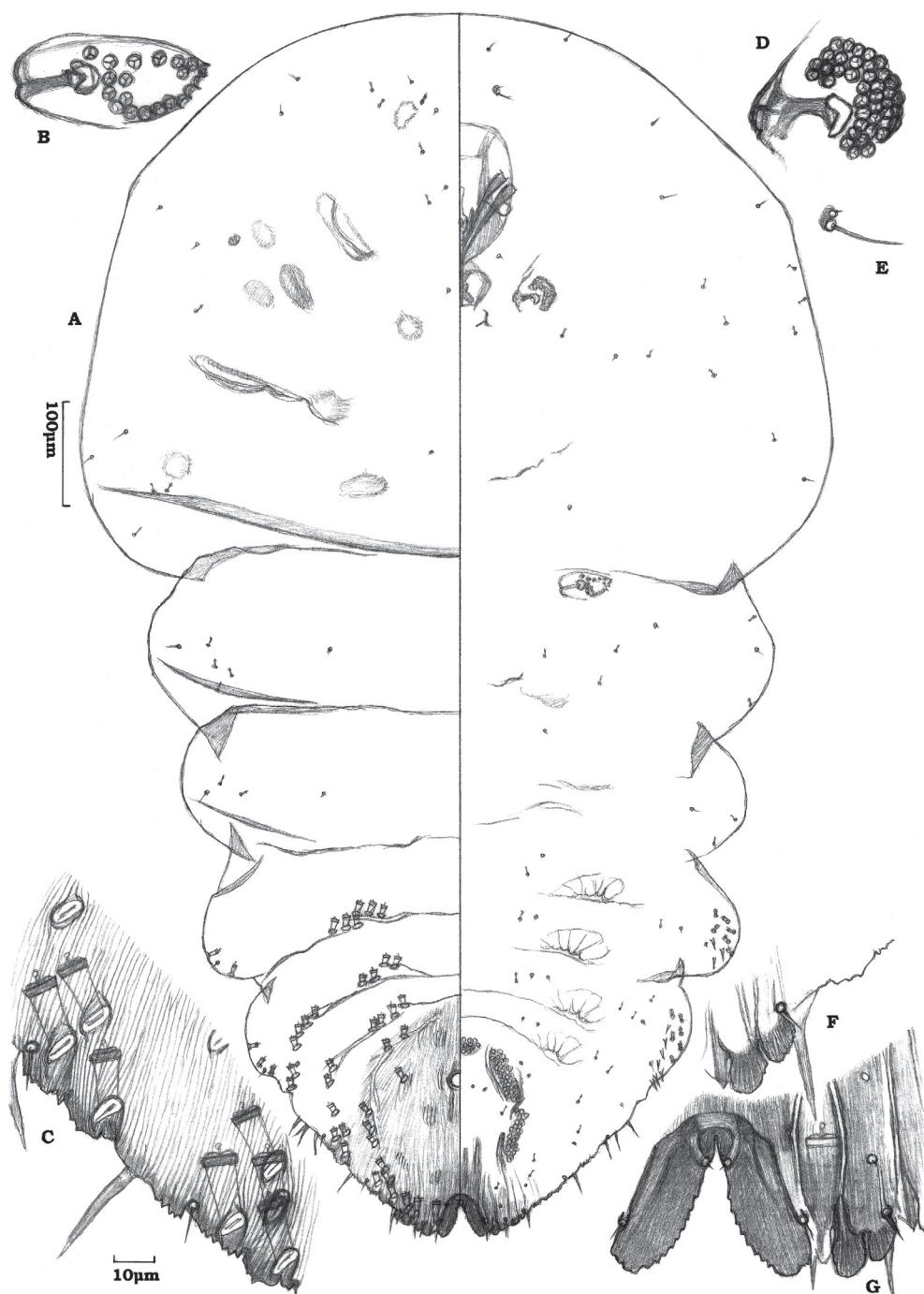


Fig. 25. *Aulacaspis megaloba*, adult female, full-grown. Sample 9. Gandaki, on *Rubus ellipticus* branch. B, posterior spiracle; C, marginal processes on abd IV and V; D, anterior spiracle; E, antenna; F, G, trullae. Scale bar, 100 μ m for A; 10 μ m for B-G.



Fig. 26. *Aulacaspis amamiana*, adult female, full-grown. Sample 3. Okinawa, on *Rubus sieboldii* leaf. B, posterior spiracle; C, lateral trullae, dorsal view; D, median trullae; E, anterior spiracle; F, antenna; G, lateral trullae, ventral view. Scale bar, 100µm for A; 10µm for B–G.



Fig. 27. *Aulacaspis amamiana*, adult females. Sample 1, Amami-Ôshima (D); Sample 2, Tokuno-Sima (E); Sample 3, Okinawa (A-C). On *Rubus sieboldii* branch. A, D, pygidia; B, median trullae; C, lateral trullae; E, trullae, marginal processes on abd V. Scale bar, 100µm for A, D, E; 10µm for B, C.