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SOME SPECIES OF AULACASPIS RELATED TO MANGROVE-ASSOCIATED AUSTRALIAN SPECIES (STERNORRHYNCHA: COCCOIDEA: DIASPIDIDAE)

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Abstract

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Six Asian species of *Aulacaspis* are studied on the supposition that they are related to *A. australis* Brimblecombe and *A. constricta* Takagi and De Faveri, mangrove-associated species in Australia: *A. crawii* (Cockerell) [=*Diaspis crawii* var. *fulleri* Cockerell], *A. mischocarpi* (Cockerell and Robinson) [=*Phenacaspis thoracica* Robinson, n.syn.], *A. alangii*, n.sp. (Borneo, on *Alangium*), *A. otophorae*, n.sp. (Palawan, on *Otophora*), *A. shoreae*, n.sp. (Malaya, on *Shorea*), and *A. fici*, n.sp. (Malaya, on *Ficus*). One of them, *A. crawii*, is closely related to *A. australis*; the other five species are lumped under the *mischocarpi* species group, which may be responsible for the origin of *A. constricta*. Four of the six species, together with *A. litsearum*, n.sp. (India, on *Litsea*) and *A. rosae* (the type species of the genus) added for comparison, are examined for their growth patterns in the stage of the adult female by means of pairing full-grown adult females with teneral ones from the same samples.

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Contents

1. Introduction

The genus *Aulacaspis* has as many as 117 known species mostly distributed in tropical and subtropical Asia and warm-temperate eastern Asia (Takagi, 2012). *Diaspis rosae*, first known from Europe taxonomically and accepted as the type species of the genus, should have its origin in temperate eastern Asia, where it occurs mainly on wild roses and certain other rosaceous plants as well as on garden roses. *Diaspis crawii* var. *fulleri* was described from South Africa and treated by some authors as a distinct species, but it is now generally accepted as synonymous with *Aulacaspis crawii*, which should be native to tropical and subtropical Asia (see Section 2.1 of this paper). *Phenacaspis kenyae* was described from Kenya, eastern Africa, as a grass-associated species (Hall, 1946). It is referable to *Aulacaspis* so far as based on the description, though the possibility that it belongs to another genus may not be excluded. If it is a true member of *Aulacaspis* and really native to Kenya, it makes a rare exception to the general geographical distribution of the genus. Some grass-associated coccoids, however, were introduced to new territories together with sugar cane. *Aulacaspis boisduvalii* var. *maculata* was described from Brazil (Cockerell, 1898b). It seems that it was simply a by-product from the circumstances that *Diaspis boisduvalii* was removed (erroneously) to *Aulacaspis* five years before and had been held in that genus. It may correctly be excluded from *Aulacaspis* apart from the question what it really represents.

Over against the eastern end of Asia, two species of *Aulacaspis* occur on the coasts of eastern and northwestern Australia in association with mangrove plants: *Aulacaspis australis* (Brimblecombe, 1959; Takagi and De Faveri, 2009; Takagi, De Faveri, and Martin, 2011) and *Aulacaspis constricta* (Takagi and De Faveri, 2011). The discoveries of these species are noteworthy, because Australia is apparently outside the main domain of *Aulacaspis*, having no native inland species of the genus, and also because it is hardly possible to imagine any human influence (except for recent mangrove restoration) on the distribution of scale insects exclusively associated with mangroves. The occurrence of the two species in Australia should therefore be attributed to the invasions of their ancestors, conspecific or not with them, from the mangrove-associated fauna in Asia under some natural conditions.

In the present paper, six species of *Aulacaspis* occurring in Asia are studied on the supposition that they are more or less related to the two Australian species. All these species belong to the *rosae* type, having the prosoma swollen into an eminent mass on the full-grown body, but are far from uniform in the body shapes of the full-grown adult females. The species-characteristic body shape is gradually formed during the growth of the adult female. In the present study, the growth pattern of the adult female is analysed in four of the six Asian species, the type species, and another species (which belongs to the *rosae* type but is extraordinary in having a much broadened postsoma) by means of pairing a full-grown adult female with a teneral one (which was collected shortly after the emergence from under the second-instar exuvial cast) from the same sample (which was collected, in principle, from the same plant at the same time).

Full-grown adult females and teneral ones in the same sample may represent two successive generations. *Aulacaspis cupulifera* shows a statistically significant difference in the total number of the dorsal macroducts and also in that of the perivulvar disc pores between successive generations, which represent seasonal phenotypes on the same plant and the same feeding site (Takagi, 2012b). In the present study, teneral specimens of the

adult female, in addition to full-grown ones, are available in some samples. They are too few or not sufficiently numerous for examining the possible occurrence of seasonal variation. Actually, they are not particularly different in the numbers of the main wax-secreting organs from the full-grown adult females in the same samples, and are united with the full-grown ones in the statistics of these numbers.

In the descriptions, the abbreviations 'abd I' to 'abd VIII' stand for the first to eighth abdominal segments. The term 'dorsal macroducts' means the submedian and submarginal macroducts combined; the 'lateral macroducts' and 'lateral gland spines' occur on the lateral lobes of the second and third abdominal segments. The numbers of the disc pores, macroducts, and gland spines are given for each side of the body except for the total number of the dorsal macroducts and that of the perivulvar disc pores. The length of the pygidium is measured along the midline between the anterior margin of the fifth abdominal segment and the apices of the median trullae; the width of the pygidium is measured between the anterolateral angles of the fourth abdominal segment, just caudad of the marginal macroducts of the third segment. Specimens mounted from the leaves of the host plants are 'foliicolous', and those from the twigs and branches are 'ramicolous'.

The term 'trullae' is adopted in place of 'lobes' or 'pygidial lobes' of authors. In addition to the strong median trullae, two pairs of lateral trullae are well developed on the seventh and sixth abdominal segments, each being divided into two lobules, mesal and lateral. Marginal macroducts occur on the seventh to third abdominal segments, one on the seventh segment (between the median and second trullae), two on each of the sixth to fourth, and one on the third at the posterolateral angle of the segment. The single marginal macroducts occurring on the seventh and third segments and the mesal ones of the paired macroducts on the sixth to fourth open in marginal processes called 'pore prominences', which are variable in development on the fifth and fourth segments and sometimes indiscernible on the third. On the fifth segment, the pore prominence is accompanied laterally with two processes; the mesal one of these processes may also be called 'pore prominence' (because it is associated with the lateral one of the marginal macroducts), but these processes may more probably be homologous with the lobules of the second and third trullae, thus representing the lobules of the 'fourth trulla'. They are greatly different from the lobules of the second and third trullae in shape and variable in development. On the fourth segment the corresponding processes tend to be reduced to low protuberances or mere serrations or to be practically obsolete.

The host plants were identified by botanists in India (Botanical Survey of India), Nepal (Department of Medicinal Plants), Malaysia (Mr K. M. Kochummen, Forest Research Institute of Malaysia; Forest Research Centre, Sabah), Singapore (Dr Hsuan Keng, University of Singapore), and the Philippines (Dr Edwino S. Fernando, University of the Philippines at Los Baños).

The holotypes of the new species described in this paper are deposited in: Museum of Natural History, University of the Philippines at Los Baños, Laguna, the Philippines (*A. otophorae*); Entomological Division, Forest Research Institute of Malaysia, Kepong, Kuala Lumpur, Malaysia (*A. alangii*, *A. shoreae*, and *A. fici*); Laboratory of Systematic Entomology, Hokkaidô University, Sapporo, Japan (*A. litsearum*).

2. Asian species for comparison

2.1. *Aulacaspis crawii*
(Tables 1, 2; Figs 1, 2a, 4–10)

2.1.1. Historical review

Diaspis crawii Cockerell, 1898: 190 [‘On stem of some woody plant from China, …’].

Diaspis crawii, Ckll., var. *fulleri* Cockerell, 1901: 225 [‘On twigs of *Melia azedarach* …, Maritzburg, Natal.’].

Aulacaspis crawii: Cockerell, 1902: 59 [‘China.’].

Aulacaspis crawii fulleri: Cockerell, 1902: 59 [‘South Africa.’].

Diaspis (*Aulacaspis*) *fulleri*: Brain, 1919: 193 [‘On *Melia azedarach*, Natal (Fuller), and Pretoria, … 1915. On *Ricinus* sp., Durban; … 1910.’].

Aulacaspis crawii: Kuwana, 1926: 25 [‘Found in California on *Elaeagnus umbellata* which came from China. … a part of material at the Plant Quarantine Office at San Francisco which was collected by the late Mr. A. Craw on plants from China.’].

Aulacaspis fulleri: Zimmerman, 1948: 381 [Oahu, Hawaii, on *Aglaia odorata*].

Aulacaspis crawii: Scott, 1952: 36 [southern China, on *Aglaia odorata*, *Smilax*, *Murraya*, *Rubus*, *Citrus*, and *Camellia*; Taiwan, on *Melia azedarach*; other ‘specimens taken at Honolulu and indicated as having come from Africa.’ *A. fulleri* ‘may very well prove to be a synonym of *A. crawii*, …’].

Aulacaspis crawii: Munting, 1977: 2 [Natal, on *Melia azedarach* (the type series of *Diaspis crawii* var. *fulleri* collected in 1901; other specimens collected in 1962); Durban on *Ricinus*. ‘No constant differences could be found between the material of *fulleri* and that of *crawii* … *fulleri* is therefore considered a synonym of *crawii*.’].

Aulacaspis crawii: Chen, 1983: 40 [southern China, on *Aglaia odorata*, *Rubus* sp., and *Smilax* sp.].

Aulacaspis crawii: Tang, 1986: 196 [Tianjin, China, on *Aglaia odorata* (under glass)].

Aulacaspis crawii: Takagi and De Faveri, 2009 [recorded from a mangrove plant: ‘Linggi Forest Reserve, Negeri Sembilan, Malaya, on the leaves of *Xylocarpus granatum* …’].

2.1.1b. Notes on other records

Kuwana (1902) recorded *Diaspis crawii* from Japan (‘Chikujo-gun, Kiushiu’) as occurring on *Elaeagnus umbellata*. No further record of the species has been made in Japan.

In Hawaii, ‘*Aulacaspis fulleri*’ was first recorded in 1924 on *Aglaia odorata*, ‘a Chinese stove-plant’, used for table decoration ‘at the Chinese banquet held during the Pan-Pacific Conference’ (Notes and exhibitions, Proceedings of the Hawaiian Entomological Society 6: 22, 1925). This scale insect was evidently introduced from China, but it was identified with the South African form *fulleri* for some unknown reason. This identification should have afforded a basis for Zimmerman’s (1948) record of *A. fulleri* in Oahu and also for Scott’s (1952) statement that *A. crawii* was introduced into Honolulu from Africa. So far as this understanding is adopted, the figures presented by these authors represent a form originally occurring in China, and Scott’s suggestion about the synonymy of *A. fulleri* with *A. crawii* was based exclusively on the material from China. Furthermore, Nakahara (1981) mentioned *Aglaia odorata* and *Murraya paniculata*, originally Asian plants, as hosts of *A. crawii* in Hawaii.

Takahashi (1930) recorded *Aulacaspis crawii* in Taiwan on *Hibiscus tiliaceus* and *Melia azedarach*.

Matile-Ferrero (1976) adopted Wallace's records of *Aulacaspis crawii* from Saint Helena Island, in which it was collected at four localities and on 'Mûrier, probablement *Rubus pinnatus*', 'rosier' (rose tree), 'Rosaceae', and '*Rubus*'. (It should be noted that *Aulacaspis rosarum* was introduced into some areas of the world probably together with garden roses: see Section 2.2.3b.)

Tang (1977) described *A. crawii* from China and mentioned some plants as its hosts. However, it is not clear which of the host plants he really confirmed. He suppressed *Aulacaspis citri* as a synonym of *A. crawii*. Chen (1983, p. 40, under *Aulacaspis citri*) remarked that Scott (1952) and Tang (1977) confused *A. citri* with *A. crawii*. He probably alluded to their records of *A. crawii* from *Citrus* in China. Later, Tang (1986) admitted that *A. citri* was distinguishable from *A. crawii* in some characters.

2.1.2. Material examined

Specimens are available for the present study from Malaya, Singapore, lowland Nepal, and Natal; a few from Hong Kong.

Sample 1–5. Cameron Highlands (Gg. Jasar and Gg. Beremban), Malaya, Malaysia, alt. within 1300–1800m, on the leaves of *Tetractomia tetrandra* (Rutaceae), 1.XII.1985 [85ML-80, Sample 1], 17.X.1986 [86ML-226, Sample 2], 22.X.1986 [86ML-283, Sample 3; -289, Sample 4; -292, Sample 5]. Sample 6. Linggi Forest Reserve (on the western coast of the Malay Peninsula), Negeri Sembilan, Malaysia, on the leaves of the mangrove plant *Xylocarpus granatum* (Meliaceae), 9.XI.1986 [86ML-430].

Sample 7. Bukit Timah, Singapore, on the leaves of *Gonystylus* sp. (cf. *confusus*) (Thymelaeaceae), 6. and 8. VII.1992 [92SP-23 and -48, united into Sample 7].

Sample 8–11. Terai (lowland belonging to the Gangetic Plain and bordering on the foothills of the Himalayas), alt. about 100–250m, Nepal. Dharan, Kosi Zone, on the leaves and twigs of *Murraya paniculata* (Rutaceae), 24.XI.1983 [83NPL-256, Sample 8]. Dharan, on the leaves of *Trichilia connaroides* (Meliaceae), 26.XI.1983 [83NPL-268, Sample 9]. Kanepokhari, near Dharan, Kosi Zone, on the leaves and twigs of *Trichilia connaroides*, 24.XII.1983 [83NPL-437, Sample 10]. On the River Pahasa, Narayani Zone, on the leaves of *Trichilia connaroides*, 20.XII.1983 [83NPL-391, Sample 11].

Sample 12. Umbogintwini, Natal, South Africa, on the twigs of *Melia azedarach* (Meliaceae), 21.VII.1964 (P. C. Wentzel).

In addition, three mounted specimens of the adult female are available from Hong Kong and from *Grewia* sp. (Tiliaceae). They are infected with fungi within the body walls (having been collected after their death on the host plant), and this condition makes detailed observations of characters difficult especially in the prepygidial region.

2.1.3. Foliicolous and ramicolous subsamples

Sample 8 and 10, which contain specimens mounted from the leaves and those from the twigs, have been examined for the extent of difference between the foliicolous and ramicolous subsamples (Tables 1, 2; Figs 1, 2a, 7, 8, 10). (Sample 12 is represented only by ramicolous specimens; the other samples examined in the present study have foliicolous specimens alone.)

Sample 8, collected on *Murraya paniculata* at Dharan, shows little evidence for the occurrence of ecophenotypic variation caused by the different feeding sites in the numbers of the main wax-secreting organs and in the shape of the median trullae. The ramicolous subsample appears to have more numerous dorsal macroducts, the mean value of the total number being larger than that in the foliicolous subsample. However,

it is too small for making a reliable comparison and, above all, the range observed in it entirely overlaps with that in the foliicolous subsample. After all, any phenotypic variation due to the different feeding sites, if perceptible, should have been unremarkable in the population which occurred on *Murraya paniculata* at Dharan and from which Sample 8 was obtained.

Sample 10, collected on *Trichilia connaroides* at Kanepokhari, a locality near Dharan, exhibits statistically significant differences in the numbers of the perivulvar disc pores, dorsal and lateral macroducts, and lateral gland spines between the foliicolous and ramicolous subsamples, which may be sufficiently large for comparison. These subsamples are definitely and widely different especially in the mean values of the total numbers of the dorsal macroducts.

Another remarkable difference is observed between the subsamples of Sample 10: a good number of enlarged dorsal microducts occur in the ramicolous specimens alone. These microducts occur submarginally on the pro- and mesothoracic areas of the prosoma, the metathorax, and the first abdominal segment, and occasionally a few ones on the second abdominal segment (Fig. 8). They are broadly variable in number, the total number ranging from 17 to 73, mean 32.8 (n=55), on each side of the body. In addition, one to three similar microducts are often observed on the ventral surface of the vertex just within the frontal margin. In the foliicolous specimens of the same sample no microducts are enlarged on both surfaces, and the submarginal dorsal microducts are much fewer than in the ramicolous subsample (Fig. 7).

There are morphological grounds for supposing that these samples (and also Sample 9 and 11) belong to the same local population (which should be part of a larger population inhabiting the Terai or a broader area of the Gangetic Plain) (Section 2.1.4, *Terai form*). On this supposition, the occurrence (in Sample10) and the absence (in Sample 8) of the noticeable variation in association with the different feeding sites are attributable not to any genetic difference between the samples but exclusively to the different influences of the different host plants on the phenotypic development of the insects. This implies another category of ecophenotypic effect in scale insects in addition to the season-caused effect on the same feeding sites (Takagi, 2012) and the site-caused effect on the same plant body in the same season (well known in many species now). In general terms, the supposed ‘host plant effect on the feeding site effect’ may induce remarkable differences in microscopic characters of scale insects on some plants but little or no difference on others between conspecific individuals feeding on different sites of the same plant body in the same season. It should be added that the ramicolous specimens of Sample 12 (Natal, on *Melia azedarach*) show no enlarged dorsal microducts.

2.1.4. Local forms

Aulacaspis crawii and *A. fulleri* were originally described from China (*Diaspis crawii*) and South Africa (*D. crawii* var. *fulleri*), respectively, and have been studied mainly on the basis of specimens from these countries, but they are generally supposed to belong to the same species now. The present study shows that the species is broadly distributed in tropical and subtropical Asia and that it should be differentiated locally. The available local forms, however, are still few. There are in these forms two contrasting types in the state of the pore prominences and the accompanying processes (‘lateral processes’) of the fourth and fifth abdominal segments: ‘flat’ and ‘rugged’ types. In the flat type all the pore prominences and lateral processes are low, none of them protruding

beyond the general line of the pygidial margin (Figs 9D, 10A–C); in the rugged type the pore prominences more or less protrude and are often pointed apically and the lateral processes are more or less raised and tend to be remarkably dentate or serrate (Figs 6D, 7E, 10E–G). These types are connected through an intermediate type, in which the margins of the fourth and fifth abdominal segments are rugged but not remarkably (Figs 4E. 5E, 10D).

Hong Kong form. Three adult female specimens, not in good condition, are available from Hong Kong (Section 2.1.2). They belong to the flat type in the margins of the fourth and fifth abdominal segments. The total numbers of the perivulvar disc pores in these specimens are 131, 140, and 141, and those of the dorsal macroducts, of which some were not clearly observed, are estimated to be 206, 208, and 209; the first abdominal segment has, on the posterolateral corner, five macroducts in one case, one in four cases, and none in one case; the fourth abdominal segment has three or four, mean 3.5 (n=6), marginal gland spines on each side. Although the available specimens are too few to show the general characters of the Hong Kong form, the numbers of the counted wax-secreting organs are not scattered but considerably concentrated together, so that the three specimens may represent average members of the form. The disc pores associated with the spiracles and the lateral macroducts and gland spines on the second and third abdominal segments were often not exactly countable, so that their numbers are not given here. The Hong Kong form should belong to a large population broadly distributed in southern China.

Natal form (Sample 12) (Tables 1, 2; Fig. 2a, 9, 10A, 10B). About 20 specimens, all from the twigs of *Melia azedarach*, have been available for study. They belong to the flat type in the margins of the fourth and fifth abdominal segments. In comparison with the other samples, they are especially characteristic in the pygidium much broader (about 1.5–1.8 times as wide as long) and in the median trullae thicker and often broadly rounded. The first abdominal segment often (about 60%, n=32) has one to three dorsal macroducts on the posterolateral corner. These specimens should represent *Aulacaspis fulleri* (Section 2.1.6).

Mangrove-associated form from Negeri Sembilan, Malaya (Sample 6) (Tables 1, 2; Fig. 2a, 10C). This form was studied once together with other mangrove-associated species of *Aulacaspis* (Takagi and De Faveri, 2009). Seven specimens, not all in good condition, are available. They belong to the flat type in the margins of the fourth and fifth abdominal segments. The first abdominal segment often (about 70%, n=14) has one to six dorsal macroducts on the posterolateral corner. The fifth abdominal segment has one or two marginal gland spines, and two with considerable frequency (about 50%, n=11), on each side. (The frequency of the occurrence of two gland spines on the segment is much lower to zero in the other samples).

Cameron Highlands form (Sample 1–5) (Tables 1, 2; Figs 2a, 4, 5, 10D). The samples were collected at various altitudes on the highlands, all on the leaves of *Tetractomia tetrandra*. The specimens are intermediate between the flat and rugged types, the pore prominences of the fourth and fifth abdominal segments tending to protrude, often with a small triangular projection laterally to the apex. The samples comprise a compact group in the numbers of the disc pores, macroducts, and gland spines. It should be added that the first abdominal segment usually or always (about 90–100%) has no dorsal macroducts on the posterolateral corner except in Sample 4, in which the segment sometimes (about 27%, n=22) has one or two macroducts on the corner.

Terai form (Sample 8–11) (Tables 1, 2; Figs 2a, 7, 8, 10E). Sample 8 was obtained from *Murrya paniculata* (Rutaceae) and the other samples from *Trichilia connaroides* (Meliaceae). Sample 8 and 10 contain foliicolous and ramicolous specimens (Section 2.1.3), and Sample 9 and 11 are represented only by foliicolous ones. The collection localities are in two widely separated areas (Dharan area and Narayani Zone, about 200km distant) in the Terai. The specimens of these samples belong to the rugged type in the margins of the fourth and fifth abdominal segments, which are rugged nearly in the same pattern throughout the samples in spite of the distant localities, the different host plants, and the different feeding sites. These samples are considerably similar to each other also in the numbers of the main wax-secreting organs (disc pores, macroducts, and gland spines) except for the total numbers of the dorsal macroducts and perivulvar disc pores in the ramicolous subsamples. On the scatter diagram Fig. 2a they appear rather scattered as compared with the samples from the Cameron Highlands. But this is caused largely by the inclusion of the ramicolous subsamples (8r and 10r), and the foliicolous samples and subsamples are plotted rather close together. Through these samples the first abdominal segment usually or always (about 90–100%) has no dorsal macroducts on the posterolateral corner.

Singapore form (Sample 7) (Tables 1, 2; Figs 2a, 6, 10F–H). The specimens collected from Singapore are characteristic in having eminently rugged margins on the fourth and fifth abdominal segments, standing in a sharp contrast especially with the samples of the flat type. The pore prominences on these segments are usually produced apically into an angular process. This sample is characteristic also in having the disc pores, macroducts, and gland spines fewer than in most of the other samples. On the scatter diagram Fig 2a it is isolated from the other samples, the latter forming a loose group. The first abdominal segment usually (90%, n=78) has no dorsal macroduct on the posterolateral corner (having one to three submarginal macroducts in the other cases). The prosoma often has five to seven dorsal microducts submarginally on each side of the prothoracic area. (The dorsal microducts occurring on this area are generally very few in the other samples except in the ramicolous subsample of Sample 10).

2.1.5. Features through the local forms

Body shape. All the local forms are similar in the body shape of the full-grown adult females, which are, however, variable in the relative width of the pygidium. The broadest pygidium, about 1.8 times as wide as long, is found in the Natal form (Sample 12), whereas the narrowest one, about 1.1 times as wide as long, in the Singapore form (Sample 7). However, each form is considerably variable in the relative width, so that all the forms broadly overlap to form a continuous series of variation. The pygidial margins of seven specimens belonging to five samples and five local forms are shown in one chart (Fig. 10). They gradually change in gradient, the degree of gradient reflecting the breadth of the pygidium. The basal three segments of the postsoma are nearly the same in width, but in the Cameron Highlands form the metathorax and the second abdominal segment are lobed laterally rather strongly, and in the Terai form the second abdominal segment tends to be broader than the preceding two segments.

Median trullae. The median trullae are similar among most of the forms, having the mesal margins divergent and finely serrate; their basal zygosis is somewhat variable in development. In the Natal form (Sample 12) they are usually very thick, roundish around the apex, and strongly zygotic basally (Fig. 10A). However, narrower median

trullae are also found in the sample (Figs 9H, 10B), and they are more or less similar to the trullae observed in the other forms. The Singapore form (Sample 7) has the median trullae usually separated basally from each other by a good space, which is not strongly sclerotized and shows little trace of zygosis (Figs 6H, 10F); this space, however, is sometimes narrower and sclerotic (Fig. 10H), and the trullae themselves appear to be not much different in shape from those in the samples from Malaya and the Terai. After all, each of the Natal and Singapore forms appears to be somewhat distinct from the other forms in the state of the median trullae but, in this feature, too, they may represent the opposite extremes of a broad variation.

Pore prominences and lateral processes on the fourth and fifth abdominal segments. The flat and rugged types of the pygidial margins on the fourth and fifth abdominal segments are distinct from each other, but they are connected through the intermediate type, and the rugged type is divisible into two subtypes somewhat different in the development of the processes. In Fig. 10 the pygidial margins of seven specimens belonging to five samples and five local forms are arranged in an ascending order of the development of the pore prominences and lateral processes. These features apparently vary stepwise from the Natal form to the Singapore form. It is natural to expect that the gaps among these forms will be bridged by further local samples.

Dorsal microducts on the prosoma. The Singapore form (Sample 7) often has five to seven dorsal microducts in a group on the prothoracic area. Some specimens, however, have only a few dorsal microducts on this area as usual in the other samples. Moreover, the ramicolous subsample of Sample 10 possesses abundant enlarged dorsal microducts on the prothorax to the basal abdominal segment, and this fact makes the Singapore form appearing much less peculiar.

Submarginal dorsal macroducts on the first abdominal segment. A few or several submarginal dorsal macroducts occur on the first abdominal segment frequently in the mangrove-associated form (Sample 6) and Natal form (Sample 12) and possibly also in the Hong Kong form. In the other forms there are usually or always no submarginal macroducts on that segment except for the occasional occurrence of a few in Sample 4, which belongs to the Cameron Highlands form.

Combined mean values of the total number of the perivulvar disc pores and that of the dorsal macroducts. On the field of the scatter diagram Fig. 2a the examined samples except Sample 7 (Singapore form) are plotted in a loose cluster (with the ranges overlapping variously). It is noteworthy that Sample 12, the Natal form, is in the midst of the cluster and situated near the samples from the Cameron Highlands. The Singapore form is isolated in the left lower corner of the diagram, having the mean values much smaller than in the other forms (and the ranges overlapping with those in none of them). However, the three specimens from Hong Kong (not shown in the diagram) are close to the Singapore form in their mean total number of the perivulvar disc pores, while not differing from the Cameron Highlands samples in the mean total number of the dorsal macroducts. This supports the view that the blank space between the Singapore form and the other samples on the diagram will be filled by samples from other localities, especially from southern China. (This statement does not mean that the Singapore form is especially close to the supposed South China form. So far as represented by the three specimens from Hong Kong, the South China form belongs to the flat type in the marginal processes of the fourth and fifth abdominal segments, thus making a remarkable contrast with the Singapore form.)

Conclusion. The local forms are far from uniform, but are not reasonably divisible into distinct units or species. They are remarkably variable especially in the marginal processes of the pygidium, in which, however, they are connected to compose a graded series. In Hong Kong, Malaya, Singapore, and the Terai the local forms were collected on wild trees, and they are probably native to their localities. In the present study it has not been possible to find any geographical trend throughout them. This may be due to the insufficient material, but it is more probable that the local differentiation depends on local ecological conditions rather than on geographical distances.

2.1.6. Notes on the Natal form

This form should correspond to *Diaspis crawii* var. *fulleri* or *Aulacaspis fulleri*, which was formally synonymized with *A. crawii* by Munting (1977) (Section 2.1.1). I agree with him about this synonymy. The Natal form appears to be different from the others in the pygidium broader and the median trullae thicker, but the view is adopted that it represents no more than an extreme of a broad variation in each of these features. In fact, South Africa is outside the natural distribution of *Aulacaspis*, and *A. fulleri* should have been introduced from Asia to South Africa a long time ago, though the original locality is unknown. It was found in 1901 in Natal on *Melia azedarach*, which was also introduced from Asia. It was collected further on that plant in South Africa at least in 1915, 1962, and 1964 (and on *Ricinus* sp. in 1910) (Section 2.1.1, 2.1.2). The main part of the South African population should have been, exclusively or at least usually, ramicolous on *M. azedarach*, a deciduous plant, for more than a century under the ecological conditions of the region. It might be worthwhile from this viewpoint to compare samples occurring in South Africa on *M. azedarach* (and also on other plants if any) with those in Asia on *M. azedarach* as well as on evergreen plants. (It should be kept in mind that *M. azedarach* and some other host plants, especially *Aglaia odorata* and *Murraya paniculata*, have long been cultivated broadly in Asia and that the distribution of *A. crawii* in Asia is probably not entirely natural.)

'A. *fulleri*' was recorded in Hawaii, but it is reasonable to assume that it was introduced from China (Section 2.1.1b).

2.1.7. Recognition characters

Full-grown adult female robust, sclerotized throughout and especially strongly on prosoma. Prosoma swollen into an eminent mass, rather square in rough outline, broader than long, broadest subbasally; frontal margin between prosomatic tubercles roundish, lateral margin behind the tubercle roundish and slanting outwards; prosomatic tubercles blunt. Postsoma robust, metathoarx about 0.8 times or so as wide as prosoma; basal three segments nearly the same in width, or metathorax and abd II, or abd II alone, lobed laterally somewhat beyond abd I.

Antennae each with basal tubercle small and simple. Peribuccal scleroses well represented. Anterior spiracles each with a compact group of many disc pores (not always countable exactly, being crowded together often too closely); posterior spiracles each with a loose cluster of disc pores, of which a few or several lateral ones are usually laid on their sides under a dermal fold. Perivulvar disc pores numerous. Dorsal macroducts numerous, occurring on abd I–VI submedially and on II–V and at times also on I submarginally; submedian macroducts arranged in distinct segmental and infrasegmental series on I–IV, 1–11 on VI; submarginal macroducts at times 1–6

occurring on posterolateral corner of I, those on II often in an irregularly double or triple row. Lateral macroducts and lateral gland spines abundant on abd II and III; marginal gland spines 2–11 on IV, 1 or at times 2 on V, on each side. Median trullae sunken into pygidium except for apices; variable in thickness and in the development of the basal zygosis, the thickest ones being nearly rounded marginally and strongly zygotic basally, but usually these trullae are longer than broad, with the mesal margins divergent and serrate and with the bases sometimes yoked only weakly.

Remarks. *Aulacaspis crawii* as understood in this study is broadly distributed in the tropics and subtropics of Asia, comprising local forms, which are diverse in various features. The description given above may be too short for recognizing this variable species. The inclusion of noteworthy characters of all the known local forms (Section 2.1.4, 2.1.5) in the description will make it too discursive and not applicable to unknown local forms. It may be better to focus the description on differences between this species and closely related ones. There have been described some species that are similar to *A. crawii*. *Aulacaspis citri* and *A. intermedia*, both described from China (Chen, 1954; Chen et al., 1980; Chen, 1983), may especially be close to *A. crawii*, but have not been available for the present study. According to Chen, *A. citri* and *A. intermedia* differ from *A. crawii* in the body constricted across the metathorax, in the disc pores associated with the posterior spiracles much fewer, and in other details. Tang (1986) stated that *A. crawii* and *A. citri* were distinguishable from each other in the number of the marginal macroducts in the second-instar female. However, in *A. crawii* these macroducts are variable in number, affording no stable diagnostic character (Takagi and De Faveri, 2009).

2.2. *Aulacaspis mischocarpi*
(Tables 1, 2; Figs 3, 11, 12)

2.2.1. Historical review

Phenacaspis mischocarpi Cockerell and Robinson, 1914: 328 [‘Los Baños, Philippine Is., Dec. 1913, on *Mischocarpus fuscescens* Blume (C. F. Baker, 2179).’].

Phenacaspis mischocarpi: Robinson, 1917: 21 [‘Luzon, Laguna, Los Baños (Baker), on *Mischocarpus fuscescens*.’].

Phenacaspis thoracica Robinson, 1917: 22 [‘Luzon, Laguna, Los Baños (Baker), December 1915, on *Morinda bracteata*.’], n.syn.

Aulacaspis mischocarpi: Scott, 1952: 38 [‘The material … was collected by C. F. Baker and is from the same lot used by Cockerell and Robinson in their original description.’].

Aulacaspis thoracica: Scott, 1952: 41 [‘Material is … from the lot used by Robinson in the original description.’].

Aulacaspis thoracica: Balatibat, 1991: 41 [‘Los Baños, Mt. Makiling, on leaves of *Pedicellia fuscescens* … 1990 …’].

Aulacaspis mischocarpi: Takagi and De Faveri, 2011 [Fig. 3, drawn by D. J. Williams on the basis of a specimen mounted from the type material].

Furthermore, ‘*Aulacaspis thoracica*’ was recorded repeatedly from China, but all these records are problematical (Section 2.2.3).

2.2.2. Material examined

Los Baños (type locality), Laguna, Luzón, Philippines, on the leaves of *Pedicellia fuscescens* (=*Mischocarpus fuscescens*) (Sapindaceae), 1.XII.1992 [92PL-62] (collected in the grounds of the

University of the Philippines at Los Baños).

Thirty full-grown and 12 teneral adult females have been examined for preparing the description.

One adult female mounted from the type material of *Phenacaspis mischocarpi* (Los Baños, on *Mischocarpus fuscescens*, 26.XII.1913, C. F. Baker) has also been examined. This specimen is briefly noted after the description based on the specimens collected in 1992 (Section 2.2.4).

2.2.3. Notes on *Aulacaspis thoracica*

In this study, *Aulacaspis thoracica* (originally *Phenacaspis thoracica*, 1917, Los Baños, on *Morinda bracteata*, Rubiaceae) is united with *Aulacaspis mischocarpi* (*Phenacaspis mischocarpi*, 1914, Los Baños, on *Mischocarpus fuscescens*, which is known also as *Pedicellia fuscescens*, Sapindaceae) as a junior synonym of the latter.

A. thoracica from Los Baños. When describing *P. thoracica*, Robinson (1917) also described *P. mischocarpi* and separated them in 'Synoptic table of the species' on the basis of the external appearance of the female test. Scott (1952) examined specimens of *P. mischocarpi* and *P. thoracica* used in the original descriptions. He described them as distinct species and separated them in 'Key to included species' by the different arrangements of the submedian dorsal macroducts and by the presence and absence of long lateral setae on the metathorax and basal three abdominal segments. Balatibat (1991) identified with *A. thoracica* his material collected at Los Baños on *Pedicellia fuscescens*.

Records of '*A. thoracica*' from China. Scott (1952) recorded '*A. thoracica*' also from southern China and stated that 'Ferris collected specimens from numerous hosts in China, and about Hong Kong'. The host plants he recorded as of '*A. thoracica*' in China were *Cinnamomum*, *Cycas revoluta*, *C. circinalis*, *Sapium sebiferum*, and rose. Chen (1983) described 'A. *thoracica*' and mentioned some southern provinces of China for its distribution range and *Cinnamomum*, *Sapium sebiferum*, and *Cycas revoluta* as its host plants in China. He compared it with *A. rosarum* and *A. mischocarpi*. Tang (1986) united *A. thoracica* with *A. rosarum*, suppressing the latter as a junior synonym of the former. He mentioned roses, *Cycas revoluta*, *Sapium sebiferum*, *Phoebe nanmu*, and *Catalpa ovata* as the host plants of his 'A. *thoracica*'. (Some of the diverse host plants mentioned by Chen and Tang agreed with those recorded by Scott, suggesting the possibility that they were mere citations from Scott.)

A. *thoracica* and *A. mischocarpi*. Dr D. J. Williams prepared a figure of *A. thoracica* on the basis of a specimen from the type material of *P. thoracica*, and the figure is published in this paper with his approval (Fig. 3). It agrees with his figure of *A. mischocarpi* published in Takagi and De Faveri (2011) and with the specimens of *A. mischocarpi* I examined (Fig. 11) (including the one from the type material of *P. mischocarpi*: Section 2.2.2) in the shape of the body, in the arrangement of the dorsal macroducts (in disagreement with the key, descriptions, and figures presented by Scott), in the pygidial margin, etc. It does not differ from the specimens of *A. mischocarpi* in the numbers of the disc pores, the dorsal macroducts, and the lateral macroducts and lateral gland spines on the third abdominal segment. (The total number of the perivulvar disc pores in the specimen of *A. thoracica* figured by Williams is estimated at about $44 \times 2=88$; that of the dorsal macroducts at about $45 \times 2=90$.) The figure of *A. thoracica* differs from *A. mischocarpi* I examined in showing no long lateral setae on the prosoma and basal three postsomatic segments. However, these setae are lost on some of these body parts in some

of the examined specimens of *A. mischocarpi*, especially in fully grown ones. It seems that these lateral setae easily drop off from their basal sockets possibly in the course of preparing specimens and especially on aged individuals with the derm sclerotized and hardened. I adopt the view that *P. thoracica* was described on the basis of specimens of *P. mischocarpi* that had lost the long lateral setae. On this understanding, *P. thoracica* and *P. mischocarpi* are objective synonyms, which were given to the syntopic (but, according to Robinson, 'allophytic') samples of the same species. After all, I cannot choose but conclude that both Robinson and Scott made inaccurate observations on the specimens of these forms they examined and that Balatibat was misled by them in identifying his material collected on *Pedicellia fuscescens* (the host plant of *Phenacaspis mischocarpi*) at Los Baños.

This species was collected at least four times at Los Baños: in 1913 (*Phenacaspis mischocarpi*), 1915 (*P. thoracica*), 1990 (*A. thoracica*: Balatibat), and 1992 (*A. mischocarpi*, the present study). We may reasonably suppose that these samples were obtained from the same population that had been (and probably is still) persisting at that locality in association, at least mainly, with *Pedicellia fuscescens*. A careful survey in Los Baños may be necessary in order to confirm whether the record of *Morinda bracteata* as the host of P. *thoracica* was correct or not.

The records of '*Aulacaspis thoracica*' from China remain problematical, requiring critical re-examinations of the specimens concerned. Now that *A. thoracica* is identical with *A. mischocarpi*, and because *A. rosarum* is distinct from *A. mischocarpi* as mentioned below, Tang's (1986) view that *A. thoracica* and *A. rosarum* belong to the same species finds no grounds. His view suggests that the records of '*A. thoracica*' in China included *A. rosarum*.

2.2.3b. Notes on *A. rosarum*

Aulacaspis rosarum was described by Borchsenius (1958) from specimens collected on the branches of *Rosa* sp., near Chengdu, Sichuan, China. I have prepared a figure from a specimen mounted from the type material (Fig. 22) for making a comparison with *A. mischocarpi* (Fig. 11). These figures show that *A. rosarum* and *A. mischocarpi* are clearly distinguishable in the shape of the body, in the length of the lateral setae in the prepygidial region of the body, in the marginal processes of the fourth and fifth abdominal segments, in the number of the marginal gland spines on the fourth abdominal segment, in the occurrence of dorsal microducts, etc. *A. rosarum* occurs broadly in China on *Rosa* and *Rubus* (Chen, 1983). This species was introduced to some other areas of the world probably together with garden roses. In Hawaii, however, it was confused with *A. rosae* (in spite of the fact that these species are distinct from each other in microscopic characters: see Fig. 22 and Fig. 23). Nakahara (1981) failed to find *A. rosae* among all specimens once referred to that species in Hawaii and re-examined by him, and he identified them with *A. rosarum*. According to Chen (1983), this species was recorded once as *A. rosae* in China. *A. rosarum* may have been confused also with *A. thoracica* in China (Section 2.2.3). Moreover, the possibility that it was confused with *A. crawii* in China and Saint Helena Island may not be excluded (see Section 2.1.1 for the occurrence of '*A. crawii*' on *Rubus* in China; Section 2.1.1b for the repeated collections from rosaceous plants in Saint Helena Island).

2.2.4. Recognition characters

Full-grown adult female about 1150μm long at maximum, pygidium about 205–260μm long, as wide as or a little wider than long. Sclerotized, especially strongly on prosoma. Prosoma swollen into an eminent mass, somewhat wider than long, widest at about posterior one fourth; margin broadly rounded between and behind the tubercles, the lateral margins gradually converging caudad on posterior one fourth; prosomatic tubercles robust. Metathorax and abd I about two thirds as wide as prosoma; abd II lobed laterally a little beyond I.

Antennae each with basal tubercle very small. Peribuccal scleroses well developed. Anterior spiracles each with a rather small compact cluster of disc pores; posterior spiracles each with a loose cluster of several disc pores, of which a few lateral ones are laid on their sides under a dermal fold. Prosoma and prepygidial postsoma with elongate lateral setae on dorsal and ventral surfaces, the setae on posterolateral corner of prosoma, metathorax, and abd I and II especially elongate, the ventral lateral seta on metathorax about 23–25μm long. Perivulvar disc pores: 6–13 in median, 13–24 in each anterolateral, and 14–29 in each posterolateral group. Submedian dorsal macroducts on abd II–VI, arranged in distinct infrasegmental and segmental series on II–IV: 2–7 in infrasegmental and 1–9 in segmental series on II, 2–6 infrasegmental and 2–7 segmental on III; 1–4 infrasegmental and 1–5 segmental on IV; 2–4 on V; 1–3, usually 1 or 2, on VI. Submarginal dorsal macroducts on abd III–V: 1–6 on III, 1–4 on IV, 2–5 on V. Lateral macroducts and lateral gland spines abundant on abd II and III; marginal gland spines 2 on IV. Median trullae sunken into apex of pygidium almost entirely, longer than broad, with mesal margins divergent, slightly rounded, and serrate; ventrally, bases with a pair of sclerites separated from each other by a narrow space and extending anteriorly to form a pair of attenuating stripes. Second and third trullae with both lobules well represented, the lateral lobule of the third asymmetrical, with lateral margin longer than the mesal, slanting, and serrate; mesal lobules of both trullae with a pair of linear scleroses basally, lateral lobules with rudimentary scleroses. Pore prominence associated with mesal marginal macroduct on abd V protruding and angular, followed laterally by rugged processes; that on IV similar, followed by a less developed process.

The specimen available from the type material (see Section 2.2.2). No difference of taxonomic value has been found between the specimen mounted from the type material and the sample collected in 1992. This adult female is not fully grown, but the whole body approaches the outline characteristic of the species. Peribuccal scleroses shaped well. Ventral lateral seta on metathorax 25μm long. Anterior spiracle with 9 or 10 disc pores; posterior spiracle with 4, 2 of them being laid on their sides in a dermal fold. Perivulvar disc pores 76 in total; 8 in median, 16 or 17 in anterolateral, 16 or 19 in posterolateral group. Dorsal macroducts on both sides 60 in total; submedian macroducts 3 or 4 in infrasegmental and 4 in segmental series on abd II, 3 in each series on III, 2 in each series on IV, 2 on V, 2 on VI; submarginal macroducts 2 or 3 on abd III and also on IV, 3 or 4 on V. Lateral macroducts 10 or 14 on abd II, 9 on III. Lateral gland spines 6 or 10 on abd II, 9 or 10 on III; marginal gland spines 2 on IV.

Remarks. On the understanding adopted in this study, this species is known only from Los Baños, Luzón Island. It is characterized especially by the prominent prosoma, the robust prosomatic tubercles, the elongate lateral setae, and the protruding pore prominences on the fourth and fifth abdominal segments. In these characters it is similar to *A. alangii* from Borneo (Section 2.3).

2.3. *Aulacaspis alangii*, n.sp.
(Tables 1, 2; Figs 13, 14)

2.3.1. Material examined

Sepilok, Sabah (northeastern Borneo), Malaysia, on *Alangium ebenaceum* (Alangiaceae), 14.XI.1988 [88ML-350]. Females occurring on the lower surface of leaves.

The description below is based on nine full-grown (one the holotype) and three teneral adult females. Not all of them are in good condition (it seems that the full-grown individuals were collected at some time after their death on the host plant).

2.3.2. Recognition characters

Full-grown adult female 1530μm long at maximum, pygidium about 260–325μm long, a little wider than long. Strongly sclerotized especially on prosoma and metathorax, and also on basal 2 abdominal segments except on median area. Prosoma swollen into an eminent mass, nearly 1.5 times as wide as long, widest across prosomatic tubercles, which are large and robust; margin between the tubercles broadly rounded, the margins behind the tubercles converging caudad gradually, then abruptly towards metathorax. Postsoma much narrower than prosoma, metathorax a little less than two thirds as wide as prosoma, abd I and II gradually wider.

Antennae each with basal tubercle very small or represented by 2 minute setae alone. Peribuccal scleroses well developed. Anterior spiracles each with a loose cluster of disc pores. Posterior spiracles each with 7–15 disc pores, all or most pores being arranged in a single transverse row laterally to the spiracle. Prosoma and basal three segments of postsoma with elongate lateral setae; ventral lateral seta on metathorax about 16–20μm long. Perivulvar disc pores: 16–25 in median, 27–39 in each anterolateral, and 22–33 in each posterolateral group. Submedian dorsal macroducts on abd II–VI, arranged in distinct infrasegmental and segmental series on II–IV; 4–10 in infrasegmental and 4–11 in segmental series on II; 4–9 infrasegmental and 3–9 segmental on III; 2–6 in each series on IV; 5–8 on V; 3 or 4, usually 3, on VI. Submarginal dorsal macroducts on abd III–V (in one specimen, 3 macroducts present on the left side of abd II), 3–8 on III, 4–7 on IV, 5–9 on V. Lateral macroducts and lateral gland spines abundant on abd II and III. Marginal gland spines 3–5 on IV. Median trullae sunken into a deep notch at apex of pygidium almost entirely, longer than broad, divergent, with mesal margins minutely serrate and rather abruptly bent outwards at about apical third; bases separated from each other by a slit, extending into a pair of attenuating sclerotized stripes on ventral surface of pygidium. Second and third trullae with oblong lobules; mesal lobules with a pair of well-developed linear scleroses basally, lateral lobules with basal scleroses less developed. Pore prominence associated with mesal marginal macroduct on abd V protruding and pointed apically, followed laterally by 2 broad processes also protruding, asymmetrical, the lateral margin being much longer and serrate; that on IV protruding, broad, followed laterally by rugged margin.

Remarks. This species is similar to *A. mischocarpi* especially in having elongated lateral setae on the prosoma, metathorax and basal three abdominal segments. It is, however, uniquely characterized by the disc pores associated with each posterior spiracle arranged in a single transverse row laterally to the spiracle. The new species is also well characterized by the very prominent prosoma, which makes the body appearing strongly constricted in the metathorax.

2.4. *Aulacaspis otophorae*, n.sp.
(Tables 1, 2; Fig. 15)

2.4.1. Material examined

Tarusan, Batarasa, Palawan, Philippines, on *Otophora fruticosa* (also known as *Lepisanthes fruticosa*) (Sapindaceae), 19.VIII.1993 [93PL-86]. Females occurring on the lower surface of leaves.

The description below is based on 30 specimens (one the holotype), which are fully grown or nearly so.

2.4.2. Recognition characters

Full-grown adult female 1550µm long at maximum, pygidium about 260–285µm long, a little wider than long. Sclerotized on prosoma but weakly and except along posterior border. Prosoma swollen into a prominent mass, nearly quadrate, about 1.3 times as wide as long, widest subbasally, broadly rounded between prosomatic tubercles, a little swollen behind the tubercles, prosomatic tubercles low and broad. Metathorax about 0.8 times as wide as prosoma, abd I a little narrower than metathorax, II lobed laterally a little beyond I.

Antennae each with basal tubercle small and often having 1 or 2 minute spiny processes. Peribuccal scleroses shaped but not strongly sclerotized. Anterior spiracles each with a rather small, loose cluster of disc pores. Posterior spiracles each with some disc pores in a loose cluster, several lateral ones laid on their sides under a dermal fold. Perivulvar disc pores: 12–22 in median, 18–38 in each anterolateral, and 20–33 in each posterolateral group. Submedian dorsal macroducts on abd II–VI, in distinct infrasegmental and segmental series on II–IV; 4–8 in infrasegmental and 5–10 in segmental series on II; 4–7 infrasegmental and 4–8 segmental on III; 2–4 infrasegmental and 2–5 segmental on IV; 4–9 on V; 1–4, usually 3, on VI. Submarginal dorsal macroducts on abd III–V: 6–11 on III, 4–7 on IV and also on V. Lateral macroducts and lateral gland spines abundant on abd II and III. Marginal gland spines on V 3–5, usually (88.3%, n=60) 3. Median trullae sunken into apex of pygidium, elongate, divergent and minutely serrate on mesal margins; basally with a pair of small sclerites separated from each other by a narrow space and extending and attenuating anteriorly on ventral surface of pygidium. Second and third trullae similar in shape; second trullae with lobules oblong, the third with lobules a little broader, asymmetrical, minutely serrate or smooth on the longer lateral margin; mesal lobules of both trullae with a pair of linear basal scleroses well represented, the lateral lobules with basal scleroses less developed. Pore prominence associated with mesal marginal macroduct on abd V somewhat protruding, ending in 1 or 2 sharp spines, followed laterally by 2 serrate processes also protruding; that on IV broader, with 1 or 2 spines, followed laterally by processes much less developed.

Remarks. This species differs from *A. mischocarpi* and *A. alangii* in the prosoma rather quadrate in outline, in the prosomatic tubercles less developed, in the peribuccal scleroses not strongly sclerotized, and in the lateral setae not particularly elongated. It is similar to the latter two, and also to *A. shoreae* (Section 2.5) and *A. fici* (Section 2.6), in the rugged margins of the fourth and fifth abdominal segments, and all these species may be more or less related to each other. It differs from the last two species in having submedian macroducts on the first abdominal segment and in other details.

2.5. *Aulacaspis shoreae*, n.sp.
(Tables 1, 2; Fig. 16)

2.5.1. Material examined

Bukit Cendana, Pulau Pinang [Penang Island], Malaya, Malaysia, on *Shorea multiflora* (Dipterocarpaceae), 21.XI.1991 [91ML-489]. Females occurring on the lower surface of leaves.

The description below is based on 28 full-grown (one the holotype) and nine juvenile adult females.

2.5.2. Recognition characters

Full-grown adult female 1300µm long at maximum, pygidium 240–280µm long, a little wider than long. Sclerotized, but only weakly and except on posterior border of prosoma and on median area of prepygidial abdomen. Body deeply constricted between prosoma and metathorax. Prosoma swollen into an eminent mass, roundish, tending to be slightly excavated medially on frontal margin, about 1.2–1.3 times as wide as long, widest across prosomatic tubercles, which are low and broad. Metathorax nearly 0.6 times as wide as prosoma, abd I and II gradually wider, the whole postsoma being rather fusiform in rough outline.

Antennae each with basal tubercle small but distinct. Peribuccal scleroses well developed. Anterior spiracles each with a small cluster of disc pores, which is partly covered by a dermal fold. Posterior spiracles each with a small cluster of disc pores, a few lateral ones laid on their sides. Perivulvar disc pores: 4–14 in median, 11–23 in each anterolateral, and 9–23 in each posterolateral group. Submedian dorsal macroducts on abd I–VI; 2–6 in segmental series and occasionally (about 5%) 2 present in infrasegmental series on I; 1–7 in segmental and often (about 44%) 2–5 in infrasegmental series on II; 2–6 in segmental and often (about 43%) 2 or 3 in infrasegmental series on III; 2–5 in segmental and sometimes (about 33%) 2 in infrasegmental series on IV; 1–4 in segmental series on V; 1 on VI. Submarginal macroducts on abd II–V, rarely 1 or 2 on I; 1–4 on II, 2–5 on III, 2–4 on IV, and 1–3, usually 2, on V. Lateral macroducts and lateral gland spines abundant on abd II and III. Marginal gland spines 2–5, often 3, on IV. Median trullae sunken into pygidium except for apices, elongate, their mesal margins parallel and separated from each other by a space on about basal half, then divergent and minutely serrate; basally with a pair of small sclerites separated from each other by a slit and extending and attenuating anteriorly on ventral surface of pygidium. Second trullae with lobules oblong and with a pair of linear basal scleroses, which are especially well developed on mesal lobule. Third trullae with lobules tending to be broader, mesal lobule with a pair of linear basal scleroses. Pore prominence associated with mesal marginal macroduct on abd V protruding and pointed apically, followed laterally by a similar process, then usually by a low protuberance; that associated with mesal marginal macroduct of abd IV similar, tending to be serrate, usually followed laterally by a smaller process.

Remarks. This species is very similar to *A. fici* and compared with the latter under that species (Section 2.6).

2.6. *Aulacaspis fici*, n.sp.
(Tables 1, 2; Figs 17, 18)

2.6.1. Material examined

Grounds of the Forest Research Institute of Malaysia, Kepong, Kuala Lumpur, Malaya, Malaysia, on *Ficus chartacea* (Moraceae), 27.IX.1986 [86ML-33]. Females and males occurring on both surfaces of leaves. Female test gently convex dorsally; first-instar exuvial cast dark brown; second-instar exuvial cast with two dark brown spots arranged longitudinally.

The description below is based on 32 full-grown (one the holotype) and four teneral adult females.

2.6.2. Recognition characters

Full-grown adult female 1550μm long at maximum, pygidium about 290–335μm long, as wide as long. Sclerotized, especially on prosoma. Body deeply constricted between prosoma and metathorax. Prosoma swollen into an enormous mass, occupying half the body length, about 1.2–1.3 times as wide as long, widest across prosomatic tubercles, swollen between the tubercles, tending to be a little excavated medially on frontal margin, roundish behind the tubercles; prosomatic tubercles moderate in size. Metathorax about 0.6–0.7 times as wide as prosoma, abd I and II a little wider than metathorax, the whole postsoma being rather fusiform in rough outline.

Antennae each with basal tubercle small but distinct. A small low tubercle sometimes (22.2%, n=36) present between antennae. Peribuccal scleroses well developed. Anterior spiracles each with some disc pores scattered anterolaterally, encircled together within a slender dermal fold. Posterior spiracles each with some disc pores scattered laterally. Perivulvar disc pores: 9–18 in median, 16–31 in each anterolateral, and 10–30 in each posterolateral group. Submedian dorsal macroducts on abd I–VI; 1–9 in segmental series and none in infrasegmental series on I; 3–9 in segmental series and sometimes (about 22%) 3 or 4 present in infrasegmental series on II; 3–9 in segmental and sometimes (about 21%) 2–4 in infrasegmental series on III; 2–8 in segmental and sometimes (about 19%) 3–5 in infrasegmental series on IV; 3–5, usually 4, in segmental series on V; 1–4, usually 2 or 3, on VI. Submarginal dorsal macroducts on abd III–V, 4–7 on III, 3–6 on IV, and 2–5 on V. Lateral macroducts and lateral gland spines abundant on abd II and III. Marginal gland spines 3–6 on IV. A small dermal pocket often present submarginally around borders between abd III and IV and also on IV, 4 in total on both sides but sometimes 1 or more of them being not discernible. Median trullae sunken into pygidium, elongate, divergent, minutely serrate on mesal margins, basally with a pair of sclerites extending into a pair of lines anteriorly on ventral surface of pygidium. Second trullae with oblong lobules, mesal lobule with a pair of linear basal scleroses. Third trullae with broader lobules. Pore prominence associated with mesal marginal macroduct on abd V protruding and triangular, slightly serrate, followed laterally by a similar process and then by a much smaller process; that on IV also protruding and triangular, serrate, followed laterally by a similar process.

Remarks. *A. shoreae* and *A. fici* are very similar to each other in the body shape of the full-grown adult female, in the arrangement of the dorsal macroducts (except for the presence and absence of submarginal macroducts on the second abdominal segment), and in the remarkably rugged margins of the fourth and fifth abdominal segments, but each of these species has an odd character. In *A. shoreae*, the disc pores associated with

each anterior spiracle are partly covered by a dermal fold. On the other hand, *A. fici* is unique in having dermal pockets ventrally and submarginally on the third and fourth abdominal segments. These structures are small and inconspicuous, and the dermal pockets are unstable in occurrence in some of the examined specimens. However, they are extraordinary not only in *Aulacaspis* but also in the family, so that they should have taxonomic significance. In addition, the prosoma in *A. fici* is more swollen on the frontal margin between the prosomatic tubercles, occupying half the body length. The perivulvar disc pores and the dorsal macroducts are more numerous in *A. fici*, and the total number of the dorsal macroducts is definitely greater in *A. fici* in spite of the fact that this species has no submarginal macroducts on the second abdominal segment (and on the first). However, in general, the numbers of these organs are liable to fluctuate locally, whereas *A. shoreae* and *A. fici* are known only by their type samples.

Tang (1986) described *Aulacaspis fuzhouensis* from Fuzhou, Fujian, China. His figure shows that it is characterized in having a fusiform postsoma partitioned from the prosoma by a deep constriction. In this character *A. shoreae* and *A. fici* are similar to *A. fuzhouensis*, but Tang's figure also shows that the last is quite different from the former two in the less prominent prosoma, in the absence of dorsal macroducts on the basal two abdominal segments, and in the low marginal processes on the fourth and fifth abdominal segments. The last character excludes *A. fuzhouensis* from the *mischocarpi* group (which is mentioned in Section 3.3). Furthermore, Tang compared *A. fuzhouensis* with *Aulacaspis latissima* and *A. distylii*, but the latter two differ from the first, above all, in body shape.

3. Australian Species and Asian Species

I have begun this study with the intention of finding Asian species that are related to *A. australis* and *A. constricta*, both these species occurring on mangrove plants in Australia and appearing to be unrelated to each other. I think that two species groups in Asia are related to these Australian species.

3.1. Two mangrove-associated species in Australia

Aulacaspis australis was described by Brimblecombe (1959) from Sandgate, Queensland, and from *Bruguiera gymnorrhiza*, and was compared with *A. crawii*. It was recorded and described from another locality of Queensland (Takagi and De Faveri, 2009). It was studied on the basis of a series of samples collected on three or so species of mangroves on the coast of Queensland and two islands in the Torres Strait between Australia and New Guinea; *Aulacaspis martini*, which was described from *Rhizophora* and from the northern coast of Papua New Guinea (Williams and Watson, 1988), was interpreted to represent a local form of *A. australis* (Takagi, De Faveri, and Martin, 2011). (Furthermore, *A. martini* was recorded from South India as occurring on mango leaves, but this record is left out of account.)

Aulacaspis constricta was described from mangroves of *Avicennia* in Northern Territory and from an undetermined mangrove (*Avicennia*?) in Western Australia. It was compared with *A. bambusae* (=*Diaspis bambusae* Green) and *A. mischocarpi*, and supposed to be related to *A. mischocarpi* (Takagi and De Faveri, 2011).

No native inland species of *Aulacaspis* has been known in Australia. When combined with this fact, the occurrence of the two mangrove-associated species on

the eastern and northwestern coasts of Australia postulates that these species or their ancestors invaded Australia from Asia through intermittent chains of mangroves, and suggests that the biogeographical region Wallacea, where little is known about the scale insect fauna, should have played some important role in their evolution and distribution (Takagi and De Faveri, 2011).

Our knowledge on mangrove-associated scale insects and their distributions are still very meagre. However, it may be reasonable to suppose that transmarine dispersal is much easier for mangrove-inhabiting scale insects than for inland ones. *Mongrovaspis quadrispinosa* is known from Lombok, Mindoro, Luzón, Iran, the Sinai Peninsula, and the Red Sea coast of Africa in association with mangroves of *Avicennia* (Takagi and Moghaddam, 2005). *Suluaspis* has two mangrove-associated species known from widely distant areas, one of them from the Philippines (Palawan and Luzón) and the other from the Solomon Islands (Vanikoro islets) (Takagi and Germain, 2008).

3.2. *A. australis* and Asian species

In describing *A. australis*, Brimblecombe (1959) remarked as follows: 'This species has a close resemblance to *A. crawii* (Cockerell) but differs in having neither dorsal ducts on the sixth abdominal segment nor any indication of a fourth pair of pygidial lobes.' *A. crawii* certainly has submedian dorsal macroducts on the sixth abdominal segment. The Singapore form of *A. crawii* has two serrate broad processes laterally to the pore prominence on the fifth abdominal segment (Fig. 10F, G), and these processes may be interpreted to be modified lobules of the fourth trulla. However, these processes are variable in development in *A. crawii*, and the Singapore form represents an extreme of a broad variation, of which the opposite extreme does not differ from *A. australis* in the state of the processes. Definite fourth trullae are absent in both *A. australis* and *A. crawii* as usual in *Aulacaspis*.

Both these species are, naturally, variable locally. Local variation in *A. australis* has recently been studied (Takagi, De Faveri, and Martin, 2011), and some local forms of *A. crawii* are presented in this paper. No specimen of *A. australis* has ever been found to have submedian macroducts on the sixth abdominal segment, whereas, through all the local forms, *A. crawii* is provided with submedian macroducts (which are variable in number among the local forms) on the segment. The absence and presence of these macroducts are stable characters adoptable in distinguishing the two species. These species do not entirely agree also in the number of the marginal gland spines occurring on the fourth abdominal segment: *A. australis* has usually two, and rarely one or three, gland spines, while *A. crawii* usually more than two, and only exceptionally two, on each side of the segment. There are other features showing slight or obscure tendencies to differ between the two species (as may generally be expected for different species).

A. crawii is broadly distributed and associated with diverse plants. It is noteworthy that a mangrove-inhabiting population of *A. crawii* exists on the coast of the Malay Peninsula. There is no further evidence for the supposed close relation between *A. crawii* and *A. australis*. On the other hand, according to the literature, there are in Asia some species more or less similar to *A. crawii*. The details of them are not clear to me, but they together with *A. crawii* and *A. australis* may form a species group, which probably includes further species still unknown. *A. australis* should have arisen within the *crawii* group, if not from *A. crawii*.

3.3. *A. constricta* and Asian species

One of the remarkable characters of *A. constricta* is that it has elongate lateral setae on the prosoma and the prepygidial segments of the postsoma. The ventral lateral setae occurring on the metathorax and the first abdominal segment are especially elongate, attaining about 30–35μm, at times about 40μm, in length. This is not a usual character in *Aulacaspis*. Among the Asian species known to me, *A. mischocarpi* occurring in Luzón and *A. alangii* described from Borneo are similar to *A. constricta* in having elongate lateral setae. These three species are also similar in the rugged margins of the fourth and fifth abdominal segments and in the general pattern of the arrangement of dorsal macroducts.

A. constricta remarkably differs from the two Asian species in having rounded median trullae and low lateral trullae. It differs from *A. mischocarpi* in the prosoma broadest across the prosomatic tubercles and in the body deeply constricted in the metathorax. In the outline of the body it is very similar to *A. alangii*, but not exactly owing to the prosomatic tubercles less developed.

In general, the shape of the body and the state of the trullae, especially of the median trullae, are not necessarily decisive for or against a close relationship. *A. alangii* is unique in the disc pores associated with each posterior spiracle arranged in a single transverse row laterally to the spiracle. This peculiar character is useful in recognizing the species, but its significance in clarifying taxonomic relationships is unknown.

Three other species, *A. otophorae*, *A. shoreae*, and *A. fici*, are also described in this paper because of their possible relationships to *A. mischocarpi* and *A. alangii*. They differ from these two in the lateral setae not particularly elongated, in the body shapes, and in other characters. However, they are similar to *A. mischocarpi* and *A. alangii* in the margins of the fourth and fifth abdominal segments rugged with protruding pore prominences and lateral processes in addition to the median and lateral trullae, which are also similar among the species. The view may be adopted, though rather tentatively, that all these five species have some relationships among them and form a loose species group, the *mischocarpi* group. (The similarity in the features of the pygidial margin was adopted also in recognizing the *calcarata* species group, which was composed of species representing two different body shapes: Takagi, 1999). The five species undoubtedly represent only part of the *mischocarpi* group, which should have further species and possibly include those resembling *A. constricta* more closely. It should be added that the Singapore form of *A. crawii* is similar to the *mischocarpi* group in having rugged margins on the fourth and fifth abdominal segments. The similarity may be due to convergence; otherwise, it suggests some relationship between the *crawii* group and the *mischocarpi* group.

4. Appendix I: An Extraordinary Form

Aulacaspis litsearum, n.sp.
(Tables 1, 2; Figs 19–21)

This species belongs to the *rosae*-type, but it is unusual for a member of that type in the body appearing obovate in outline. It is out of the main theme of the present paper. It is described here and added to the comparisons made in Appendix II (Section 5).

4.1. Material examined

Grounds of the Forest Research Institute, Dehra Dun, Uttar Pradesh (now in Uttarakhand divided from U.P.) (on the foothills of the western Himalayas), India, alt. 670m, on *Litsea polyantha* and *Litsea glutinosa* (Lauraceae), 13.XI.1978 [78IND-155, -158]. Females and males occurring on the twigs of both host plants; adult female specimens associated with the leaf-blade and petiole are also available in the sample from *L. glutinosa* [78IND-158].

The two samples, collected at the same spot and at the same time, are united together in the description, which is based on 59 ramicolous adult females: 30 full-grown (one the holotype) and nine teneral specimens mounted from the lot [78IND-155] plus 20 full-grown ones from [78IND-158]. Three foliicolous adult females and two petiole-associated ones were also mounted [78IND-158], and are briefly noted below the description.

4.2. Recognition characters

Full-grown ramicolous adult female about 1400μm long at maximum, pygidium 290–335μm long, about 1.5 times as wide as long. Prosoma swollen, depressed semicircular in rough outline, about 1.5–1.7 times as wide as long; no obvious prosomatic tubercles. Postsoma robust; metathorax about 0.8–0.9 times as wide as prosoma, the free abdominal segments gradually narrowing caudad. Dorsal surface of prosoma tending to be sclerotized for a considerable part, with many small sclerotized patches; dorsal surface of prepygidial segments of postsoma with sclerotized patches submedially and submarginally.

Antennae each with basal tubercle well developed. Peribuccal scleroses present but not completely shaped, being represented by a pair of small sclerotized pieces detached from rostrum. Anterior spiracles each with a compact cluster of disc pores. Posterior spiracles each with a loose cluster of disc pores. Perivulvar disc pores: 20–47 in median, 30–62 in each anterolateral, and 21–45 in each posterolateral group. Submedian dorsal macroducts on abd III–VI, tending to be divided into segmental and infrasegmental series on III–V, but not always clearly; 5–15 on III, 7–12 on IV, 3–12 on V, and 1–6 on VI. Submarginal dorsal macroducts on abd III–V, 8–18 on III, 5–13 on IV, and 5–10 on V. Lateral macroducts and lateral gland spines abundant on abd III, less numerous on II. Marginal gland spines 5–9 on IV. Median trullae with basal halves sunken into pygidium; robust, roundish and minutely serrate marginally. Second trullae with lateral lobule much smaller than the mesal. Third trullae with lobules shortened. Both lateral trullae without linear basal scleroses. Pore prominences little protruding.

The specimens from the leaf-blade and petiole are not especially different from the ramicolous specimens in the numbers of the disc pores, macroducts, and gland spines and in the pygidial margin.

The second-instar male (Fig. 21) is characteristic in having abundant macroducts on both dorsal and ventral surfaces.

Remarks. The new species, *A. litsearum*, belongs to the *rosae* type in body shape, having an enlarged prosoma. Exceptionally to a species of that type, however, it has also a much broadened postsoma, which makes the whole body appearing obovate in outline. It is very similar to *Aulacaspis machili*, which occurs in Taiwan and Japan on lauraceous plants of *Persea* and, according to Chen (1983), in southern China on another lauraceous plant, *Phoebe nanmu*. *A. machili* is variable in body shape at full growth, but is not definitely referable to the *rosae* type (Takagi, 2012). Nevertheless, these two species do not appear to be much different in body shape. This is because in the full-

grown adult female of *A. litsearum* the prosoma does not appear to be so swollen as in many other species of the *rosae* type owing to the much broadened postsoma (Section 5). *A. litsearum* differs from *A. machili* also in having a pair of small but distinct sclerotized pieces laterally to the rostrum (which may correspond to the peribuccal scleroses) and small sclerotized patches on the dorsal surface of the prosoma and prepygidial postsoma. (In *A. machili*, full-grown individuals sometimes show a pair of slender inconspicuous scleroses laterally to the rostrum.) Further differences between these species are trifling or indistinct. The close similarity between the two species may largely be attributed to convergence, but it is also possible that they are really closely related to each other. In the latter case, these species afford another example in favour of the view (Takagi, 2012) that dividing the species of *Aulacaspis* into the typical forms (with the body of the *rosae* type) and the atypical ones is primarily a matter of convenience and does not necessarily have phylogenetic significance.

The second-instar male of *A. litsearum* is noteworthy in having the ducts mostly developed into macroducts on both surfaces. The second-instar male of *A. machili* has many of the ducts replaced with microducts as usual in the genus. This remarkable difference does not necessarily mean that these species are remotely related. In some known cases, the second-instar males are much different between species that are closely related to each other so far as based on the adult females.

5. Appendix II: Growth Patterns in the Adult Females
(Fig. 2b; Fig. 4 vs. Fig. 5; 11 vs. 12; 13 vs. 14; 17 vs. 18; 19 vs. 20; 23 vs. 24)

The adult females of the Coccoidea are interpreted to be neotenic in general body structure and, in principle, continue to grow during a long span after the last moult, more or less changing the body shape. In a sense, they are nymphs provided with organs, functions, and behaviours necessary for reproduction. The diaspidid adult females except those of the pupillarial forms greatly increase in the size of the prepygidial region. The different parts of this region grow in more or less different rates, and this contributes to the taxon-characteristic body shape at full growth (Takagi, 1990, Figs 1.1.2.1.1, 1.1.2.1.2). In the present study, teneral adult females have been available in *A. crawii*, *A. mischocarpi*, *A. alangii*, and *A. fici*. A preliminary study has been attempted to clarify the growth rates of some body parts in these species and in two other species added for comparison, *A. rosae* (the type species of the genus) and *A. litsearum* (Section 4), the last representing an extraordinary form of the *rosae* type.

A. mischocarpi, *A. alangii*, and *A. fici*, all referred to the *mischocarpi* group in this study, are very similar to each other in the teneral adult females, which are broadly obovate and more or less constricted in the metathorax. Their full-grown adult females are, in contrast, remarkably different from each other in body shape and especially in the outline of the prosoma. *A. crawii* and *A. rosae* do not appear to be closely related to each other, but are similar in the teneral adult females in having the body constricted not in the metathorax but in the first abdominal segment. The full-grown adult female of *A. litsearum* belongs to the *rosae* type in body shape, having a swollen prosoma, but it has, exceptionally to the *rosae* type, also a much broadened postsoma, the whole body being obovate in outline. The teneral adult female of this species has a broad body, with no constriction, and is not much different from the full-grown adult female in body outline except that the prosoma is not particularly swollen.

The body shape of the full-grown adult female should have some adaptive significance. It may be generalized from the case of *A. litsearum* that the genetic change caused by this adaptation retroactively influences the formation of the adult female body within the second-instar female and changes the body shape of the teneral adult female to a greater or lesser extent.

The growth of the body means, in principle, the change of the size, mass, shape, etc. of the body with time in the same individual. In the present study on the growth of the adult female, a full-grown adult female is paired with a teneral one belonging to the same sample (but, as a possibility, representing the succeeding generation), and six pairs from the six species (instead of the same growing individuals) are used for comparison. The prosoma, the metathorax, and the first to fourth abdominal segments are measured for width, and the ratios of the measurements in the full-grown adult female to those in the teneral one on the corresponding body parts are adopted as the 'growth rates' of those parts. The growth rates obtained in each pair are connected part by part graphically by the use of straight lines to show the 'growth pattern', and the growth patterns of the six species are put together in one chart for comparison (Fig. 2b).

The measurement has actually been made not on the specimens but on the figures mentioned just below the heading of this section. The figures were drawn with the use of a camera lucida, and should give considerably exact sizes of the body parts under measurement. In any sample, however, the full-grown adult females are variable in size and shape to some extent and the teneral ones, too, are not perfectly uniform. Different pairs from the same sample probably do not give the same ratios. In these respects, the growth patterns shown in Fig. 2b are no more than approximations to real ones, which should be based, in principle, on the same growing individuals and, nevertheless, should not necessarily be stable in the same species owing to individual variation and environmental conditions. After all, the simple method adopted in this study may give rough but practically useful ideas about the growth patterns in the adult females of the six species.

In all the growth patterns shown in Fig. 2b the growth rates rapidly decrease from the prosoma to the fourth abdominal segment except that the second abdominal segment has relatively high values in two species. The width of the fourth abdominal segment, measured between the anterolateral angles of the segment, is the width of the pygidium. This part of the body does not grow, but may vary a little in size, being stretched by the broadening third abdominal segment. The largest amount of growth is found in the prosoma, and the growth patterns in Fig. 2b may be divided into three groups according to the relative amount of the growth of the prosoma to that of the metathorax.

One of the groups, represented by *A. rosae* alone, has the lowest growth rate of the prosoma and the smallest difference between the rate of the prosoma and that of the metathorax; it has the rate of the second abdominal segment relatively high. In the full-grown body the prosoma is moderately swollen and the second abdominal segment is lobed laterally beyond the first and third segments.

A second group contains *A. litsearum* and *A. crawii*. These species have very high values of the prosoma growth rate, so that they should have the prosoma very prominent at full growth. However, they have also the growth rates of the postsomatic segments higher than in the other groups. As a result, they have the postsoma considerably robust and the prosoma appearing relatively not so prominent at full growth. This is especially true with *A. litsearum*, in which the postsomatic segments are much broadened already in

the teneral adult female; the full-grown body is, thus, obovate in outline, appearing to be much different from the mushroom-shaped bodies in many species of the *rosae* type.

A. alangii, *A. fici*, and *A. mischocarpi* belong to the last group. They have the growth rate of the prosoma very or considerably high (*A. alangii* having the highest value among the examined species). On the other hand, they show the difference between the rate of the prosoma and that of the metathorax largest among the examined species. These facts make the prosoma appearing enormously swollen at full growth. Their teneral adult females are more or less constricted across the metathorax, and their low metathorax growth rates keep the full-grown bodies markedly constricted.

The *Aulacaspis* species of the *rosae* type are characterized by the prosoma much swollen during the growth of the adult female. The observations above show that the body shape at full growth is determined not only by the enlargement of the prosoma but also by the incipient shape of the body and the growth of the postsoma. *A. fici*, *A. litsearum*, and *A. crawii* closely agree in having high prosoma growth rates. Their full-grown adult females, however, are very different in body shape, because they are different in the incipient shape of the body and in the growth rates of the postsomatic segments. These species also differ at full growth in the details of some prosomatic features. The longitudinal as well as the transverse expansion of the prosoma, the development of the prosomatic tubercles, the curving of the margin between the tubercles and of those behind the tubercles — all these features contribute to the outline of the prosoma characteristic of the species concerned at full growth, but they are beyond the scope of the present analysis.

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Tables and Figures

In each of Figs 4–24 except 8 and 21, parts drawn around the body are magnified at the same rate, with a scale bar for 10μm to be applied to all of them.

Table 1. Number of disc pores associated with each anterior or posterior spiracle; total number of perivulvar disc pores in all the five groups; total number of dorsal macroducts on both sides of the body.

	Anterior spiracular disc pores	Posterior spiracular disc pores	Total perivulvar disc pores	Total doral macroducts
A. crawii 1f	21—31.9—43 n=18	10—14.9—21 n=27	159—201.7—233 n=14	134—192.0—228 n=12
A. crawii 2f	26—30.0—37 n=12	11—14.5—20 n=22	166—199.5—224 n=11	156—197.9—237 n=11
A. crawii 3f	21—32.3—44 n=12	5—15.2—24 n=41	168—211.9—260 n=21	107—191.8—238 n=19
A. crawii 4f	18—25.6—32 n=11	8—13.3—17 n=29	174—204.1—228 n=15	188—219.9—235 n=10
A. crawii 5f	25—30.5—33 n=8	11—15.1—25 n=26	186—213.1—235 n=15	210—233.8—263 n=14
A. crawii 6f	ca. (16—○—25)	ca. (6—○—11)	163—197.0—245 n=6	237—283.5—309 n=6
A. crawii 7f	14—23.1—35 n=63	6—10.0—15 n=83	67—127.3—157 n=39	43—144.9—215 n=34
A. crawii 8f	19—21.7—31 n=27	9—16.3—22 n=34	168—222.4—280 n=16	187—250.0—330 n=12
A. crawii 8r	14—21.6—25 n=9	15—18.5—22 n=14	184—236.1—267 n=8	260—298.3—327 n=6
A. crawii 9f	23—29.8—41 n=32	11—17.1—29 n=70	158—217.4—247 n=35	222—280.6—336 n=31
A. crawii 10f	21—25.9—34 n=17	11—17.6—25 n=62	178—206.0—242 n=31	189—284.6—334 n=30
A. crawii 10r	23—28.6—42 n=8	9—15.9—25 n=62	124—182.6—233 n=32	126—217.4—292 n=31
A. crawii 11f	ca. (17—○—31)	6—13.5—20 n=18	162—184.7—215 n=9	242—262.6—308 n=5
A. crawii 12r	ca. (24—○—37)	9—15.0—19 n=28	174—198.3—257 n=16	180—223.4—250 n=14
A. mischocarpi f	7—10.7—15 n=84	3—5.0—8 n=84	66—86.0—104 n=42	38—75.0—105 n=41
A. alangii f	18—22.8—27 n=24	7—10.4—15 n=23	117—134.9—161 n=10	83—126.3—159 n=11
A. otophorae f	13—18.5—24 n=57	6—7.9—13 n=60	110—127.6—151 n=30	96—115.9—137 n=29
A. shoreae f	7—9.9—15 n=24	3—5.1—9 n=41	57—74.2—89 n=37	42—62.7—78 n=33
A. flci f	9—12.6—16 n=59	6—8.3—14 n=69	74—111.2—133 n=34	78—98.8—107 n=32
A. litsearum r	18—35.4—55 n=104	7—11.4—18 n=114	155—189.5—230 n=59	92—119.2—139 n=59

1—12 under *A. crawii*: sample number
f: foliicolous specimens; r: ramicolous specimens
21—31.9—43: lowest, mean, and highest values
n: sample size

Table 2. Number of lateral macroducts on each side of abd II and also of III; number of lateral gland spines on each side of abd II and also of III; number of marginal gland spines on each side of abd IV.

	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
A. crawii **1f**	**10–18.8–27 n=13**	**10–16.5–22 n=16**	**7–12.1–18 n=14**	**12–16.5–23 n=18**	**3–5.8–9 n=23**
A. crawii **2f**	**13–17.9–22 n=21**	**11–15.6–19 n=20**	**9–12.8–16 n=22**	**14–16.6–19 n=20**	**5–6.2–7 n=20**
A. crawii **3f**	**11–18.2–25 n=45**	**9–15.6–20 n=43**	**8–13.0–23 n=45**	**12–17.6–28 n=43**	**4–6.5–9 n=44**
A. crawii **4f**	**14–18.7–24 n=29**	**11–15.4–22 n=28**	**11–14.2–18 n=29**	**16–18.9–25 n=28**	**5–6.1–8 n=30**
A. crawii **5f**	**18–22.4–28 n=26**	**14–17.7–23 n=28**	**12–15.9–20 n=26**	**18–20.2–24 n=28**	**5–6.6–8 n=28**
A. crawii **6f**	**17–21.4–25 n=10**	**12–17.5–21 n=10**	**11–12.4–15 n=10**	**13–16.5–20 n=10**	**6–6.9–9 n=11**
A. crawii **7f**	**6–12.3–18 n=74**	**5–12.1–17 n=74**	**3–10.2–14 n=71**	**6–13.0–19 n=71**	**2–3.8–5 n=75**
A. crawii **8f**	**15–22.7–28 n=28**	**11–16.0–19 n=27**	**10–14.3–18 n=30**	**11–15.5–20 n=28**	**4–5.9–8 n=33**
A. crawii **8r**	**21–23.4–27 n=11**	**10–16.7–18 n=12**	**12–14.4–17 n=11**	**12–15.4–18 n=12**	**5–6.0–8 n=14**
A. crawii **9f**	**21–25.3–32 n=64**	**13–18.4–25 n=63**	**11–15.8–19 n=64**	**11–17.5–25 n=65**	**6–7.3–11 n=68**
A. crawii **10f**	**15–22.1–27 n=57**	**12–16.7–22 n=60**	**10–14.1–19 n=57**	**11–16.3–20 n=60**	**4–6.2–9 n=60**
A. crawii **10r**	**13–18.8–27 n=62**	**10–14.8–21 n=62**	**8–11.8–16 n=62**	**9–13.9–18 n=62**	**4–5.8–8 n=64**
A. crawii **11f**	**22–23.8–28 n=15**	**14–17.5–20 n=15**	**11–14.9–19 n=15**	**14–16.9–19 n=17**	**3–5.7–7 n=18**
A. crawii **12r**	**11–13.7–17 n=31**	**8–10.5–13 n=29**	**4–6.8–10 n=29**	**8–11.9–14 n=29**	**5–6.3–8 n=31**
A. mischocarpi **f**	**7–11.3–14 n=76**	**5–9.1–12 n=78**	**6–9.7–15 n=73**	**8–11.3–14 n=78**	**2 n=80**
A. alangii **f**	**10–16.1–23 n=13**	**11–13.8–19 n=13**	**9–10.8–15 n=12**	**10–14.4–19 n=13**	**3–3.7–5 n=17**
A. otophorae **f**	**8–10.4–13 n=57**	**7–9.2–11 n=59**	**8–10.8–15 n=54**	**9–12.6–18 n=60**	**3–3.1–5 n=60**
A. shoreae **f**	**6–10.7–13 n=65**	**4–7.0–10 n=67**	**4–9.1–11 n=63**	**5–9.2–13 n=64**	**2–2.9–5 n=64**
A. fici **f**	**8–10.3–15 n=67**	**6–7.5–9 n=67**	**9–11.3–13 n=66**	**9–11.9–14 n=66**	**3–4.7–6 n=68**
A. litsearum **r**	**3–4.8–7 n=118**	**2–4.2–6 n=117**	**8–12.0–15 n=117**	**8–12.7–18 n=116**	**4–6.4–9 n=118**

1–12 under *A. crawii*: sample number
f: foliicolous specimens; r: ramicolous specimens
10–18.8–27: lowest, mean, and highest values
n: sample size

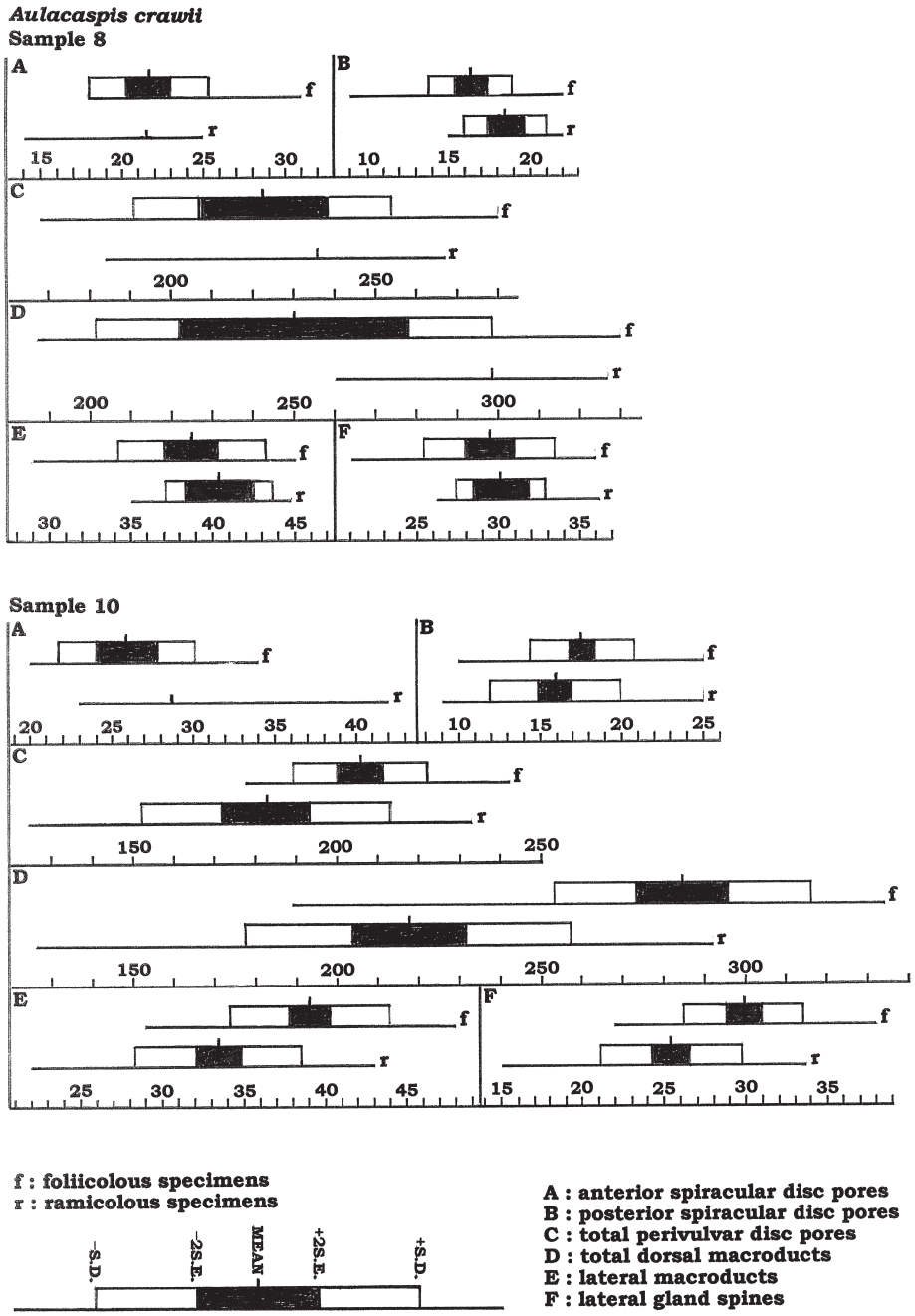

Fig. 1. *Aulacaspis crawii*, adult females. Comparisons between the foliicolous and ramicolous subsamples of Sample 8 (Terai, on *Murraya*) and also of Sample 10 (Terai, on *Trichilia*) in the number of the disc pores associated with each spiracle, in the numbers of the lateral macroducts and the gland spines on each side of the body (those on abd II and III being added together), and in the total numbers of the perivulvar disc pores and the dorsal macroducts.

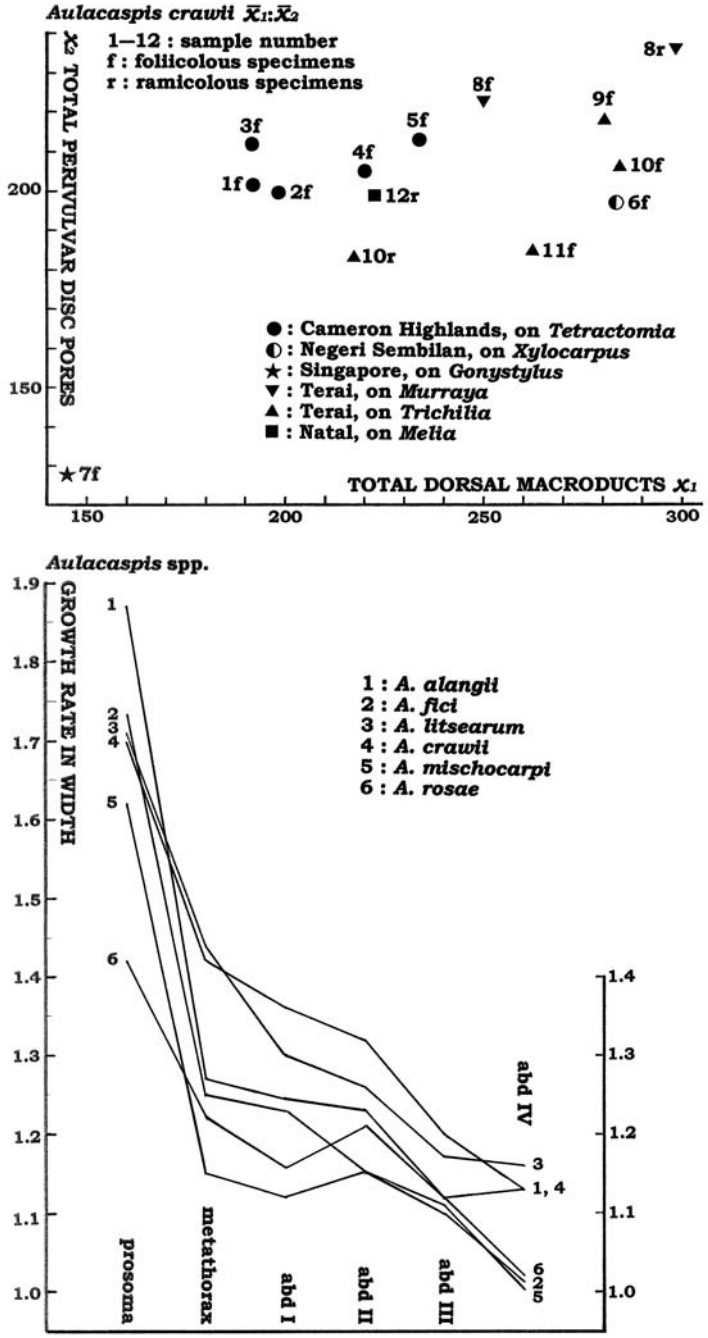

Fig. 2a (upper). *Aulacaspis crawii*, adult females. Mean total number of perivulvar disc pores against mean total number of dorsal macroducts.

Fig. 2b (lower). *Aulacaspis crawii*, *A. mischocarpi*, *A. alangii*, *A. fici*, *A. litsearum*, and *A. rosae*, adult females. Growth rates of prosoma, metathorax, and abd I–IV.

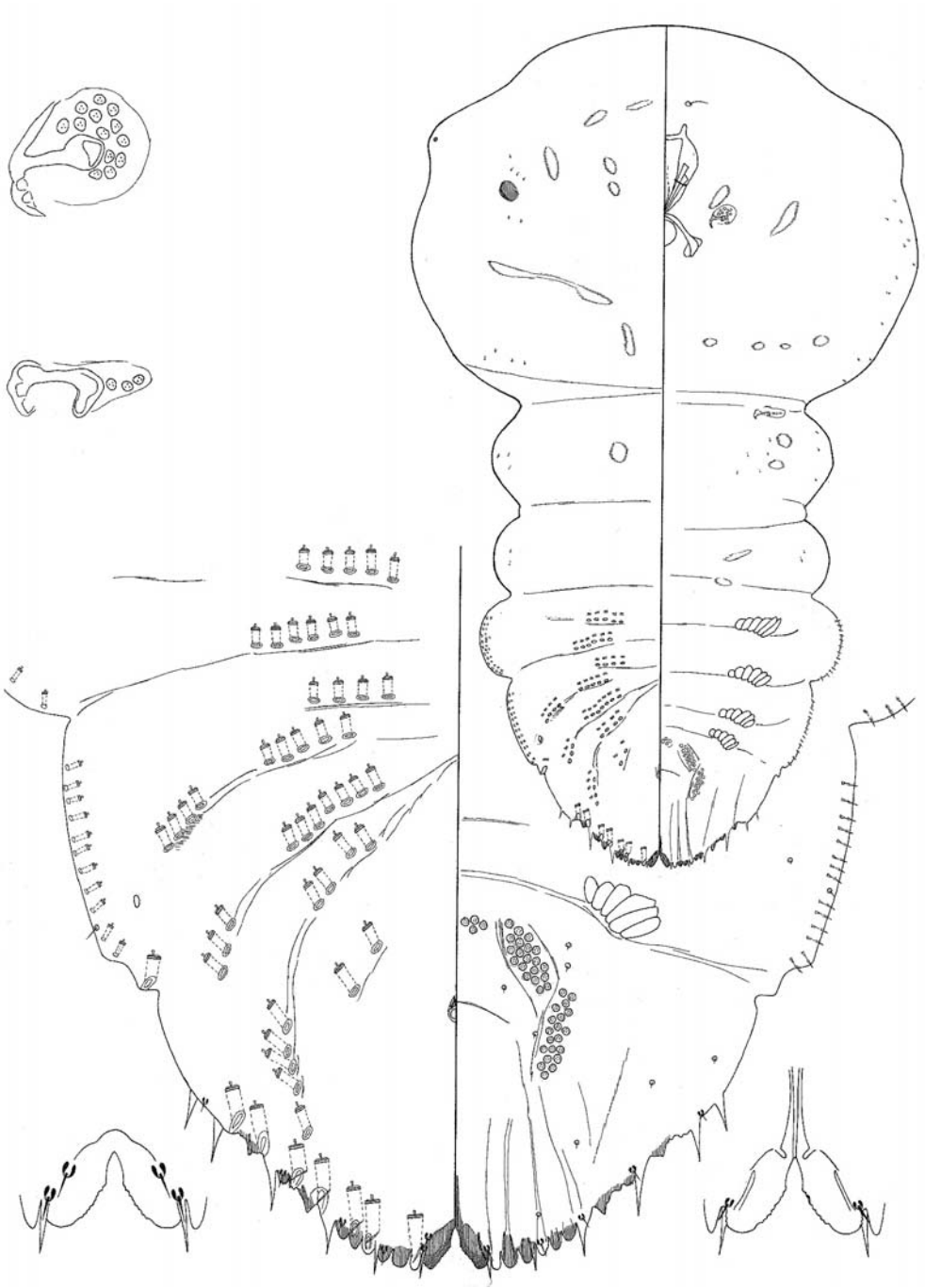

Fig. 3. '*Aulacaspis thoracica*, Philippines, Laguna, Los Baños, *Morinda bracteata*, C. F. Baker, xii 1915 (USNM)' (D. J. Williams).

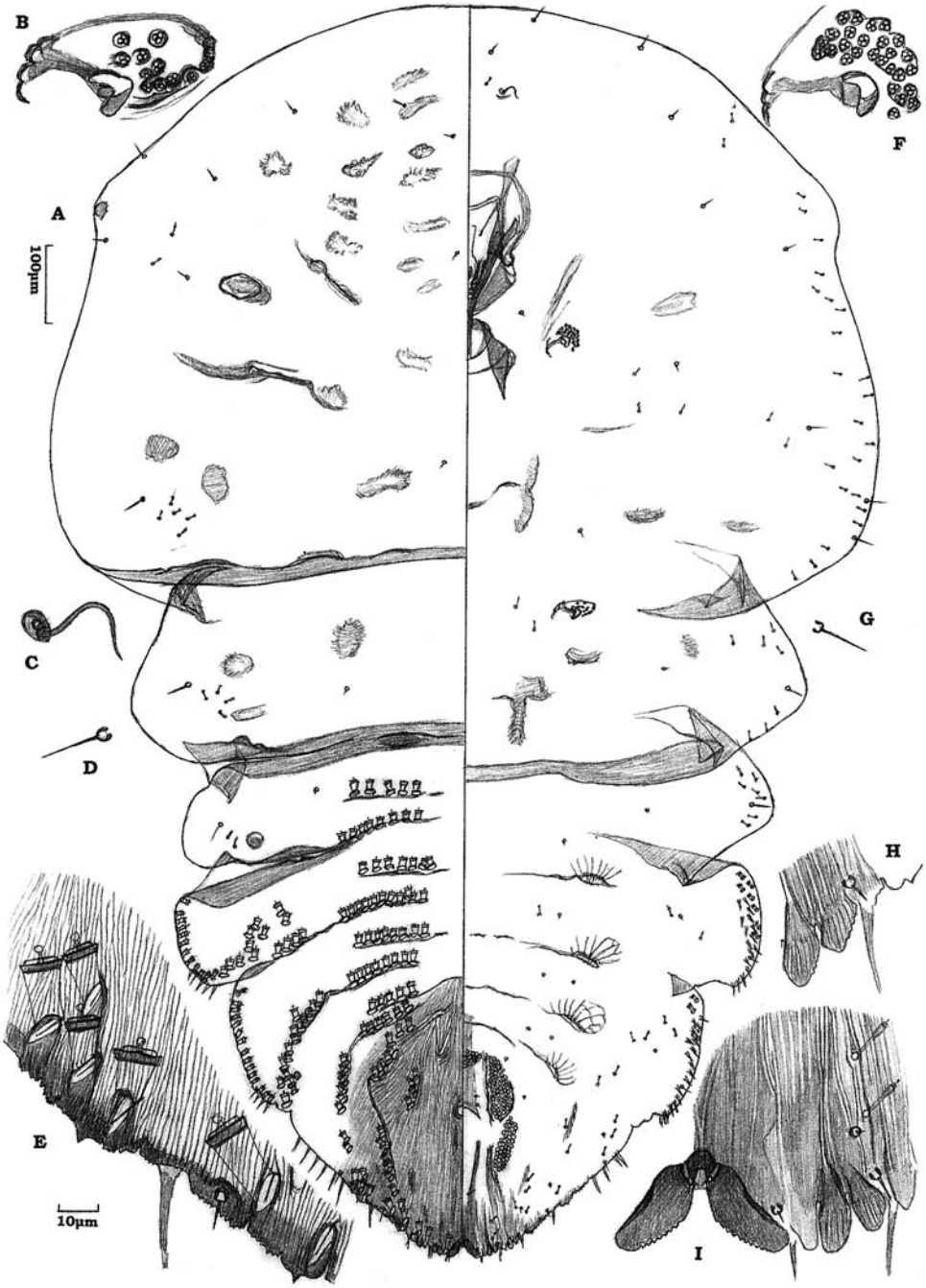

Fig. 4. *Aulacaspis crawii*, adult female, full-grown. Cameron Highlands, on *Tetractomia*, leaf, Sample 2 [86ML-226]. B, posterior spiracle; C, antenna; D, lateral seta on dorsal surface of metathorax; E, pygidial margin, abd IV and V, in dorsal view; F, anterior spiracle; G, lateral seta on ventral surface of metathorax; H, third trulla; I, median and second trullae.

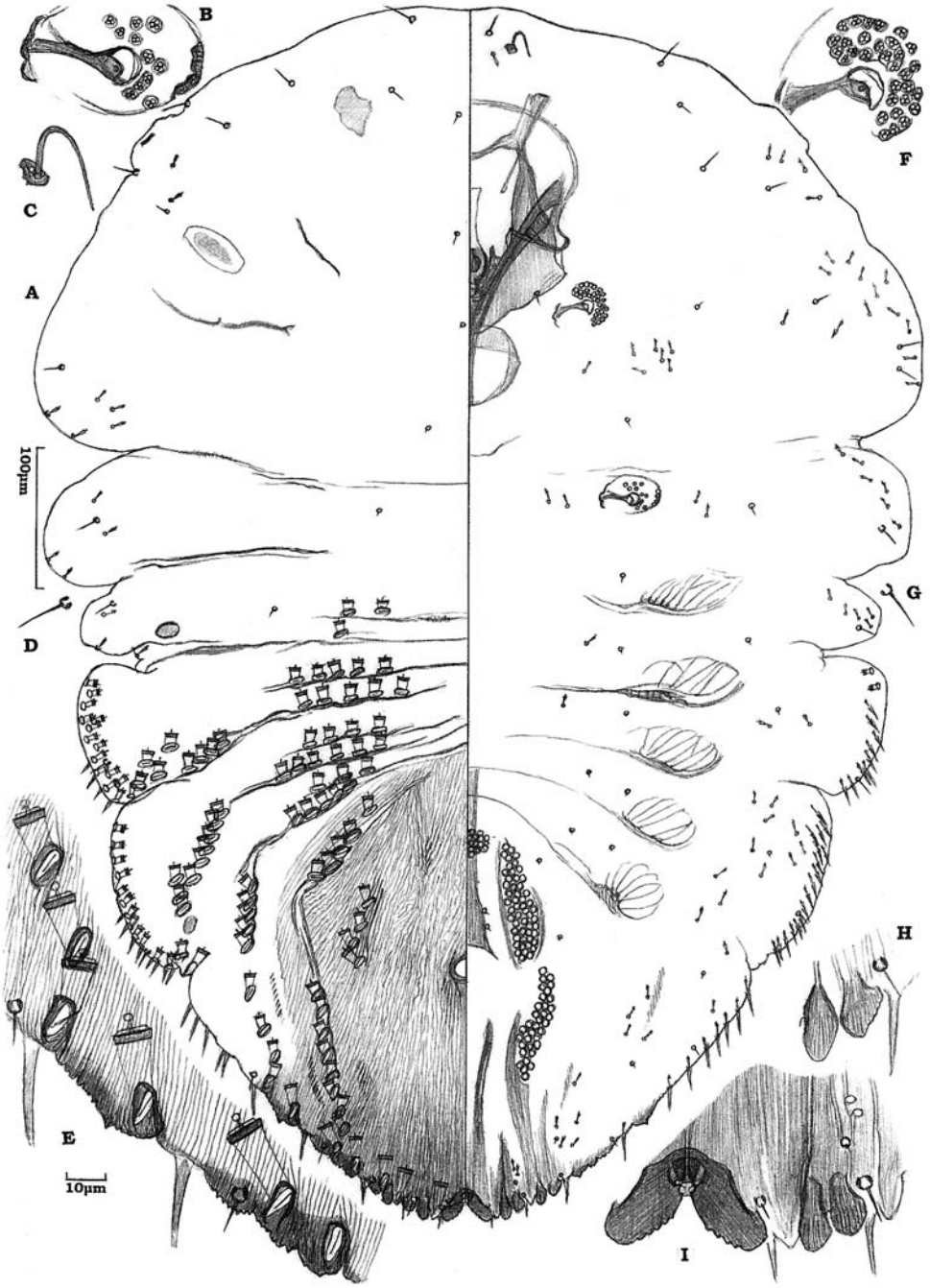

Fig. 5. *Aulacaspis crawii*, adult female, teneral. Cameron Highlands, on *Tetractomia*, leaf, Sample 2 [86ML-226]. B, posterior spiracle; C, antenna; D, lateral seta on dorsal surface of metathorax; E, pygidial margin, abd IV and V, in dorsal view; F, anterior spiracle; G, lateral seta on ventral surface of metathorax; H, third trulla; I, median and second trullae.

Fig. 6. *Aulacaspis crawii*, adult female, teneral. Singapore, on *Gonystylus*, leaf, Sample 7 [92SP-48]. B, microducts on dorsal surface of prosoma; C, lateral seta on dorsal surface of metathorax; D, pygidial margin, abd IV and V, in dorsal view; E, microducts on ventral surface of prosoma; F, lateral seta on ventral surface of metathorax; G, third trulla; H, median and second trullae.

Fig. 7. *Aulacaspis crawii*, adult females, full-grown. Terai, on *Trichilia*, leaf (A–C, E–K) and twig (D), Sample 10 [83NPL-437]. B, posterior spiracle; C, lateral seta on dorsal surface of metathorax; D, median trullae (in ramicolous specimen); E, pygidial margin, abd IV and V, in dorsal view; F, anterior spiracle; G, antenna; H, peribuccal sclerosis; I, lateral seta on ventral surface of metathorax; J, third trulla; K, median and second trullae.

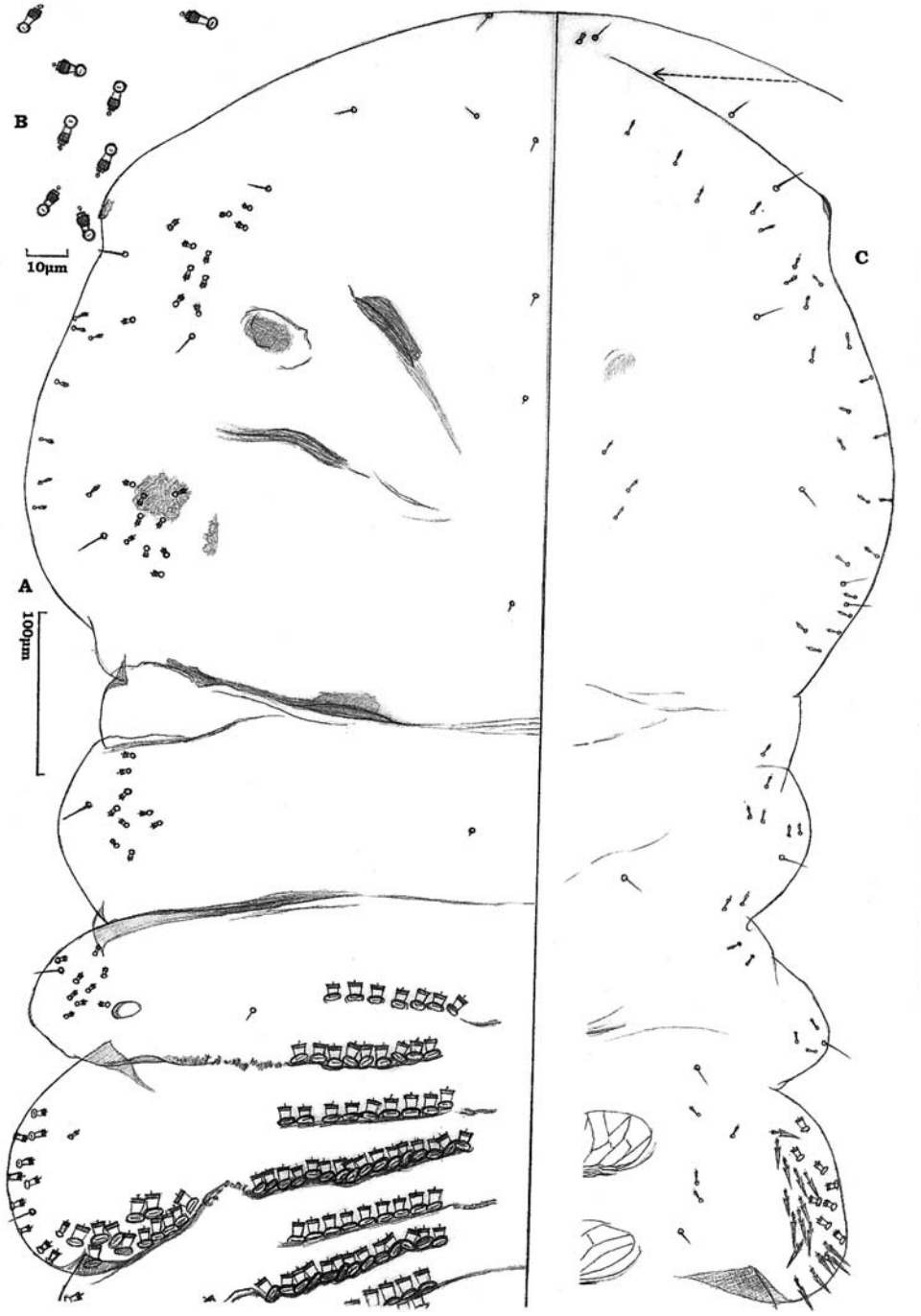

Fig. 8. *Aulacaspis crawii*, adult female, juvenile. Terai, on *Trichilia*, twig, Sample 10 [83NPL-437]. A, prosoma and anterior postsoma, dorsal half; B, enlarged microducts on dorsal surface of prosoma; C, prosoma and anterior postsoma, ventral surface, marginal to submarginal area.

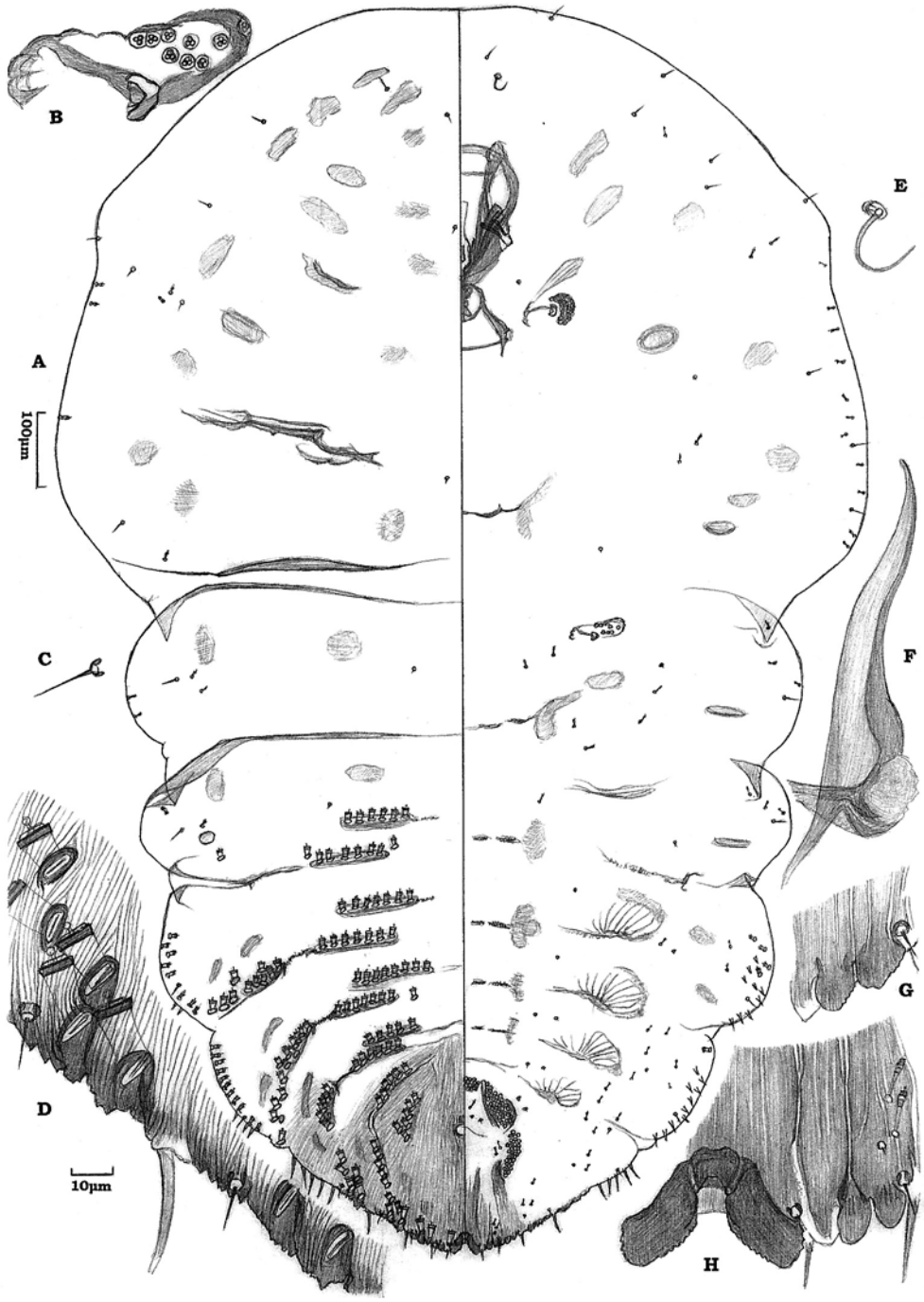

Fig. 9. *Aulacaspis crawii*, adult female, full-grown. Natal, on *Melia*, twig, Sample 12. B, posterior spiracle; C, lateral seta on dorsal surface of metathorax; D, pygidial margin, abd IV and V, in dorsal view; E, antenna; F, peribuccal sclerosis; G, third trulla; H, median and second trullae.

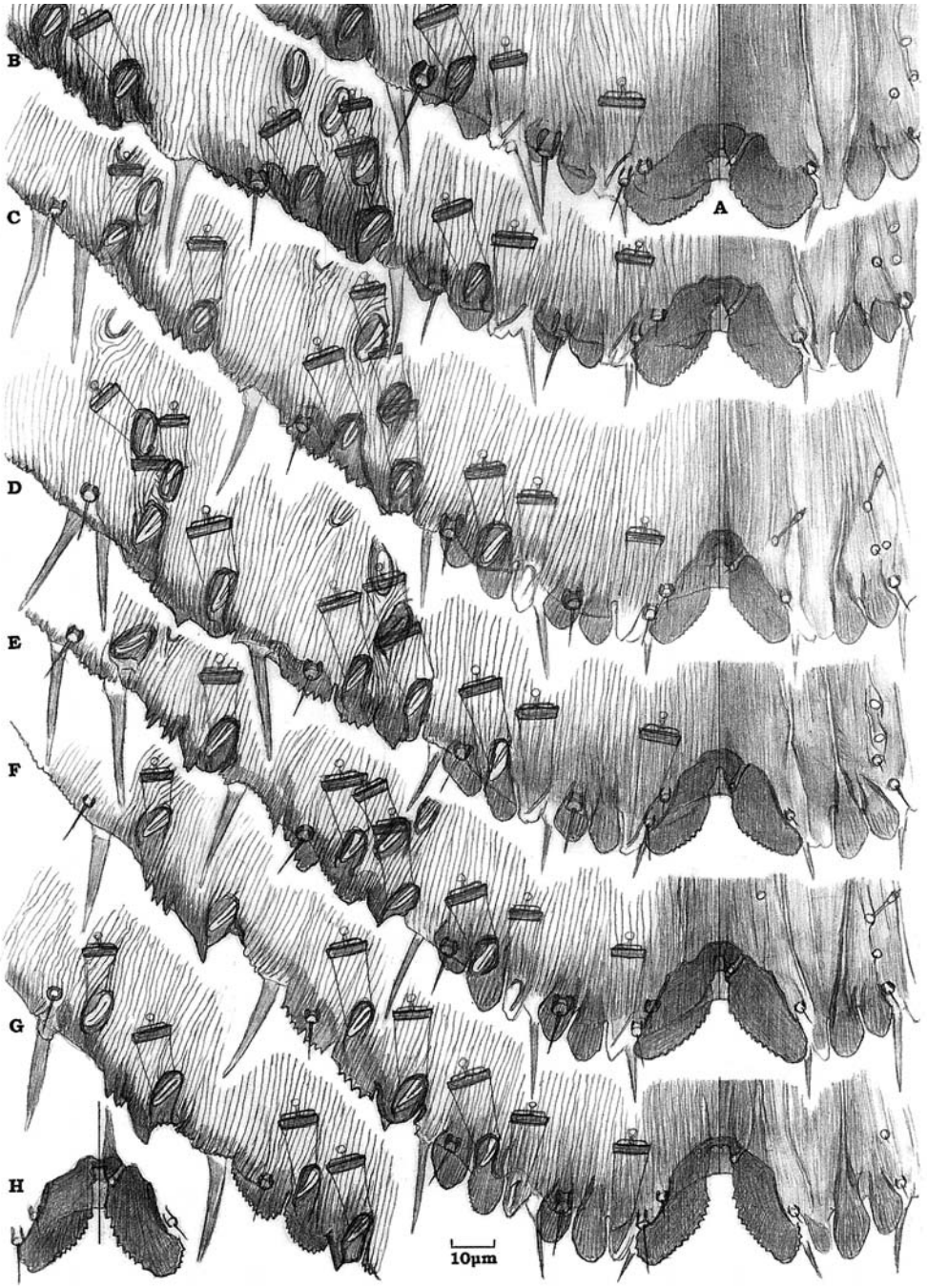

Fig. 10. *Aulacaspis crawii*, adult females, full-grown. Pygidial margins. A and B, Natal, on *Melia*, twig, Sample 12; C, western coast of Malaya, on *Xylocarpus*, leaf, Sample 6 [86ML-430]; D, Cameron Highlands, on *Tetractomia*, leaf, Sample 4 [86ML-289]; E, Terai, on *Murraya*, twig, Sample 8 [83NPL-256]; F–H, Singapore, on *Gonystylus*, leaf, Sample 7 [92SP-48].

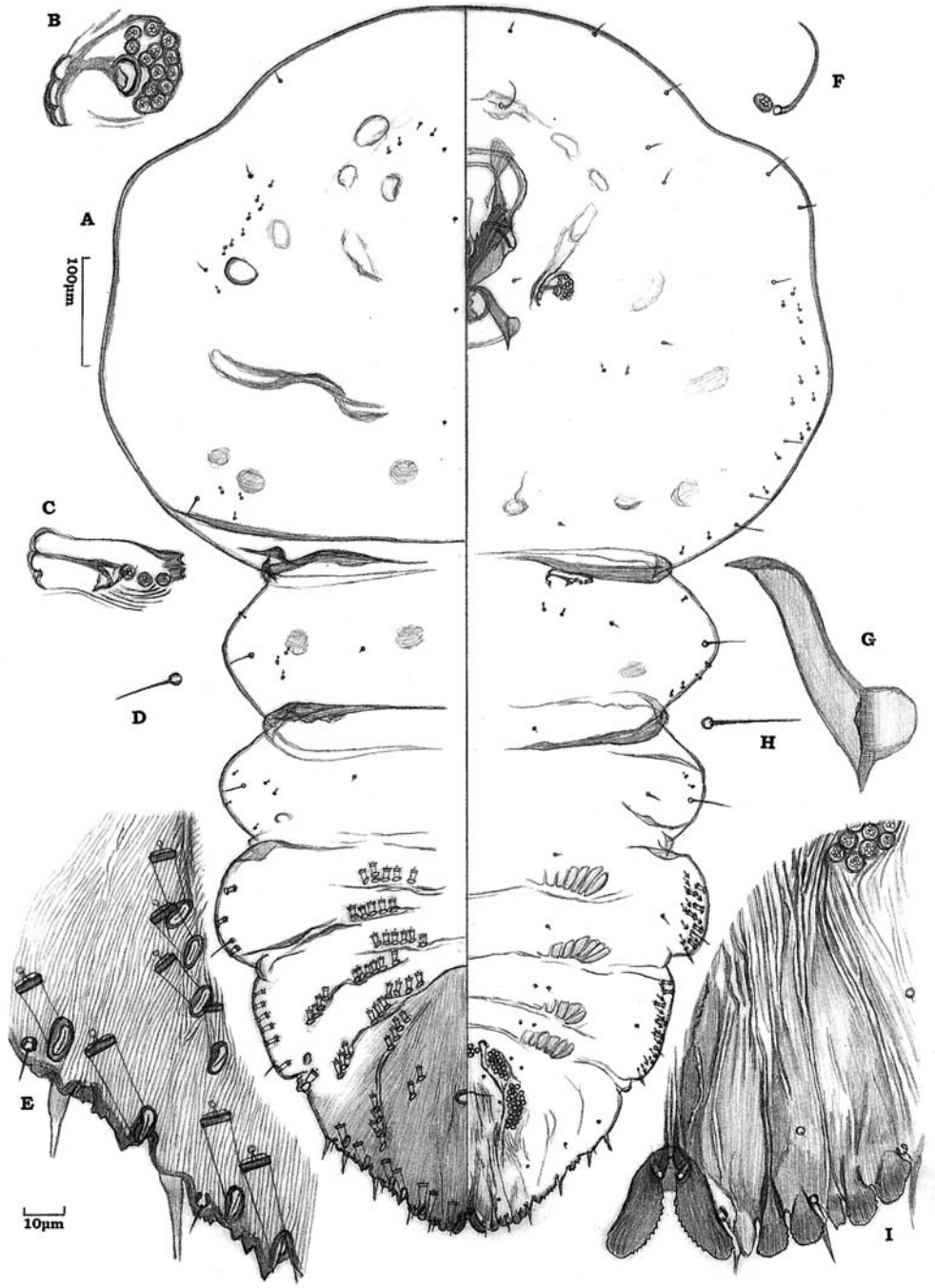

Fig. 11. *Aulacaspis mischocarpi*, adult female, full-grown. Los Baños, on *Pedicellia*, leaf [92PL-62]. B, anterior spiracle; C, posterior spiracle; D, lateral seta on dorsal surface of metathorax; E, pygidial margin, abd IV and V, in dorsal view; F, antenna; G, peribuccal sclerosis; H, lateral seta on ventral surface of metathorax; I, trullae.

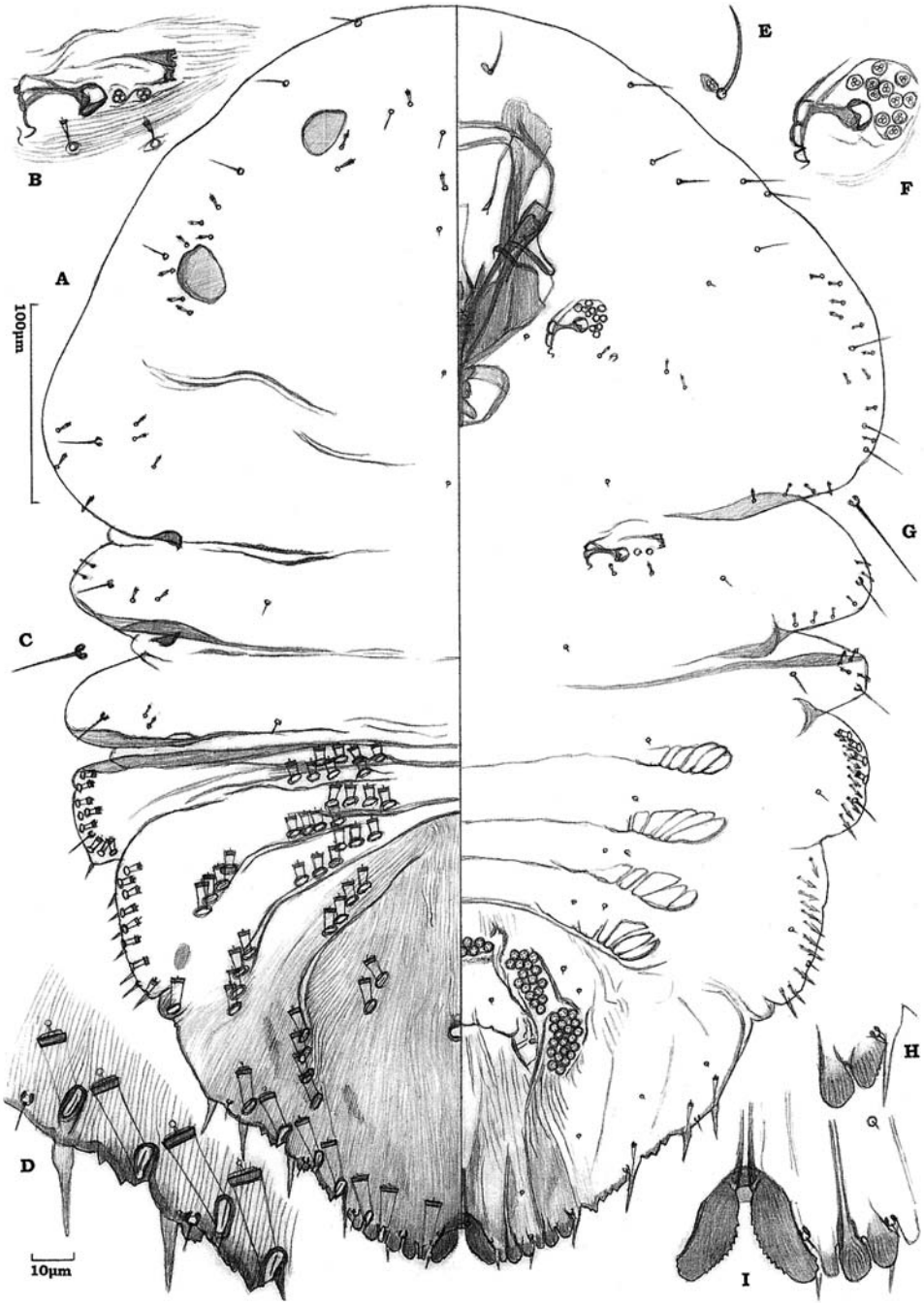

Fig. 12. *Aulacaspis mischocarpi*, adult female, teneral. Los Baños, on *Pedicellia*, leaf [92PL-62]. B, posterior spiracle; C, lateral seta on dorsal surface of metathorax; D, pygidial margin, abd IV and V, in dorsal view; E, antenna; F, anterior spiracle; G, lateral seta on ventral surface of metathorax; H, third trulla; I, median and second trullae.

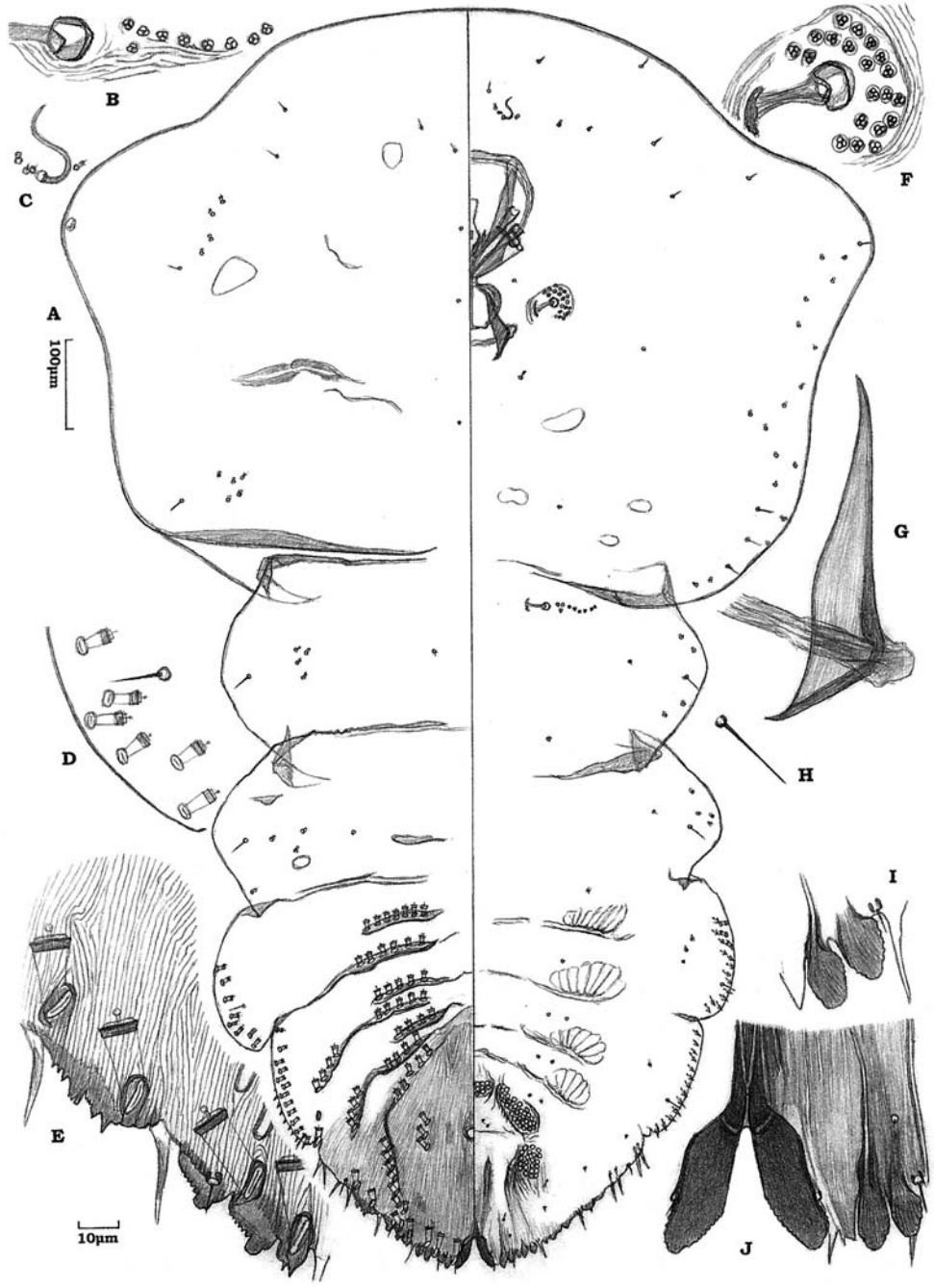

Fig. 13. *Aulacaspis alangii*, adult female, full-grown. Sepilok, on *Alangium*, leaf [88ML-350]. B, posterior spiracle; C, antenna; D, part of lateral lobe of abd II, dorsal surface; E, pygidial margin, abd IV and V, in dorsal view; F, anterior spiralce; G, peribuccal sclerosis; H, lateral seta on ventral surface of metathorax; I, third trulla; J, median and second strullae.

Fig. 14. *Aulacaspis alangii*, adult female, teneral. Sepilok, on *Alangium*, leaf [88ML-350]. B, posterior spiracle; C, antenna: D, lateral seta on dorsal surface of metathorax; E, pygidial margin, abd IV and V, in dorsal view; E, anterior spiracle; G, lateral seta on ventral surface of metathorax; H, trullae.

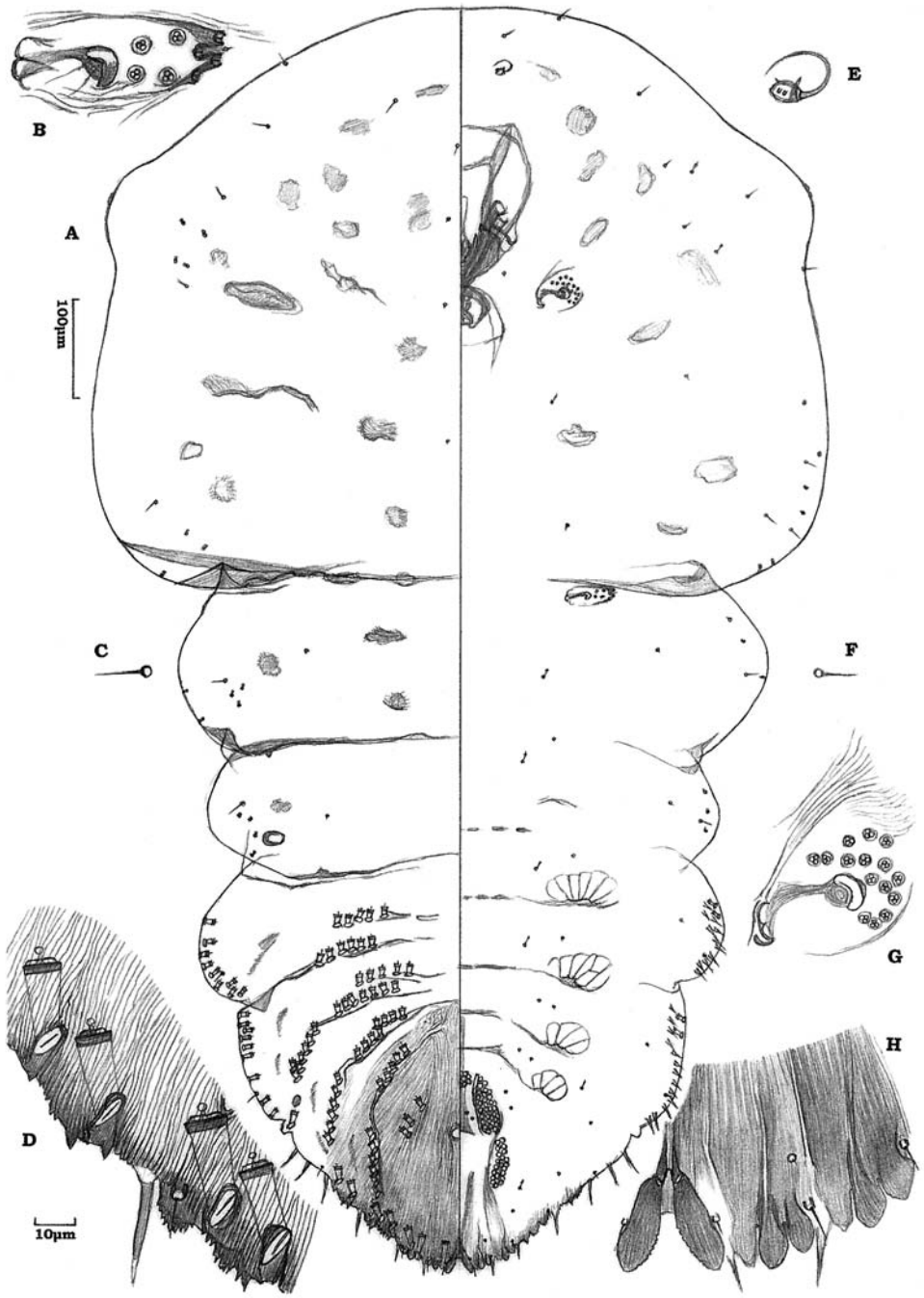

Fig. 15. *Aulacaspis otophorae*, adult female, full-grown. Palawan, on *Otophora*, leaf [93PL-86]. B, posterior spiracle; C, lateral seta on dorsal surface of metathorax; D, pygidial margin, abd IV and V, in dorsal view; E, antenna; F, lateral seta on ventral surface of metathorax; G, anterior spiracle; H, trullae.

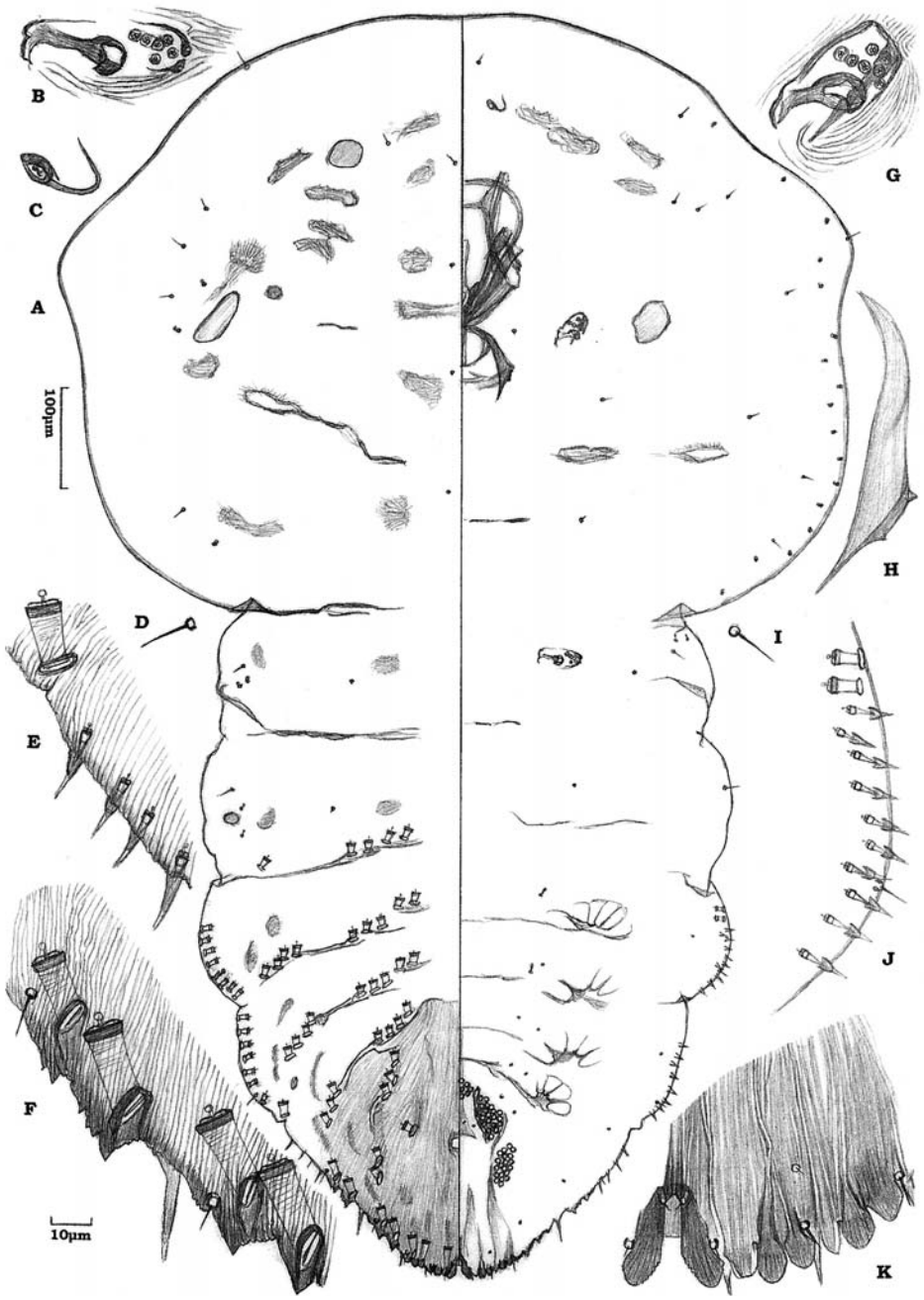

Fig. 16. *Aulacaspis shoreae*, adult female, full-grown. Pulau Pinang, on *Shorea*, leaf [91ML-489]. B, posterior spiracle; C, antenna; D, lateral seta on dorsal surface of metathorax; E, marginal gland spines on abd IV and marginal macroduct on III; F, pygidial margin, abd IV and V, in dorsal view; G, anterior spiracle; H, peribuccal sclerosis; I, lateral seta on ventral surface of metathorax; J, lateral margin of abd II in ventral view; K, trullae.

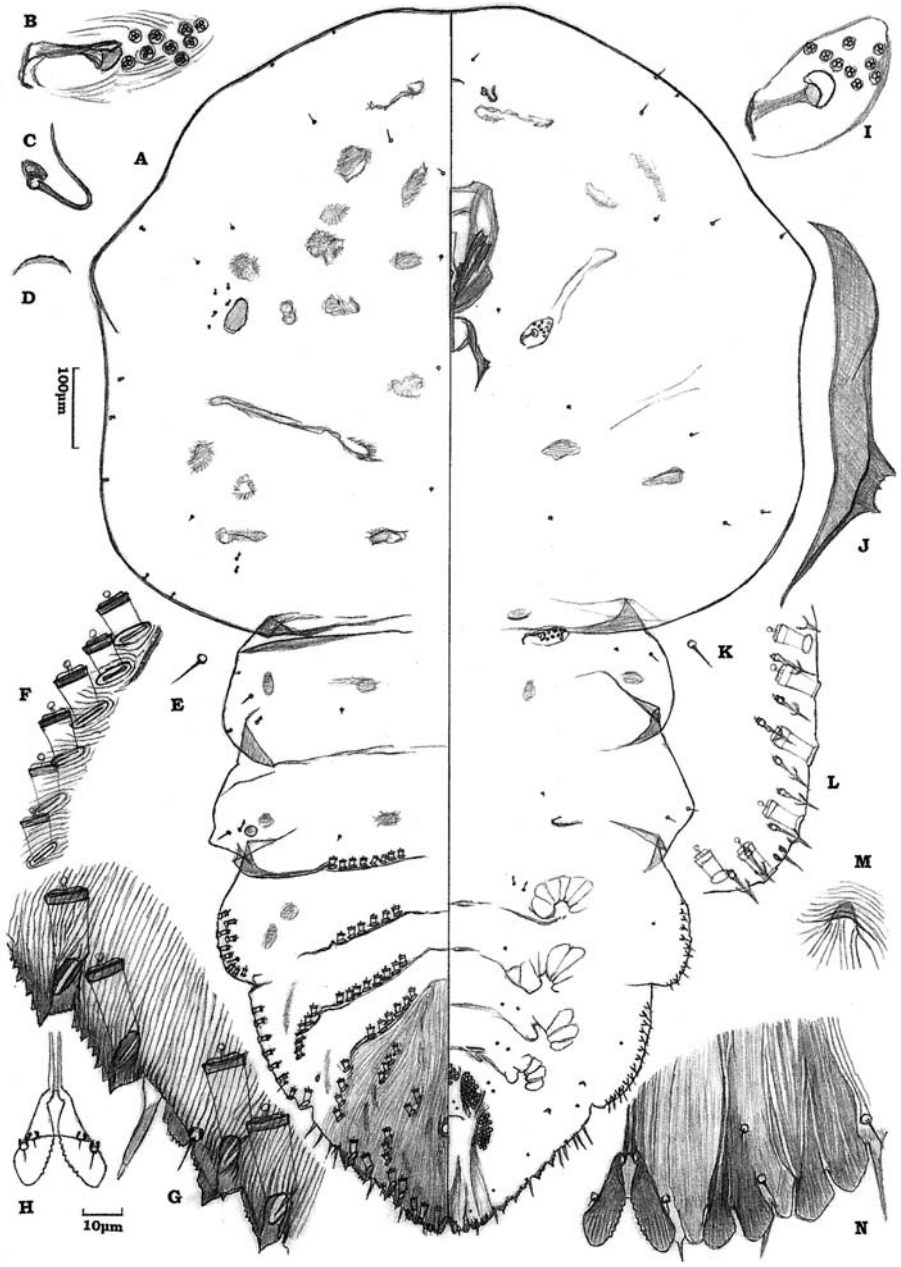

Fig. 17. *Aulacaspis fici*, adult female, full-grown. Kuala Lumpur, on *Ficus*, leaf [86ML-33]. B, posterior spiracle; C, antenna; D, interantennal prominence; E, lateral seta on dorsal surface of metathorax; F, submarginal macroducts on abd III; G, pygidial margin, abd IV and V, in dorsal view; H, median trullae in dorsal view, showing marginal setae of abd VIII and IX; I, anterior spiracle; J, peribuccal sclerosis; K, lateral seta on ventral surface of metathorax; L, lateral margin of abd II in ventral view; M, derm pocket on submarginal ventral surface of abd IV; N, trullae.

Fig. 18. *Aulacaspis fici*, adult female, teneral. Kuala Lumpur, on *Ficus*, leaf [86ML-33]. B, posterior spiracle; C, antenna; D, interantennal prominence; E, lateral seta on dorsal surface of metathorax; F, pygidial margin, abd IV and V, in dorsal view; G, median trullae in dorsal view, showing marginal setae of abd VIII and IX; H, anterior spiracle; I, lateral seta on ventral surface of metathorax; J, derm pocket on submarginal ventral surface of abd IV; K, trullae.

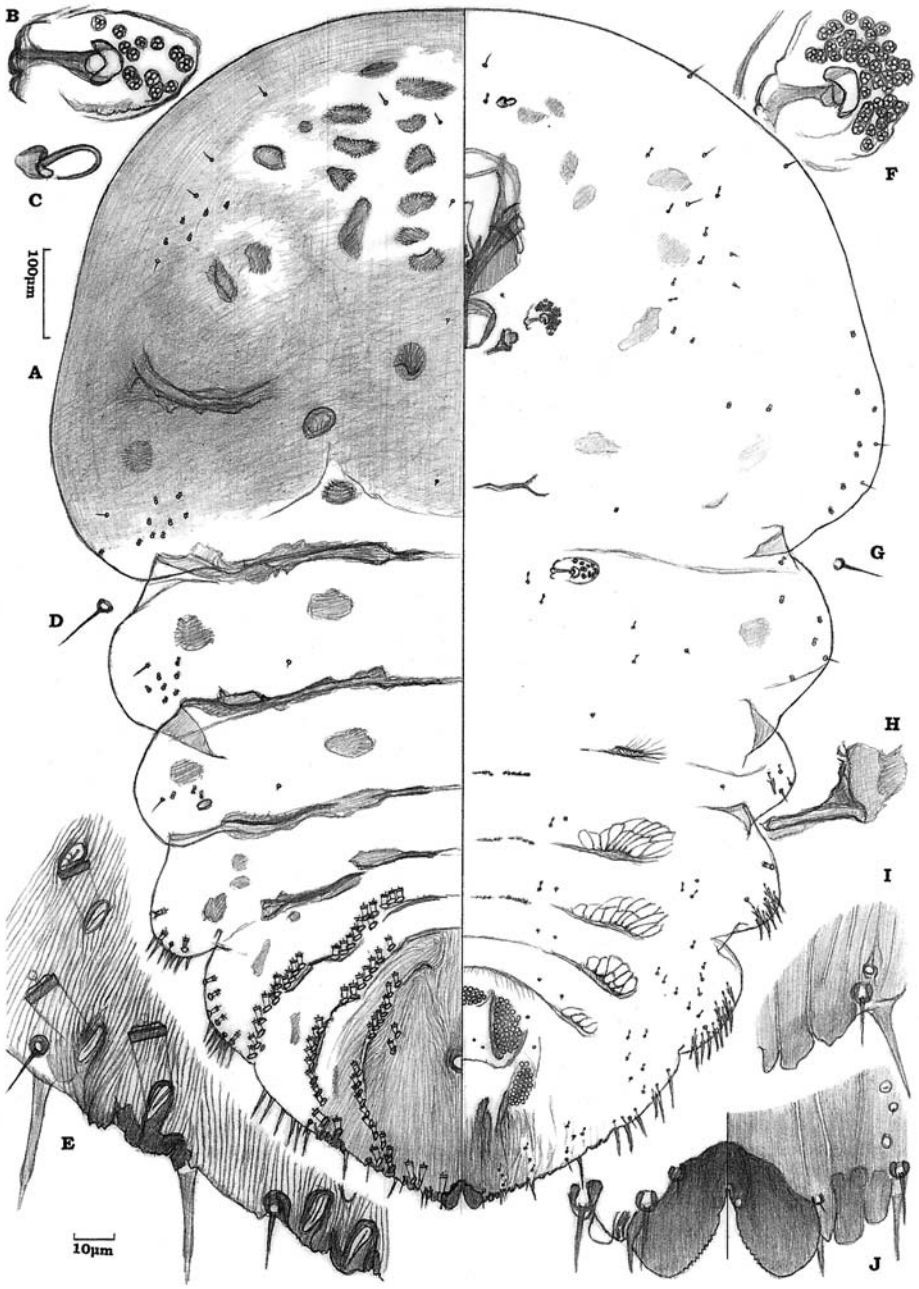

Fig. 19. *Aulacaspis litsearum*, adult female, full-grown. Dehra Dun, on *Litsea*, twig [78IND-155]. B, posterior spiracle; C, antenna; D, lateral seta on dorsal surface of metathorax; E, pygidial margin, abd IV and V, in dorsal view; F, anterior spiracle; G, lateral seta on ventral surface of metathorax; H, peribuccal sclerosis; I, third trulla; J, median and second trullae. (The pattern of dermal sclerotization on the ventral surface of the prosoma, if any, is unobservable owing to the sclerotized dorsal surface.)

Fig. 20. *Aulacaspis litsearum*, adult female, teneral. Dehra Dun, on *Litsea*, twig [78IND-155]. B, posterior spiracle; C, antenna; D, lateral seta on dorsal surface of metathorax; E, pygidial margin, abd IV and V, in dorsal view; F, anterior spiracle; G, lateral seta on ventral surface of metathorax; H, trullae.

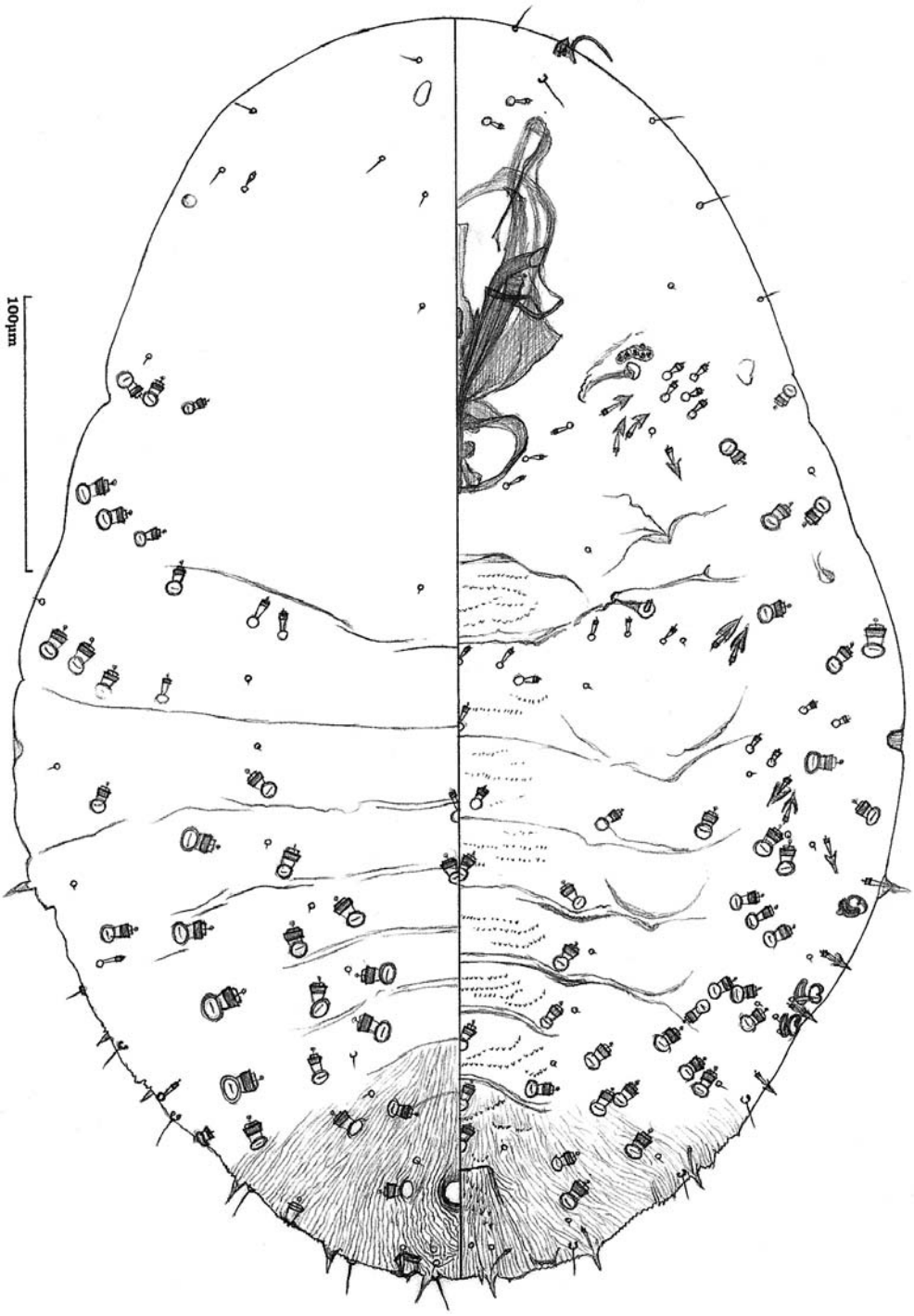

Fig. 21. *Aulacaspis litsearum*, second-instar male. Dehra Dun, on *Litsea*, twig [78IND-155].

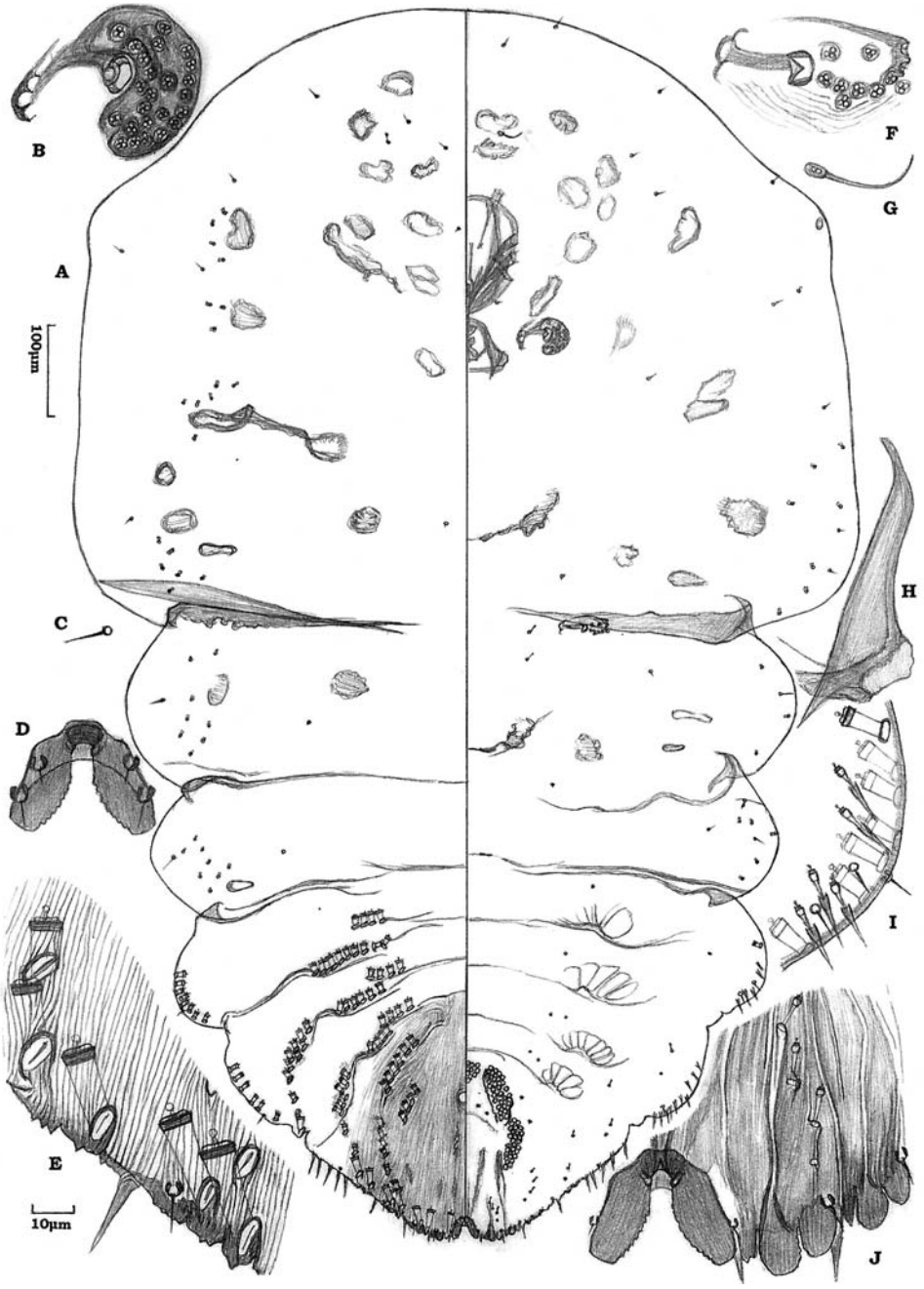

Fig. 22. *Aulacaspis rosarum*, adult female, full-grown. Figured from a specimen mounted from the type material: near 'Chengtu' [Chengdu], China, on *Rosa* sp., twig, 5.XII.1954. B, anterior spiracle; C, lateral seta on dorsal surface of metathorax; D, median trullae (another specimen, in dorsal view); E, pygidial margin, abd IV and V, in dorsal view; F, posterior spiracle; G, antenna; H, peribuccal sclerosis; I, lateral margin of abd II in ventral view; J, trullae.

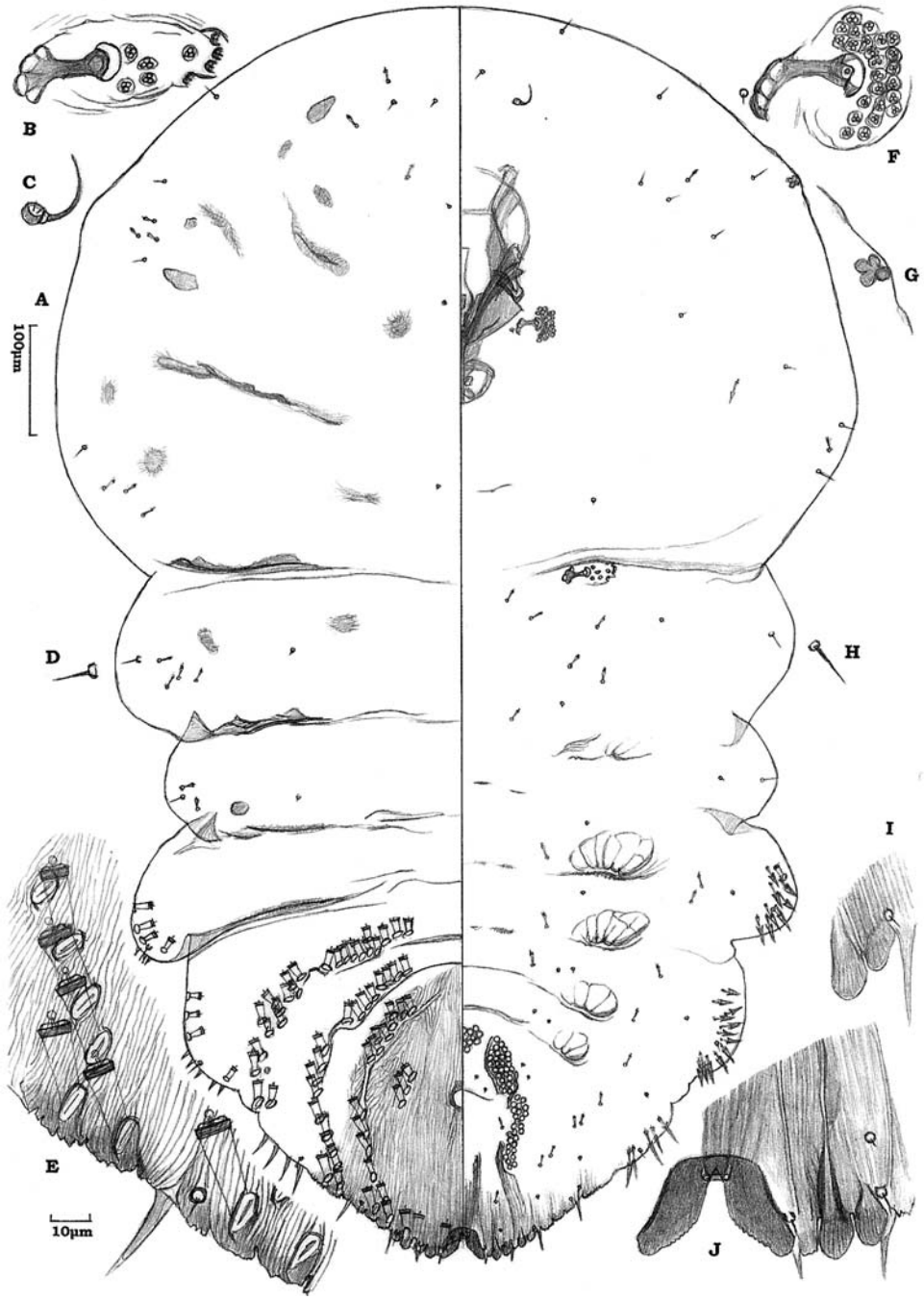

Fig. 23. *Aulacaspis rosae*, adult female, full-grown. Sapporo, Japan, on garden rose, stem, 4.XI.1962. B, posterior spiracle; C, antenna; D, lateral seta on dorsal surface of metathorax; E, pygidial margin, abd IV and V, in dorsal view; F, anterior spiracle; G, eye spot; H, lateral seta on ventral surface of metathorax; I, third trulla; J, median and second trullae.

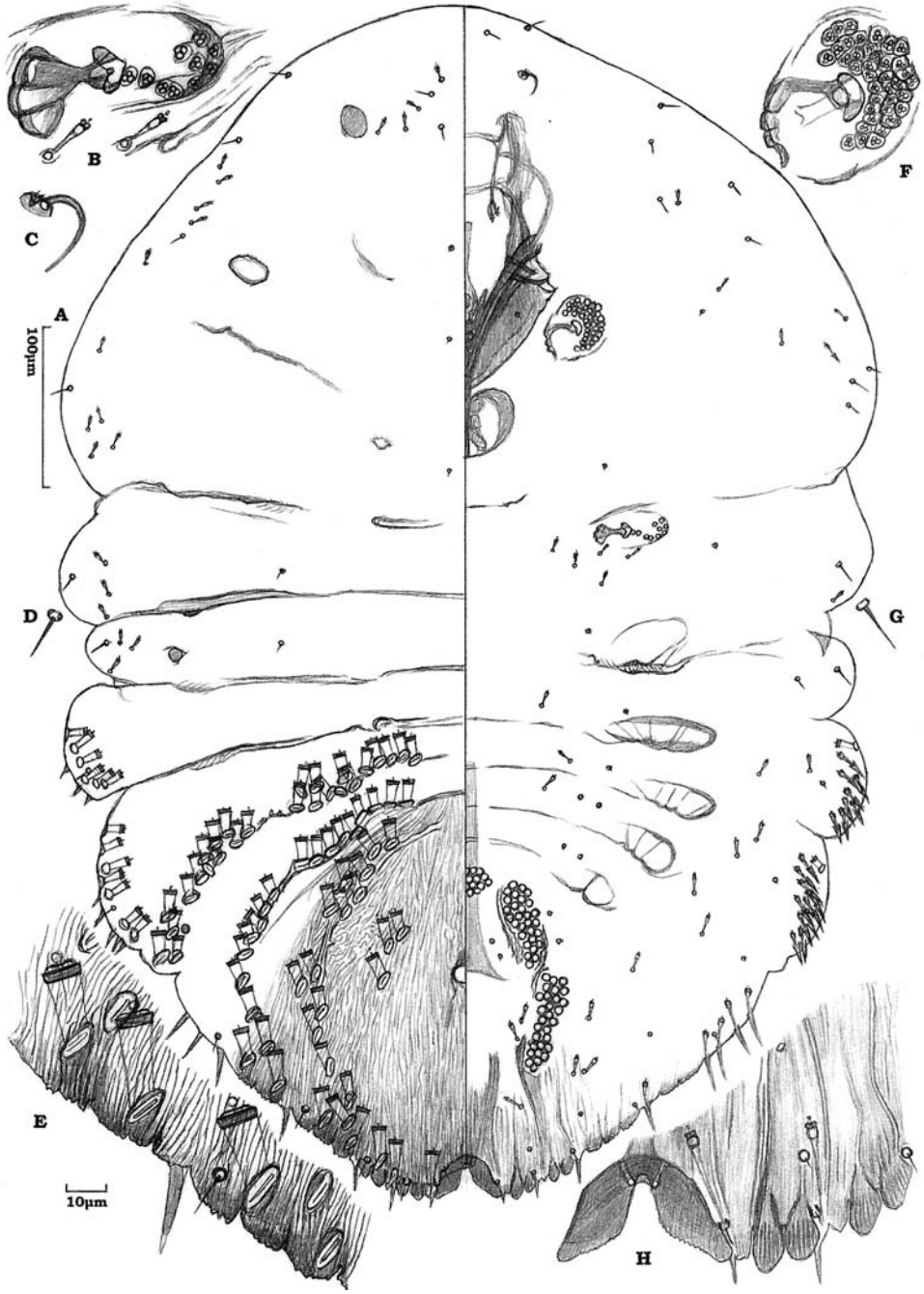

Fig. 24. *Aulacaspis rosae*, adult female, teneral. Sapporo, Japan, on garden rose, stem, 4.XI.1962. B, posterior spiracle; C, antenna; D, lateral seta on dorsal surface of metathorax; E, pygidial margin, abd IV and V, in dorsal view; F, anterior spiracle; G, lateral seta on ventral surface of metathorax; H, trullae.

Correction

Takagi, S., 2010. The *tubercularis* species group of *Aulacaspis* (Sternorrhyncha: Coccoidea: Diaspididae). Insecta Matsumurana New Series 66: 57–114.

Page 64, line 16 from bottom. Correct ‘Himachal Pradesh’ to ‘Uttar Pradesh’.