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**ONE NEW SUBFAMILY AND TWO NEW TRIBES OF THE DIASPIDIDAE
(HOMOPTERA: COCCOIDEA)**

By SADAO TAKAGI

Abstract

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Ulucoccinae, subfam. n., and Thysanaspini and Smilacicolini, tribb. n., are erected on the basis of *Ulucoccus*, *Thysanaspis*, and *Smilacicola*, respectively. The subfamily Ulucoccinae is one of very primitive forms of the Diaspididae, lacking distinct pygidial appendages, and may approach a remote ancestor of the Diaspidini, Diaspidinae, being similar to the second instar males of some species of the tribe, especially of the Chionaspina. The tribe Thysanaspini represents the most primitive form of the Aspidiotinae in the pygidial appendages, which are composed of well-developed pectinae alone in the nymphal stages. *Thysanaspis* is pupillarial, so that the nymphal stages of the genus give some idea of the putative ancestor of the extant Aspidiotinae. The Smilacicolini inhabit a constricted space on the plant body as the Odonaspini do, and may have derived from a group of forms related to, but more primitive than, the extant Parlatoriini, to which the Odonaspini are also related. Five other diaspidids are described or figured for comparison with the Thysanaspini and the Smilacicolini. Two of them, occurring in the Philippines, are new species belonging to a new genus: *Ligaspis maculata* and *L. pala*. Another species, *Mongrovaspis quadrispinosa*, is newly recorded from eastern Asia and is redescribed. The new higher taxa and the other higher taxa mentioned in this study are primarily gradal units, and comments are made on the reason why such a view of taxa is adopted.

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1. INTRODUCTION

Some diaspidid genera I have studied are not settled in the formal classification of the Diaspididae. *Ulucoccus*, *Thysanaspis*, and *Smilacicola* are among such genera and especially noteworthy for their isolation. For many years I have been looking for further forms which may come close to them, but I have failed to find such forms in my surveys. In the following lines I propose to establish for them new higher taxa, one subfamily and two tribes, which are all monobasic [2]. Their evolutionary significance is discussed [3]. For comparison with the Thysanaspidini and the Smilacicolini, two new species belonging to one new genus are described [5] and figures of three other species, especially of their nymphal stages, are presented. One of the three species is newly recorded from eastern Asia, and is redescribed [4]. In the Diaspididae, the nymphal stages are expected to be useful in revealing taxonomic relationships especially when features of the adult female are much reduced owing to the pupillarial mode of life or much modified in association with peculiar habitats. However, detailed studies of diaspidid nymphal forms are still limited, and, therefore, no generalization is attempted in this paper on the nymphal character patterns of diaspidid higher taxa. The figures are presented for showing examples, instead.

The new subfamily and tribes as well as the other subfamilies and tribes of the Diaspididae recognized in this paper are understood primarily as gradal units. Comments are given at the end of this paper for explaining why I have adopted such a view of taxa in spite of the recent spread of cladistics [6].

Terms and abbreviations. In diaspidid taxonomy 'lobes' and 'plates' have generally been applied to pygidial appendages, but these terms, having broad meanings, can also be used for other roundish projections and flat structures. Recently I have replaced them with 'trullae' and 'pectinae', which were formerly used by some authors. The term 'nymphs', universal in hemimetabolous insects, is applied to the first and second instars instead of 'larvae', which I have long used. The abbreviations 'abd I–VIII' stand for the first to eighth abdominal segments.

Acknowledgements. In this study are included three species collected in the Philippines in connection with the project 'Systematic and Ecological Surveys on Some Plant-parasitic Microarthropods in Southeast Asia'. Surveys in the Philippines were carried out with the co-operation of Dr Venus J. Calilung. Material collected by Dr K. Ozaki in Indonesia was also examined. SEM photographs were taken at the Electron Microscope Laboratory, Graduate School of Agriculture, Hokkaidô University (Mr T. Ito in charge). Dr S. Naomi and an anonymous reviewer critically read the manuscript.

2. DESCRIPTIONS OF ONE NEW SUBFAMILY AND THREE NEW TRIBES

2.1. *Ulucoccinae*, subfam. n.

Type genus: *Ulucoccus* Takagi, Tho, and Khoo (1990). This subfamily is represented by the type genus alone. The adult female and the second instar female and male are very similar in principal characters. The body is globular, wholly membranous, and obscurely segmented. The pygidium is not well demarcated from the preceding part of the body, but in the adult female it seems to comprise the segments of the abdomen posterior to the fifth. There are on the pygidial margin no appendages or no well-formed ones except for minute gland spines. There are larger gland spines in the prepygidial

region along the body margin. There occur minute ducts and larger, thick ducts, the latter being of the geminate type at the inner end. The antennae are reduced to tubercular processes, each bearing one or two long setae. In the first instar nymph the antennae are four- or five-segmented; the terminal segment is elongate but not annulate, and the apex bears one seta; the tarsus is joined to the tibia with a distinct articulation, and there is no seta on its ventral surface. As usual in diaspidids, the adult female is armoured with the exuvial casts of the first and second instars, and the male test consists of the exuvial cast of the first instar and an amount of wax. Both female and male produce flossy wax.

The genus *Ulucoccus* was proposed for *U. gombakensis* and *U. danumensis*, which were described from Malaya and Sabah (Borneo Island), respectively (Takagi et al., 1990). Later, *U. gombakensis* was collected in Sarawak (Borneo Island) and *U. danumensis* in Luzón, the Philippines, and further observations on the first instar nymphs of the two species and the adult female of *U. danumensis* were given on the basis of the new material (Takagi, 1998). These species are associated with bamboos, both sexes occurring on the lower surface of leaves.

2.2. Thysanaspidini, trib. n.

Type genus: *Thysanaspis* Ferris (1955). This genus, which alone represents the new tribe, is pupillarial, and, therefore, the second instar rather than the adult female is useful for recognizing the tribe. In both female and male of the second instar there occur on the pygidial margin well-developed pectinae but no trullae and no gland spines. These pectinae are dentate rather than fimbriate and not glanduliferous. There are within the pygidial margin very large ducts, which are of the geminate type at the inner end. The segmentation of the abdomen is traceable as posteriorly as the eighth segment, whereas the pygidium, as defined by the occurrence of the pectinae and enlarged marginal ducts (in *T. litseae*), is interpreted to comprise the segments posterior to the fifth. There are conical gland tubercles within the prepygidial margin. The antennae are tubercular and multisetose. In the first instar nymph, too, there are pectinae but no trullae and no gland spines on the pygidial margin; the antennae are five-segmented; the terminal antennal segment is annulate, and the apex bears two setae; the tarsus is joined to the tibia with a distinct articulation, bearing a well-developed seta on its ventral surface; there are macroducts along the body margin and also submedially on the dorsal surface, the submedian macroducts are larger than the marginal. The adult female is very similar to that of the Leucaspidini in having multisetose antennae, a cluster of ducts laterally to each anterior spiracle (paraspicular ducts), and quinquelocular disc pores submarginally on posterior prepygidial abdominal segments.

The genus *Thysanaspis* was erected for *T. acalyptus* Ferris (1955) described from southern China (Guangzhou ['Canton'], Hong Kong, and Macao). *T. litseae* Takagi (1961) occurs in southern Kyûsyû and the Ryûkyû Islands, Japan, and *T. perkinsi* Takagi (1969) in Taiwan. The host plant of *T. acalyptus* was not identified. The other two species are associated with plants of the family Lauraceae, occurring on the lower surface of leaves. The descriptions and figures of the *T. acalyptus* adult female and second instar female given by Ferris may not be complete, so that the diagnosis of the tribe is based largely on the other two species. I have newly prepared figures of the adult female, the second instar female and male, and the first instar nymph of *T. litseae* (Figs. 1–4). In this species the exuvial cast of the second instar female is wholly sclerotized and plump (thus appearing like a plant seed or an insect egg), with the pygidium produced, and the male

test is a loose mass of flossy wax.

For comparison I present figures of the second instar male and the first instar nymph of *Lopholeucaspis japonica* (Cockerell, 1897) (Figs. 5, 6), which may be the most generalized form of the Leucaspidini. *Mongrovaspis quadrispinosa* (Green, 1934), another leucaspidine (Figs. 7–10, 22) [4], and two new species of *Ligaspsis*, gen. n., a pupillarial genus belonging to the Parlatoriini (Figs. 11–17, 23–26) [5], are also presented here. Although the second instar female exuvial casts of *Thysanaspis*, *Mongrovaspis* and *Ligaspsis* are not similar in external appearance, all of them are strongly sclerotized throughout, thus completely enclosing the body of the adult female.

2.3. Smilacicolini, trib. n.

Type genus: *Smilacicola* Takagi (1969). This tribe is represented by the type genus alone. The adult female has no marginal appendages on the pygidium, which comprises the segments of the abdomen posterior to the fifth. There are strewn small macroducts on the dorsal surface and minute ducts on the ventral. The antennae are tubercular and multisetose. In the second instar, especially the male, there occur unilobed trullae and glanduliferous pectinae in a continuous series on the whole pygidial margin and gland tubercles in the prepygidial region, especially on the thorax; there are macroducts, which are thickly rimmed around the orifice, on the dorsal surface in segmental rows and along the body margin. The first instar nymph is also provided with trullae and glanduliferous pectinae; the antennae are six-segmented; the terminal antennal segment is rather short and not annulate, and the apex bears two setae; the tarsus is joined to the tibia with a distinct articulation, and bears a well-developed seta on its ventral surface; the longitudinal row of submedian dorsal setae is complete through the thorax and abdomen as posteriorly as the seventh segment.

The genus *Smilacicola* was erected for *S. apicalis* Takagi (1969) occurring in Taiwan. Another species, *S. crenatus* Takagi (1983), was described from Hong Kong, and *Rugaspidiotus heimi* Balachowsky (1947) described from Vietnam was transferred to the genus. The former two are associated with lianoid plants belonging to the genus *Smilax*, Liliaceae, and occur exclusively under the stipules, whereas the last was found under the mycelium of *Septobasidium xylostroma* on 'une liane ampelid e indeterminate', which should also be a *Smilax* species. Takagi (1983) revised the three species. The figure of the first instar nymph of *S. apicalis* in the revision (Takagi, 1983: Fig. 6) is, however, erroneous in depicting three submedian microducts as occurring on the ventral surface. In reality, these microducts are opened on the dorsal surface. In the course of the present study I tried to mount crawlers from the almost exhausted dry material of *S. crenatus* and got a few specimens. Though these specimens, too, are not in good condition, I have carefully prepared a figure from one of them in the hope of showing the correct character pattern of the first instar nymph (Fig. 19). A figure of the second instar male of *S. apicalis* (Fig. 18), newly prepared from a re-stained specimen, is presented to show how closely it is similar to the adult female and second instar of *Parlatoria*, the tribe Parlatoriini, except for the multisetose antennae. The figures of the nymphal stages of *Ligaspsis* (Figs. 12–14, 16, 17) may serve to show the resemblance and difference between the Smilacicolini and the Parlatoriini. I also present, for comparison, figures of the second instar male and the first instar nymph of *Odonaspis arcusnotata* Ben-Dov (1988) (Figs. 20, 21), the tribe Odonaspidini, which is another group related to the Smilacicolini [3.4].

3. EVOLUTIONARY SIGNIFICANCE OF THE NEW HIGHER TAXA

3.1. A classification scheme of the Diaspididae

Table 1 presents a scheme formulated for dividing the Diaspididae on the basis of the composition of pygidial appendages. It is substantially the same as the schemes in Takagi (1981; 1990). I hold the view that the pygidial appendages have evolved primarily in the adult female in association with manner in forming the test, and that the pattern of appendages evolved in the adult female is also manifested in the nymphal stages. In this respect, the groups formed by this scheme are gradal units. Logically Level I, II, and III represent successive stages in the differentiation and organization of pygidial appendages in each of the subfamilies Diaspidinae and Aspidiotinae. Level 0 means the absence of pygidial appendages, suggesting the primeval state of the pygidial margin. The Ulucoccinae, lacking differentiated appendages except for minute gland spines, are referred to this level. The Odonaspidini and the Smilacicolini are settled in the Level III group of the Aspidiotinae on the basis of the nymphal forms that have well-developed pygidial appendages, which are composed of unilobed trullae and glanduliferous pectinae. Differentiation of pygidial appendages has proceeded in parallel between the Diaspidinae and the Aspidiotinae. In the Diaspidinae, the Diaspidini extend over Level I–III and the Lepidosaphidini (also spelled Lepidosaphedini) cover Level II and III, both tribes showing no essential difference corresponding to the levels in features other than the pygidial appendages, whereas in the Aspidiotinae no tribe appears at more than one level. In SEM observations of perivulvar or abdominal disc pores of diaspidids some different types have been recognized. Table 2 shows that these types well fit in with the scheme. Because these disc pores have no concern with the manner of test formation, the fit of their types with the scheme suggests that the groups formed by the scheme reflect natural relationships within the family.

Not all the known forms of diaspidids readily find their places in the scheme. *Smilacicola*, once referred to the Rugaspidiotini but now the type genus of the Smilacicolini, is referred to Level III on the basis of nymphal characters. Other ‘rugaspidiotine’ genera and some odd ones are supposed to be related to diaspidines, lepidosaphidines, aspidiotines, odonaspidines, or parlatoriines mainly on the basis of their first instar nymphs (Takagi, 1995; Takagi et al., 1997). However, in the second instar nymphs they do not faithfully manifest their probable ancestral patterns with well-developed pygidial appendages, so that their taxonomic positions are not clear. The tribes Ancepaspidini and Antakaspidini, either, cannot be settled in the scheme in the present state of our knowledge about them. *Phoenicococcus* and *Xanthopthalma* have no trace of pygidial appendages and appear very primitive in other features, too. It is now a general tendency to exclude *Phoenicococcus* from the Diaspididae to form the family Phoenicococcidae, which may be restricted to the genus or may include other genera. *Xanthopthalma* should be kept in the Diaspididae, because the adult female is armoured with the nymphal exuvial casts. It may be referred to Level 0, but apparently has no relationship to the Ulucoccinae.

The Level III groups constitute a greater part of the family. Subdividing them into subtribes is not yet successful especially in the Diaspidini and Lepidosaphidini. There have been proposed many subgroups in the Diaspidini, but in Table 1 are mentioned for the Level III Diaspidini only three subtribes, which appear to represent natural groups so far as their type genera and some other genera apparently related to the type genera

are concerned. Under the Level III Lepidosaphidini are also given the names of three subtribes, which are, however, only provisional.

3.2. Ulucoccinae

The heteromorphic second instar males of some Diaspidini, especially of Chionaspidina, are similar to the adult female and the second instar female and male of *Ulucoccus*. This genus, therefore, is supposed to represent the character pattern of a remote ancestor of the Diaspidini, or at least of the Chionaspidina (Takagi et al., 1990; Takagi, 1998; for a recent summary of the homomorphism and heteromorphism in the diaspidid second instar, see Takagi, 2001, p. 78, 79). The heteromorphic second instar males of the Diaspidini are not uniform, and it is uncertain whether the Diaspidini have one origin or more. In any case, *Ulucoccus* gives us an image about forms that existed before the emergence of the Diaspidini.

The view is adopted that the appearance of well-formed pygidial appendages was a key innovation in the evolution of Diaspididae, and that the differentiation of appendages in structure and function in association with test formation has brought a great success to the family. There should be a great gap in 'adaptive potential' (Brock, 2000) before and after the appearance of pygidial appendages. I have proposed, therefore, to erect the subfamily Ulucoccinae, contrasting it with the subfamilies Diaspidinae and Aspidiotinae. In part of the latter two the manifestation of once developed pygidial appendages is suppressed in the adult female as exemplified by the Smilacicolini and Odonaspidini. In general, such forms have a sclerotic and depressed pygidium, which is strewn with abundant ducts on both surfaces, and are adapted for inhabiting depressed or confined spaces on the plant body (Takagi, 1995). Although they appear to have returned to the primeval state in the absence of pygidial appendages in the adult female, they are quite different from *Ulucoccus* in their habitat niches.

In Table 1 the Lepidosaphidini are included within the Diaspidinae, because they cannot be distinguished from the Diaspidini in the composition of pygidial appendages. These tribes also agree in having perivulvar disc pores of the capitate type (Table 2). The recently discovered *Mempelaspis serpentina* Takagi (2000) differs from the other known lepidosaphidines in having pectinae (mostly glanduliferous but partly non-glanduliferous) in addition to trullae and gland spines on the pygidial margin, and the subtribe Mempelaspidina was erected accordingly. So far as the pygidial appendages are concerned, this subtribe represents the most primitive form among the known Lepidosaphidini, and stays at Level II, whereas the other lepidosaphidines have attained Level III. It approximately corresponds to the subtribe Kuwanaspidina, Diaspidini, in the composition of pygidial appendages, but otherwise there is no character particularly common to them (Takagi, 2000). There has been known no lepidosaphidine staying at Level I, either. It is uncertain, therefore, how the Lepidosaphidini and the Diaspidini can be related phylogenetically. Under these circumstances it is not clear whether the subfamily Ulucoccinae has any relationship to the Lepidosaphidini.

3.3. Thysanaspidini

In Borchsenius' (1966) catalogue the genus *Thysanaspis* is referred to the tribe Leucaspidini, of which all the known species are also pupillarial. Indeed, it cannot be distinguished from leucaspidines in the adult female, which is much simplified in features owing to the pupillarial mode of life, thus completely lacking pygidial

appendages. In the nymphal stages, however, *Thysanaspis* stays at Level I, thus being distinct from the tribe Leucaspidini at Level II. In the second instar nymphs of both sexes *Thysanaspis* is further characterized by the enormous marginal macroducts, of which the inner end shows a geminate structure, and in the first instar nymph by the submedian dorsal macroducts, which are much larger than the marginal macroducts. In comparison with the Parlatoriini it is characterized in common with the Leucaspidini by the pectinae bearing no microduct and by having a distinct articulation between the tibia and tarsus in the first instar nymph. So far as known, these three tribes are remarkably different from each other in the SEM-observed structure of the perivulvar disc pores (Table 2). Although the acquirement of the pupillarial mode of life has obscured the taxonomic position of *Thysanaspis*, the erection of the new tribe may be justified by the morphological traits mentioned above.

The tribe Thysanaspidini exhibits the most primitive pattern of pygidial appendages among the known Aspidiotinae in the nymphal stages, which, therefore, afford some idea about the ancestor (which should be non-pupillarial) of the extant Aspidiotinae. It is difficult to suppose any particular relationship between the Thysanaspidini and the Protodiaspidina, the taxa representing the Level I forms of the Aspidiotinae and the Diaspidinae, respectively. The phylogenetic relationship between these subfamilies, therefore, remains unknown.

3.4. Smilacicolini

The genus *Smilacicola* and the tribe Odonaspidini are similar in the adult females, and the second instar nymphs of both these taxa exhibit a character pattern common to the tribe Parlatoriini in the pygidial appendages and macroducts. As compared with the Odonaspidini and the Parlatoriini, *Smilacicola* is primitive in having multisetose antennae in the adult female and the second instar female and male, and in having a distinct articulation between the tibia and tarsus and a complete longitudinal row of submedian dorsal setae in the first instar nymph. In all these characters it agrees with the Thysanaspidini (Level I) and the Leucaspidini (Level II). Furthermore, it is characterized in having six-segmented antennae in the first instar nymph, though the evolutionary significance of this character is unclear. Considering all this, *Smilacicola* should have derived from a putative group comprising forms related to, but more primitive than, the extant forms of the Parlatoriini.

The tribe Odonaspidini is hardly distinguishable from the Parlatoriini in the parlatoriine-patterned second instar male, and also in the first instar nymph except for the third segment of the five-segmented antennae peculiarly elongate. It may have derived from the tribe Parlatoriini (as represented by the extant forms), but its character pattern is also derivable from *Smilacicola* in supposing changes in the antennae of the adult female and nymphs and the legs and chaetotaxy of the first instar nymph.

Smilacicola, the Odonaspidini, and the Parlatoriini, therefore, should be related phylogenetically. Two 'gradograms' [6.4] are possible for them, both starting with the putative group that was parlatoriine-patterned as a whole but had some primitive characters. In one of the gradograms the Parlatoriini and the Odonaspidini are more closely related phylogenetically, and the similarity in the adult females between *Smilacicola* and the Odonaspidini is due to convergence in association with their cryptic mode of life. In the other gradogram, in which *Smilacicola* and the Odonaspidini are more closely related, their similarity in the adult females has a phylogenetic basis. In

any case, *Smilacicola* and the Odonaspidini have exploited their own habitat niches on *Smilax* and Poaceae, respectively, where they have undergone speciation, thus suggesting their stasigenetic state. On this understanding, these groups are distinct as gradal units. They are also characterized in the morphology of the first instar nymphs, which has no direct concern with the niche exploitation in the adult females. In consideration of all this, they are good taxa, and there seems to be no problem in erecting the tribe Smilacicolini. In fact, the tribe Odonaspidini has generally been recognized as a distinct taxon on the basis of the adult female characters (Ben-Dov, 1988). However, I would like to propose the tribe Smilacicolini rather for bringing forth a problem: how to treat other 'rugaspidiotine' genera and also odonaspidine-like forms in formal classification [3.1].

4. APPENDIX I: A REVISION OF MONGROVASPIS QUADRISPINOSA

Mongrovaspis quadrispinosa, a mangrove-associated scale insect, was originally described as a member of *Leucaspis* from the Red Sea coast of Egypt. It seems that the genus *Mongrovaspis* has no closely related forms both in the maritime fauna and in the inland fauna. I have examined specimens of this genus collected in the Philippines and Indonesia, and I am much inclined to believe that they are referable to *M. quadrispinosa* as will be discussed. The occurrence of the species at the remotely separated districts may be surprising, but is very probably natural. Mangrove restoration has begun only recently, and it is difficult to imagine any human influence on the geographical distributions of coccoids exclusively associated with mangroves. Whether the eastern Asian and Red Sea forms of *Mongrovaspis* are conspecific or not, the present discovery requires further investigations of mangroves especially in the Indian Ocean not only for revealing the distribution pattern of the genus but also for estimating dispersal ability of mangrove coccoids in general.

4.1. *Mongrovaspis* Bodenheimer, 1951, Leucaspidini

Bodenheimer, 1951: 331 ['Type: *Mongrovaspis*, olim from the Red Sea coast of Egypt *Leucaspis quadrispinosa* Green, 1934 (Egypt), also including *M.*, olim *Fiorinia pygosema* Green, 1923 (Tanganyika)'].

Balachowsky, 1953: 182 ['J'ai donc retenu le g. *Mongrovaspis* pour une seule espèce, *M. quadrispinosa* Green qui appartient indiscutablement à la tribu des Leucaspidina'].

Green (1934) supposed *Fiorinia (Adiscofiorinia) pygosema* Green and Laing (1923) to be closely related to *Leucaspis quadrispinosa*, and Bodenheimer followed him in referring it to *Mongrovaspis*. I agree with Balachowsky in his view that it should be excluded from *Mongrovaspis*, which is represented by the type species alone [4.4].

4.2. *Mongrovaspis quadrispinosa* (Green, 1934)

Green, 1934: 110 [*Leucaspis*; 'Egypt (Mersa Halaib): Discovered by Dr. H. Priesner, on *Avicennia officinalis*, 23.IX.1933'].

Bodenheimer, 1951: 331 [erection of *Mongrovaspis*, with *L. quadrispinosa* as the type species].

Balachowsky, 1953: 183 [adult female redescribed on the basis of 'le co-type de cette espèce'].

Material examined. Collected in the Philippines and Indonesia: Suqui, Calapan, Mindoro, on *Avicennia officinalis*, 12.VIII.1994 [94PL-20]; Abucay, Bataan, Luzón, on *A. officinalis*, 19.VIII.1994 [94PL-68]; Gilisulat, Lombok, on *Avicennia marina*, I.1997 [K. Ozaki leg.; denoted

by 'G' in the description below]. The slide-mounted specimens prepared from the material collected at Suqui and Abucay include adult females, second instar females and males, and first instar nymphs (crawlers). Two adult females (not good in condition) and 2 exuvial casts of the second instar female were mounted from the material collected at Gilisulat.

Host association. Green described *Leucaspis quadrispinosa* as occurring on *Avicennia officinalis* in the Red Sea. According to Spalding et al. (1997), however, *A. officinalis* is restricted to South and Southeast Asia in distribution, and *A. marina*, which is best adapted to harsh environmental conditions and widely distributed in the South Pacific Region to the Indian Ocean, occurs in the Red Sea, instead. *Mongrovaspis quadrispinosa* has been collected on *Avicennia marina* as well as on *A. officinalis* in eastern Asia as shown above. The genus *Avicennia* represents the family Avicenniaceae, which is related to and was included in the Verbenaceae. It is widely distributed in the Pacific, Indian, and Atlantic Oceans, comprising 8 species of mangroves.

Adult female (Fig. 7). Entirely enclosed within enlarged and sclerotized exuvial cast of second instar female. Body, when fully grown, elongate, with lateral margins straight and parallel; derm membranous, transversely spinulate medially on ventral surface of thorax, slightly rugose, with some irregularly shaped sclerotic patches, on dorsal surface of pygidium. Rudimentary antennae situated in front of mouth-parts, separated from each other by a space narrower than frame of mouth-parts, each with 3–5 (usually 4) well-developed stiff setae and often also with 1–3 short, slender setae. Anterior spiracles each with 1–8 5-locular disc pores (1–6, mean 4.0, sample size 37 in 94PL-68; 2–5, sample size 12 in 94PL-20; 5–8, sample size 4 in G). Short small ducts forming a rather close cluster laterally to each anterior spiracle (paraspicular ducts), 6–14 (6–14, mean 10.8, sample size 38 in 94PL-68; 9–14, sample size 12 in 94PL-20; 8–12, sample size 4 in G). Perivulvar disc pores present in 5 groups in front of vulva, the median and/or anterolateral often subdivided; 3–8 medians (5–8, mean 6.6, sample size 19 in 94PL-68; 3–6, sample size 7 in 94PL-20; 7, sample size 2 in G), 3–14 anterolaterals (3–14, mean 8.1, sample size 38 in 94PL-68; 5–8, sample size 14 in 94PL-20; 6–10, sample size 4 in G); and 4–11 posterolaterals (6–10, mean 7.9, sample size 38 in 94PL-68; 4–10, sample size 14 in 94PL-20; 7–11, sample size 4 in G); total 27–46 (32–44 in 94PL-68; 27–36 in 94PL-20; 39 and 46 in G); belonging to the 'spatulate type' in scanning electron microscopy. Anus set posterior to centre of pygidium. Four long processes on apical to subapical pygidial margin, slender and tapering, directed backward, often cleft; mesal ones of these processes each with 1 and the outer ones each with 2 minute dorsal ducts basally.

Second instar female (Fig. 8). Body elongate, when young with free segments gently lobed laterally; front growing forward; pygidium round on free margin. Antennae with 3 or 4 curved setae and, sometimes, 1 short seta. Anterior spiracles each with 6–9 5-locular disc pores forming an oblique elongate cluster. Gland tubercles conical, situated within body margin as follows: 2 between anterior and posterior spiracles (probably belonging to pro- and mesothorax), and usually 2 on each of metathorax and abd I–III (at times 1 on metathorax and abd III and 1 or 3 on II). Small ducts arranged in a transverse row across ventral surface of abd II and III each, 9–15 on II and 7–11 on III (22 on II and 12 on III in the 2 exuvial casts mounted from G). One submedian macroduct on abd VII and I at times on VI; 2–4 submarginal macroducts on IV–VII (1 or 0 on IV, usually 1 present on V, and 1 on VI and VII each); 1 small marginal duct at apex of pygidium (between median trullae), followed by 2 similar ducts laterally on each side (on abd VII and VI),

these followed by macroducts occurring as anteriorly as metathorax marginally on dorsal surface (on posterior segments) or within margin on ventral surface (on anterior segments); 1 or a few small submarginal ventral ducts on thoracic segments and abd I–III each. Pygidial margin with 2 pairs of well-developed tricuspid trullae; median trullae set close, with no processes between; second trullae unilobed, less produced than the median; 1 pectina between median and second trullae; 1 much broader pectina laterally to second trulla, followed by rudimentary ones occurring on the preceding segment. Anus a little posterior to centre of pygidium. Exuvial cast (Fig. 22) elongate, about 5 times as long as wide, flat, strongly sclerotized on both dorsal and ventral surfaces, and dark chestnut-brown; front elongate, gently narrowing anteriorly; lateral margins nearly parallel on thorax and abd I and II, abd III–V gently lobed laterally; pygidium broadly triangular apically, the ventral derm with a transverse rupture running submarginally along the whole pygidial margin.

Second instar male (Fig. 9). Similar to the second instar female, but remarkably different in having more macroducts both dorsally and ventrally on prepygidial segments. Many triangular spines on front, in a cluster on each side; sometimes rudimentary or well-developed spines between the clusters. Anterior spiracles each with 6–10 5-locular disc pores. Abd VI with a cluster of 2–8 5-locular disc pores submarginally; abd V usually with 1–3 (at times with none). Test elongate, a little expanded posteriorly, flat, grayish white.

First instar nymph (crawler) (Fig. 10). Body elongate elliptical. Antennae 5-segmented; segment II–IV short, V shorter than I–IV combined, tapering, annulate, the apex with 1 seta. Anterior spiracles each with 1 3-locular disc pore. Tibiotarsal articulation distinct, oblique; tarsi each with a well-developed seta ventrally. Submedian dorsal setae occurring as posteriorly as abd VII. A series of marginal ducts as follows on each side: 5 macroducts on abd III–VII and 1 slender duct on VIII; 2 small ventral ducts occurring marginally on thorax (probably on pro- and metathorax). Small dorsal ducts occurring as follows: 5 on head and thorax and 1 on abd II laterally to row of submedian dorsal setae, 1 near eye, and 1 submarginally on mesothorax. A pair of well-developed tricuspid trullae at apex of pygidium, separated by a space narrower than one of them, with no processes between, each with a broad pectina laterally. Two gland tubercles laterally to meso- and metacoxa, conical and robust. Caudal setae shorter than abdomen. Anus situated about centre of pygidium.

4.3. Identification of the eastern Asian form with *M. quadrispinosa*

Mongrovaspis quadrispinosa was described mainly on the basis of the adult female, which is much simplified and modified in external features owing to the pupillarial mode of life. The identification of the eastern Asian form with *M. quadrispinosa* on the basis of the adult female alone, therefore, may appear unreliable. Actually, however, it agrees closely in the numbers of the spiracular disc pores, paraspiracular ducts, and perivulvar disc pores with the descriptions given by Green and Balachowsky in spite of the great distance separating the localities in eastern Asia from the Red Sea. Such an agreement, involving different kinds of external secretory organs, may hardly be expected if these forms belong to different species. As stated in the description, minute ducts are present on the bases of the long pygidial processes in the examined specimens. Green and Balachowsky did not mention this character for the Red Sea form, but these ducts are so minute that they have been clearly recognized only in oil-immersion microscopy.

These ducts are probably rudiments of marginal macroducts, whereas the long pygidial processes may be homologous with the 2 pairs of trullae that are well represented in the second instar female and male.

Green erroneously mentioned the paraspiracular ducts as 'parastigmatic pores', while neglecting the real spiracular disc pores. Balachowsky in his figure showed two disc pores associated with the anterior spiracle. He described and illustrated the paraspiracular ducts as 'tubercules glandulaires coniques', but in the eastern Asian form none of them is associated with a conical tubercle. I do not think that this difference raises a serious difficulty in identifying the eastern Asian form with *M. quadrispinosa*, because, in diaspidids in general, small gland tubercles are often replaced by microducts.

The immature stages are unknown for the Red Sea form except for the short description and simple figure of the pygidium of the second instar female exuvial cast given by Green. Detailed examinations of the Red Sea form especially in the second instar nymphs of both sexes are necessary for confirming the present identification.

4.4. Relationship to other species

Green (1934) supposed *Fiorinia (Adiscofiorinia) pygosema* to be closely related to *Leucaspis quadrispinosa*, because these species are commonly characterized by having unusually long processes on the pygidium, and also because the former was collected 'on sea-coast south of Dar-es-Salaam, on leaves of an unknown plant of the mangrove type growing at high-water mark' (Green and Laing, 1923, my italics), thus agreeing with the latter in habitat, too. *F. pygosema*, based on the description, disagrees with *M. quadrispinosa* in the following characters of the adult female: 1) absence of spiracular disc pores, 2) absence of paraspiracular ducts, 3) absence of perivulvar disc pores, and 4) presence of 2 pairs of short conical processes, in addition to the remarkably elongate processes, on the pygidial margin. Character 4) is especially noteworthy, because the conical processes are very probably trullae. This allows us to interpret the long processes of *F. pygosema* as gland spines or modified pectinae, whereas the long processes of *M. quadrispinosa* can be modified trullae (see the preceding section). I therefore adopt the view that these two species are not congeneric.

Mongrovaspis quadrispinosa as represented by the adult female, which is much modified and peculiarly characterized in the pygidial fringe, has no close relative in the Leucaspidini. In the pygidial fringe of the second instar it is somewhat similar to *Salicicola vayssierei* Balachowsky (1928) and *S. kermanensis* (Lindinger, 1906), both studied in detail by Balachowsky (1953), but this similarity may be due to parallelism associated with their highly derivative state.

5. APPENDIX II: DESCRIPTIONS OF LIGASPIS, GEN. N., AND TWO NEW SPECIES

Pupillarial forms of the tribe Parlatoriini are well represented in the tropics of eastern Asia, with many undescribed forms. The current classification of their genera may be largely tentative because the adult females are simple-featured and much modified owing to the pupillarial mode of life, and also because the second instar nymphs are generally similar among parlatoriines, whether the adult females are pupillarial or not. The described pupillarial genera and their compositions should be critically reviewed on the basis of detailed comparisons and also with due consideration for homoplasy in adult female characters. The erection of another pupillarial genus, *Ligaspis*, is therefore

rather tentative.

5.1. *Ligaspis*, gen. n., Parlatoriini

Type species. *Ligaspis maculata*, sp. n.

Adult female. Entirely enclosed within enlarged and sclerotized exuvial cast of second instar. Body obpyriform, with prepygidial segments forming a round mass, and with pygidium (composed of abd V and succeeding segments marginally) produced; segmentation indistinct. Spiracular disc pores, when present, 3-locular (in *L. pala* usually each anterior spiracle with 1 disc pore and in *L. maculata* rarely with 1). Perivulvar disc pores in a small submedian group on each side at the position corresponding to the anterolateral group in the usual 5 group arrangement (the last prepygidial segment also with 1 or 2 submedian disc pores in *L. pala*). Two small marginal macroducts on each side of pygidium, belonging to abd VI and VII. Two pairs of unilobed trullae, small, conical or irregularly incised, and sclerotized. Glanduliferous pectinae occurring between trullae and laterally to second trullae, longer than trullae, modified to elongate tubercular processes with a slender membranous apical projection. Small ducts or gland tubercles arranged within margin in prepygidial part of body. Anus relatively large, situated about centre of pygidium.

Second instar female. Anterior spiracles each with 1 5-locular disc pore. Pygidial margin with a continuous series of appendages composed of well-developed unilobed trullae and pectinae; 4 pairs of trullae pointed apically, often variously incised; pectinae roughly serrate, each with a slender membranous apical projection, through which a microduct leads to its opening; 2 between median trullae, 2 between the median and second, 3 between the second and third, 3 between the third and fourth, and several ones laterally to the fourth, succeeded by a sparse row of well-developed conical gland tubercles occurring within margin on prepygidial abdomen and thorax. Three well-developed marginal macroducts on each side of pygidium, belonging to abd V–VII, succeeded by smaller marginal macroducts occurring on preceding segments. Anus large, situated about centre of pygidium. Exuvial cast sclerotized on both dorsal and ventral surfaces, the pygidium produced, cleft on ventral surface along margin.

Second instar male. Body obovoid to oblong. With features nearly as in the second instar female, but remarkably different in having submedian and submarginal macroducts and in the prepygidial gland tubercles rounded.

First instar nymph. Ovoid to oblong. Antennae 5-segmented, segment V shorter than I–IV combined, annulate, the apex with 2 setae. Tibia and tarsus completely united, with a well-developed tarsal seta ventrally. Anterior spiracles each with 1 invaginated disc pore (which is apparently 3-locular in *L. pala*). Submedian dorsal setae absent on abd IV and succeeding segments (in female, absent also on abd I). Submedian ventral setae absent on prepygidial abdomen. Trullae slender, pointed apically. Pectinae rudimentary or modified into spinous processes. Anus large, near apex of pygidium.

Distribution and host association. The two new species occur in Luzón, the Philippines, and are associated with *Semecarpus cuneiformis* (Anacardiaceae; local name: Ligas), both sexes occurring on the lower surface of the leaves.

Remarks. As usual for pupillarial parlatoriines, it is not easy to find the phylogenetic relationships of this genus to other parlatoriines. This genus is here compared with *Silvestraspis* Bellio (1923), another pupillarial genus. These genera are similar in the adult female pygidial fringe. In *Silvestraspis*, however, the pectinae are swollen just

before narrowing to form a membranous apical projection, whereas this is not the case with *Ligaspis*. In *Silvestraspis uberifera* (Lindinger, 1911) the thorax of the adult female is produced to form a pair of eminent wing-like lobes, but in *S. ficaria* Williams and Watson (1988) the lobes are small conical processes, suggesting that the presence of the thoracic lobes is not a constant character of the genus. In this connection it is noteworthy that *Porogymnaspis angulata* Green (1916) and *P. silvestrii* Bellio (1928) have pectinae of the *Silvestraspis* type. *Ligaspis* is distinct from *Silvestraspis* and other pupillarial parlatoriines in the second instar, in which the pectinae are serrate rather than fimbriate and the bases of the trullae do not have a wedge-shaped basal extension on the ventral surface of the pygidium. *Ligaspis* is characteristic, above all, in the second instar female exuvial cast, which is evenly sclerotized on both dorsal and ventral surfaces, and of which the pygidium is much produced.

5.2. *Ligaspis maculata*, sp. n.

Material examined. Collected in Luzón, the Philippines: the grounds of the University of the Philippines at Los Baños, Laguna, 24.XI.1992 [92PL-15] and 7.VIII.1994 [94PL-10]; Bagac, Bataan, 22.VIII.1994 [94PL-92]. Specimens prepared from 94PL-10 include adult females, second instar females and males, and first instar nymphs, so that the description below is mainly based on them. Holotype, adult female [94PL-10], deposited in the collection of the Natural History Museum, the University of the Philippines at Los Baños.

Adult female (Fig. 11). Anterior spiracles usually with no disc pore, rarely with 1. Perivulvar disc pores 1–4 (usually 3) in submedian group. Trullae conical. Pectinae, when completely represented, 9 in total: 1 between median trullae, 2 between the median and second, and 2 laterally to the second, the outermost at times lacking. Small ducts forming a sparse row on prepygidial part of body along margin, about 11–28 on one side.

Second instar female (Fig. 12). Prepygidial marginal macroducts 4–7 on one side: 4 always present on abd I–IV; others, when present, occurring on thorax. About 10 large conical gland tubercles on one side of prepygidial part of body. A few or several ventral microducts at times occurring on prepygidial abdomen. Exuvial cast (Fig. 23) black except for a broad marginal area, which is pale brown.

Second instar male (Fig. 13). Three submedian dorsal macroducts on each side, belonging to abd V–VII. Submarginal dorsal macroducts occurring on abd I–VI. Submarginal ventral macroducts in a double row on abdomen. Some ventral microducts on prepygidial abdomen. Test (Fig. 24) oblong, pale brown.

First instar nymph (Fig. 14). Trullae with median pair alone well represented. Abdominal segments each with 1 marginal microduct. Pectinae rudimentary, occurring on abd II–VIII.

5.3. *Ligaspis pala*, sp. n.

Material examined. Collected in Luzón, the Philippines: Puerto Azul, Ternate, Cavite, 8.XII.1992 [92PL-102]. Holotype, adult female, deposited in the collection of the Natural History Museum, the University of the Philippines at Los Baños.

Adult female (Fig. 15). Anterior spiracles each usually with 1 disc pore, rarely none. One or 2 (usually 2) perivulvar disc pores on each submedian group; usually 1 or 2 similar submedian disc pores present on the last prepygidial segment (abd V), rarely none. Two pairs of trullae distinct, conical or irregularly incised, the third trulla at times suggested by a small conical process. Pectinae 2 between median trullae, 2 between the

median and second, and 2 laterally to the second; several rudimentary spiniform pectinae laterally to third trulla (or the expected position of the third trulla). About 11–33 small gland tubercles (partly replaced by ducts) scattered within margin of prepygidial part of body as anteriorly as mesothorax.

Second instar female. Prepygidial marginal macroducts 2 on each side, occurring on abd III and IV, none on anterior segments. Exuvial cast (Fig. 25) wholly pale brown.

Second instar male (Fig. 16). Three submedian macroducts on abd V–VII on dorsal and ventral surfaces each. A single row of submarginal macroducts on abdomen on dorsal and ventral surfaces each. Test (Figs. 25, 26) glabrous, pale brown.

First instar nymph (Fig. 17). Trullae in 2 pairs. Pectinae bi- or tricuspid, or modified into spinous processes. Marginal microducts absent on abd II–IV.

Remarks. This species is easily distinguishable from *L. maculata* by the characters given above. The presence of prepygidial abdominal disc pores in the adult female is especially characteristic of this species, and the rather well-represented marginal appendages of the abdomen in the first instar nymph are also noteworthy. These characters may arouse some doubt about the generic position of *L. pala*. However, prepygidial abdominal disc pores also occur in the Thysanaspidini and Leucaspidini. *L. pala* suggests that this feature potentially persists in the Parlatoriini. The first instar nymphs of the two species agree in the slender trullae and other characters. The occurrence on the same plant species may also support the view that *L. pala* is closely related to *L. maculata*.

6. APPENDIX III: EXPLANATORY COMMENTS

In establishing the new subfamily and tribes I have adopted a gradistic view of taxa. Because cladistics dominates the literature, I should explain why I have not followed it. The standpoint I take is that of traditional taxonomy, which, I think, can be more harmonious with certain perspectives on evolution provided especially by the fields of molecular biology and developmental biology.

6.1. Clade, cladon, or sector of evolution

In traditional or evolutionary taxonomy the terms monophyly and clade (monophyletic group) have been defined for qualifying taxa (e.g., Simpson, 1961). Hennig (1966) turned the situation upside down, divorced the concept of monophyly from taxa, making it clear-cut in appearance but tautological in meaning, and thus has caused confusion in the usage of the terms. The fact is that one is often puzzled about the meanings of the terms one encounters in books and papers published after 1966. ‘A clade of the Hennigian system does not correspond to a taxon of the Darwinian classification and should therefore be given a different technical name’ (Mayr, 1997). I agree with Mayr in his view just cited, but ‘cladon’, the term he coined in 1995 for Hennig’s clade, may still be confusable. Mayr revoked the name cladistics, which he had long applied to the Hennigian method and system, and proposed ‘cladification’ instead. This term, too, is ambiguous, failing to distinguish between clade (in the traditional usage) and cladon (Hennig’s clade).

‘The facts of stasigenesis usually enable us to delimit the anagenetic grades actually involved in any particular *sector of evolution*’ (Huxley, 1958, my italics). The term sector originally means part of a circle lying between two straight lines drawn from the centre

to the circumference. Huxley's sector apparently corresponds to Hennig's clade and Mayr's cladon. I would like to use the term in a broader sense, and to apply 'evolutionary sector', abbreviated to 'ES' or simplified to 'sector', to any branching evolutionary structure arising from one point, whether it is composed of genes, enzymes, characters, species, or higher taxa. The Hennigian system is, in its essence, an ES reconstruction at the species level based on derivative morphological characters. To reconstruct a clade (*sensu* Hennig), a cladon (Mayr), or a sector [of species] (Huxley) may be justified apart from some problems, among which a major one concerns how to convert the reconstructed sector to a hierarchical set of taxa (for the deficiencies of the Hennigian manner of conversion, see Mayr, 1997). But it is justifiable on the premise that species emerge through branching, whereas branching of species is understood as branching of 'vertical inheritance' (the passing on of genetic information from parent to offspring). Monophyly in any usage of the term implies vertical inheritance. Thus any reconstructed sector of species is expected to reveal their genealogical (i.e., hereditary) relationships. This premise is now seriously challenged.

6.2. Horizontal gene transfer, introgression, and hybrid speciation

In the late 1950's it was discovered that plasmids carrying genes resistant to multiple antibiotics were transferred from *Escherichia coli* to another bacterium of *Shigella*. Recently, studies on 'horizontal gene transfer' (HGT) have greatly advanced (Syvanen and Kado, eds., 2002). Comparative analysis of complete genome sequences has shown that the occurrence of HGT is far from rare among prokaryotes. It has been revealed that in eukaryotes, too, genes can be transferred horizontally, and that viruses, retroviruses, and bacteria act as gene delivery vectors. HGT can take place between taxa of higher taxonomic categories (as exemplified by the transposon family named mariners, which repeated migration among various animals belonging to different orders, classes, or phyla) and even between prokaryotes and eukaryotes. The role of HGT in the evolution of organisms is still largely speculative, but this phenomenon potentially gives a great impact to evolutionary thinking. 'Macroevolution occurs when there is extensive horizontal exchange of genes between taxa at levels higher than at the species level. This exchange of genes is triggered by catastrophes in the biosphere and allows the organism to adapt to the radical alteration of the environment due to the catastrophe' (Hartman, 2002). It is true that branching is primarily responsible for the occurrence of numberless extinct and extant species. According to the catastrophe-HGT hypothesis, however, evolution also involves complex, reticulate relationships of genomes and species due to HGT. In genetic engineering recipient cells for artificial HGT are treated with chemicals, heat, or electricity, and this practice is congruous with the view that HGT can be accelerated in stressful environments caused by catastrophic events. Rampant HGT may increase the chances that foreign genes, when not degraded in recipient cells, take part in genomic evolution to give rise to new types of organisms. It is now generally accepted that the eukaryotes originated with 'endosymbiotic gene transfer' 2000–2200 million years ago when a global catastrophic event occurred—the appearance and accumulation of oxygen in the atmosphere due to the emergence of the cyanobacteria and oxygenic photosynthesis. The hypothesis supposes 'a massive intrusion of prokaryotes (eubacteria and archaeobacteria) into a host cell, which was not a prokaryote and which resulted in the formation of nucleus' (Hartman, 2002). HGT is of special interest in other aspects of evolution. It gives a new explanation for the ubiquitous occurrence of phenotypic

parallelism and also for the emergence of certain higher taxa that are supposed to have originated from more than one lineage (e.g., ‘pachyphyletic’ emergence of angiosperms: Krassilov, 2002). More important, ‘interactions between coevolving organisms appear in a new light not only as competitive, but also cooperative, including at least episodic sharing of a communal gene pool, thus enforcing the idea of community as an evolutionary unit’ (Krassilov, 2002).

Reticulate relationships also arise through introgressive hybridization. Application of molecular marker data to natural populations has detected numerous cases of introgression not only in plants but also in animals. The accumulation of data strongly suggests a wide migration of alleles, and challenges the current theories of species and speciation. ‘Species appear able to diverge at some loci while evolving in concert at others due to introgression’ and ‘are more correctly viewed as groups of populations at different adaptive peaks, which are primarily maintained by selection’ (Rieseberg and Welch, 2002). Endorsed by these observations, ‘the view of species genomes as mosaics of chromosomal blocks with different pedigrees, represents a substantial challenge to current methods of phylogenetic reconstruction, which generate trees that are exclusively dichotomous and branching’ (Rieseberg and Welch, 2002).

‘Recombinational speciation’ refers to the hybrid origin of a new species, either diploid (e.g., Ungerer et al., 1998) or allopolyploid (Ferguson and Sang, 2001), through a rapid process of reorganizing the chromosomes from the parental species into a stabilized homoploid state. This mode of speciation is still rare, with less than 20 documented examples in flowering plants and even fewer in animals. The rarity, however, may partly be due to ‘the difficulty of detecting and rigorously documenting homoploid hybrid species, particularly if the hybridization events are ancient’ (Rieseberg, 1997). In the study of animal evolution, no great importance has been attached to introgression and hybridization owing to far too few documented cases, but ‘misperception and negative attitudes have contributed to an apparent scarcity’ (Dowling and Secor, 1997). Contrary to popular belief, ‘hybridization may be a more plausible mechanism than population bottlenecks for generating the genetic or chromosomal reorganization proposed in founder effect or saltational models of speciation’ (Rieseberg, 1997).

6.3. Emergent reality and gradistic taxa

HGT, transposons, endosymbiotic gene transfer in the origin of the eukaryotic cell, rapid chromosomal reorganization in hybrid speciation—these heretical but now established phenomena reveal the dynamic nature of the genome in different but related aspects. The occurrence of introgression may not be uncommon even in animals. All these phenomena suggest diverse modes of evolution, which far exceed the framework of cladification (ES reconstruction at the species level on the supposition that species emerge through branching of vertical inheritance, followed by grouping species according to branching sequence). Another factor, which is essential and universal, also makes cladification disputable—development. ‘The dynamics of the developmental process interpose between genes and phenotype and provide the only proper logic for translating from one to the other’, thus giving rise to discrepancy between genes and morphology, and ‘without a logic of development, it is impossible to define the relation between forms’ (Ho, 1992). The point in dispute concerns the assertion ‘that the genealogical tree is quite distinct from the ontogenetic tree, and that a reconstructed cladogram is at best a confounded mixture of the two’ (Ho, 1992). Needless to say,

HGT, introgression, and hybridization make genealogy complicated and the relation between genealogy and ontogeny quite intricate. The dispute does not end with that. ‘The Cambrian pananimalia genome’ has been proposed on the supposition that ‘all those diverse animals of the early Cambrian period, some 550 million years ago, were endowed with nearly identical genomes, with differential usage of the same set of genes accounting for the extreme diversity of body forms’ (Ohno, 1996). According to this hypothesis, evolution involves a phase in which genealogy has little significance! Apparently an organism is something else than the sum of its genes. We might ‘imagine organismal lineages to have a sort of emergent reality—just as we think of ourselves as real and continuous over a lifetime, while knowing that we contain very few of the atoms with which we were born’ (Doolittle, 1999). Taxonomy, having to do with organisms, their populations, and their lineages, is not a matter of genes and their pedigrees, but is to be formulated, to use Doolittle’s words, in terms of emergent reality in organismal lineages.

In spite of the spread of cladification, ‘many taxa tend to be naturally gradistic rather than cladistic in nature’ (Brock, 2000). Organisms exist as adaptive entities or grades, which ‘are evolutionary phenomena, and gradistic classification is in no way “artificial”!’ (Brock, 2000). The gradistic view is that taxa should be stabilized (i.e., stasigenetic) units corresponding to grades, of which the adaptive traits are reflected in their phenotypes including morphological patterns. As a rough generalization, hierarchically correlated morphological characters among organisms lead to hierarchical taxa. The material basis of hierarchical taxa may reasonably be attributed to the hierarchical organization of gene expression, which should generate ‘grand developmental schemes’ (GDS’s) (Takagi, 2001) corresponding to taxa. Genes in a genome perform multiple functions, which are organized and integrated in the hierarchical structure of the organism. Not genes themselves, nor accumulated genes, but their organized functions essentially concern evolution. It is now evident that, besides branching of vertical inheritance, there are various means through which genetic substance is transmitted to evolving populations. Foreign genes introduced into a genome through HGT or introgression may or may not change the GDS emerging from the genome’s activity. Hybridization or a massive intrusion of alien genes, when successful, should give rise to a new or novel GDS. It does not matter whether the origins of individual genes comprising a stabilized genome and participating in its integrated activity are vertical or horizontal. It makes no difference whether such a genome is pure or mixed. (Is there any pureblooded genome at all? Above all, the eukaryotes originated with endosymbiotic gene transfer. Is there, then, any good reason to reject the idea that foreign genes or genomes played a large role in the diversification of eukaryotes?) In the light of new knowledge about gene transmission the premise that taxa should necessarily be clades or monophyletic groups (in the traditional usage of the terms) is far from the reality. Gradistic taxa, which are not primarily concerned with genealogy, can meet various ways of genomic reorganization and various modes of evolution. Taxa emerge and tend to persist. While genes widely migrate, resulting in their complicated, reticulate pedigrees, there may be formed dominant patterns of gene coalescence maintained by both internal and external factors.

Phylogeny, literally meaning ‘origin of race’, is to explain the origins of taxa. It is an inquiry into the past, not always resulting in a tolerable approach, whereas taxa, based on material before us, afford evidence necessary for carrying on the inquiry. Now that there are various routes of genomic evolution, the so-called phylogenetic systematics,

with the coach (phylogeny) set before the horses (taxa), cannot run any more. Of course, reciprocal illumination and adjustment between the recognition of taxa and the building of a phylogenetic hypothesis are not to be denied. But how is it possible to perform such an adjustment? Monophyly or shared ancestry is no longer the criterion of taxonomic reality. I wonder if there will be any consistent criterion to be applied to adjustment between taxa and phylogeny. Anyway, phylogeny follows taxa, not vice versa, but whenever there is found any contradiction between them, we should re-examine both.

6.4. Evolutionary sectors: significance of reconstruction

In concluding my comments I would like to refer to the significance of ES reconstruction. A great number of cladograms (reconstructed sectors of species based on derivative morphological characters) have been published and declared to be genealogical trees. HGT is supposed to have been a very powerful process in evolution episodically, but it is not recognizable in routine taxonomic work. Introgression has traditionally been studied in flowering plants by the use of morphological hybrid index. It is now documented by molecular data, and, according to a recent view, it occurs in animals as frequently as in plants. Actually, however, introgression has generally been neglected in the study of animal species. Homoploid hybrid species may hardly be detected as such particularly when the hybridization events are ancient, and we are ignorant about their frequency. Considering all these circumstances, the supposed branching of species in those cladograms should, in reality, not all be restricted to branching of vertical inheritance. It is certainly possible that a cladogram or a reconstructed sector of species approaches their real genealogical relationships at least to some extent, because there must be a phase of evolution that branching of vertical inheritance dominates. This may be expected especially when a sector is composed of closely related species, which must be similar in their 'logic of development'. But it is also possible that a reconstructed sector includes species that emerged through other means of genomic reorganization. Such a reconstruction is partly or largely false as a genealogical tree, but it may still be significant in reflecting the relationships of all the component species in some aspect other than genealogy. Probably it traces the changes in development responsible for the varying phenotypes of the species. It follows that a reconstructed sector of species may be interpreted as a type of phenogram irrespective of genealogy. Taxa of higher categories have also been employed as units for reconstructing a sector, which may be justified so far as branching of vertical inheritance dominated their evolution. From the viewpoint of gradistics, however, the reconstruction may be significant irrespective of genealogy, because traditional higher taxa are principally delimited as 'anagenetic grades' (Huxley, 1958). It is a 'gradogram', which is to illustrate gradal evolution. (Species should also be grades, forming the base of a gradal hierarchy, but, as pointed out by Brock, 2000, species proliferation does not necessarily show a clear correlation with anagenetic change.) Sectors are also reconstructed of phenotypic or molecular characters. Chronoclines and morphoclines are reconstructed sectors of morphological characters. Reconstructed sectors of genes, enzymes, or other macromolecules have been called 'molecular phylogenies' by authors, but they do not axiomatically represent phylogenetic hypotheses. They may serve to detect HGT, introgression, and hybridization as well as parallelism, convergence, and recurrence in the compositions of the molecules. Sector reconstruction is not wholly the same as phylogeny, but it contributes to the latter. We may say following Olendzenski et al.

(2002) that with any reconstructed sector we should be thoughtful to understand what the reconstruction is really telling us and should keep an open mind regarding possible alternative interpretations.

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Table 1. Major divisions of the Diaspididae based on the combination of pygidial appendages.

	Diaspidinae		Aspidiotinae
Level III	[Tt+D+Sg] Diaspidini Chionaspina Fioriniina Diaspidina, etc.	[Tt+D+Sg] Lepidosaphidini Lepidosaphidina Coccoxylina Howardiina	[T+Pg] Aspidiotini Odonaspini Parlatoriini Smilacicolini
Level II	[Tt+P+Sg] Diaspidini Kuwanaspina	[Tt+P+Pg+Sg] Lepidosaphidini Mempelaspidina	[T+P] Leucaspini
Level I	[P+Sg] Diaspidini Protodiaspidina		[P] Thysanaspini
Level 0	[Sg] Ulucoccinae		

[T] trullae; [Tt] bi- or multilobulate trullae; [D] pore prominences; [P] pectinae; [Pg] glandiferous pectinae; [Sg] gland spines. The Diaspidinae are primarily provided with gland spines on the pygidial margin. In the Aspidiotinae there are no pygidial gland spines, but glandiferous pectinae are often modified into spine-like processes. The trullae are principally bilobulate in the lateral pairs (and potentially also in the median pair) in the Diaspidinae and often multilobulate in the Kuwanaspina, whereas unilobed in the Aspidiotinae.

Table 2. Types of perivulvar or abdominal disc pores in the major divisions of the Diaspididae, superimposed on the frame of Table 1.

	Diaspidinae	Aspidiotinae
Level III		Septal processes sulcate
Level II	Septal processes capitate	Septal processes spatulate
Level I		Septa ridged, not produced
Level 0	Simply septate	

Based on Takagi (1990) and other works. No species of the Smilacicolini has been examined for the structure of perivulvar disc pores. In the course of the present study the perivulvar disc pores of *Thysanaspis litseae* (with ridged septa), *Mongrovaspis quadrispinosa* (with spatulate septal processes), *Ligaspis maculata*, and *L. pala* (both species with sulcate septal processes) were SEM-observed. *Mitulaspis malayana* (Diaspidinae: Lepidosaphidini) is exceptional in having simple-septate disc pores.

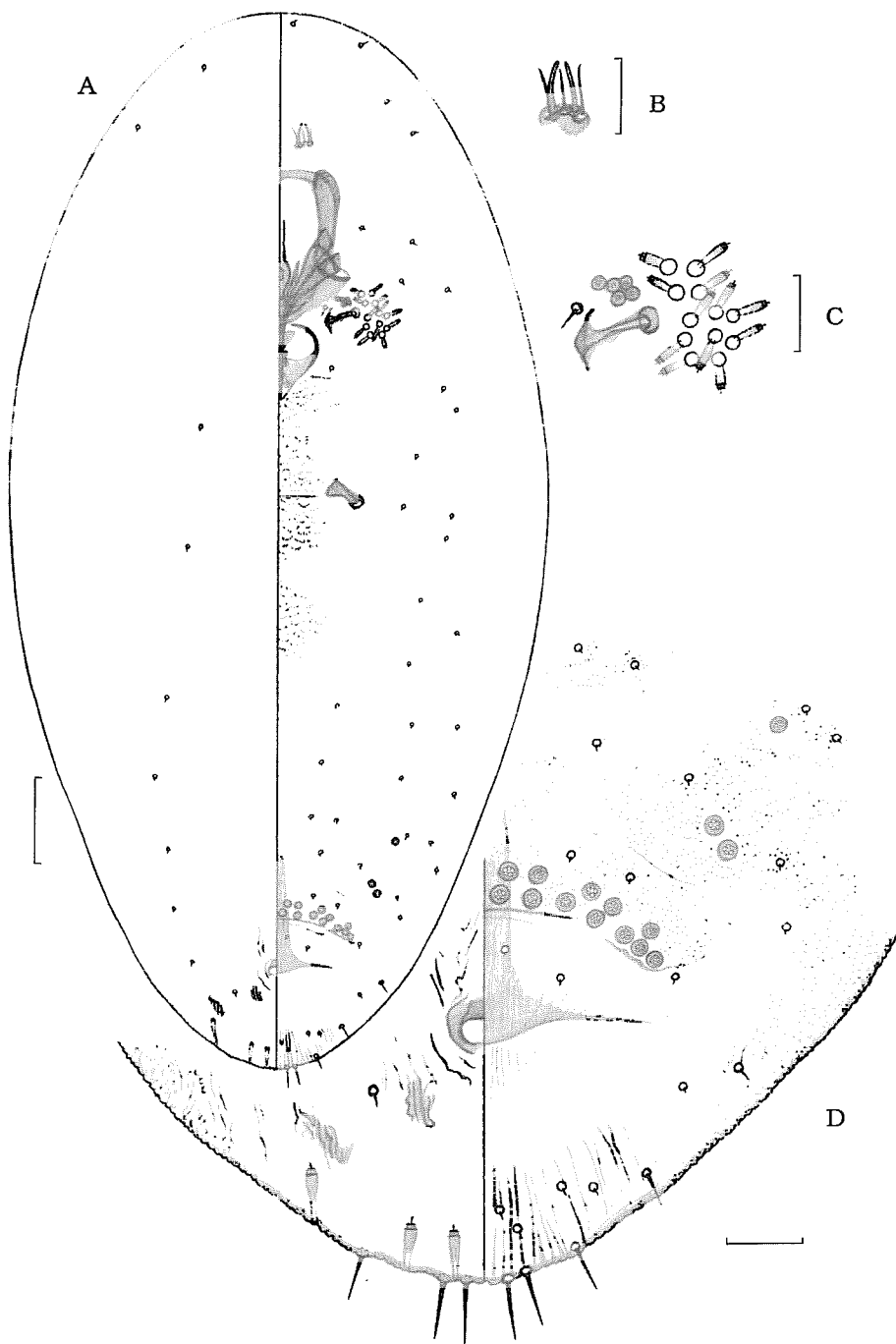


Fig. 1. *Thysanaspis litseae*, adult female. B: antenna; C: anterior spiracle with paraspiracular ducts; D: pygidium. Scales: A, 50 μ m; B–D, 10 μ m. Sata-Misaki, Kagosima-ken, Japan, on *Litsea japonica*.

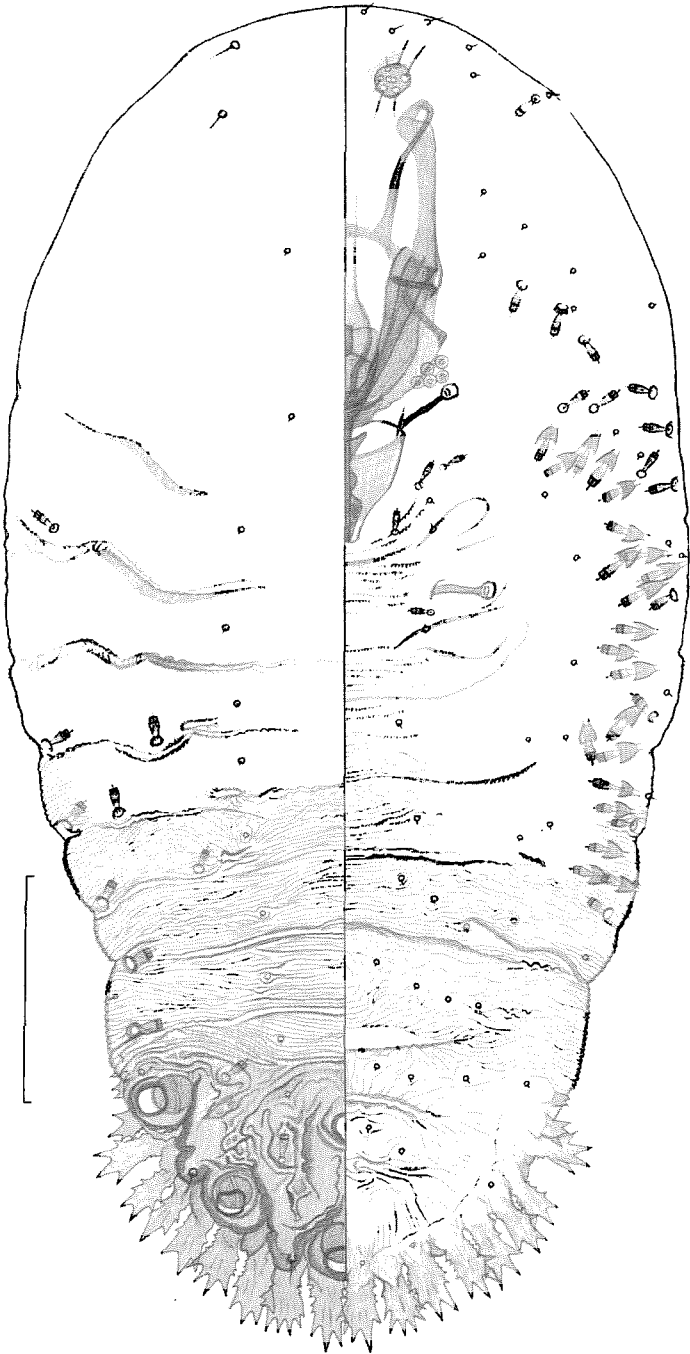


Fig. 2. *Thysanaspis litseae*, second instar female. Scale: 50 μ m. San, Tokuno-Sima, Japan, on *Litsea japonica*.



Fig. 3. *Thysanaspis litseae*, second instar male. B: pectinae. Scales: A, 50 μ m; B, 10 μ m. San, Tokuno-Sima, Japan, on *Litsea japonica*.



Fig. 4. *Thysanaspis litseae*, first instar nymph. B: antenna; C: anterior spiracle; D: posterior tibia and tarsus; E: pygidial margin. Scales: A, 50µm; B-E, 10µm. San, Tokuno-Sima, Japan, on *Litsea japonica*.



Fig. 5. *Lopholeucaspis japonica*, second instar male. B: antenna; C: anterior spiracle; D: prepygidial glanduliferous processes; E: pygidial margin, ventral surface. Scales: A, 50 μ m; B-E, 10 μ m. Toyama, Toyama-ken, Japan, on *Enkianthus perulatus*.



Fig. 6. *Lopholeucaspis japonica*, first instar nymph. B: antenna; C: anterior spiracle; D: posterior tibia and tarsus; E: pygidial margin. Scales: A, 50 μ m; B-E, 10 μ m. Toyama, Toyama-ken, Japan, on *Enkianthus perulatus*.



Fig. 7. *Mongrovaspis quadrispinosa*, adult female. B: antenna; C: anterior spiracle with paraspiracular ducts; D: pygidium. Scales: A, 50 μ m; B–D, 10 μ m. 94PL-68.

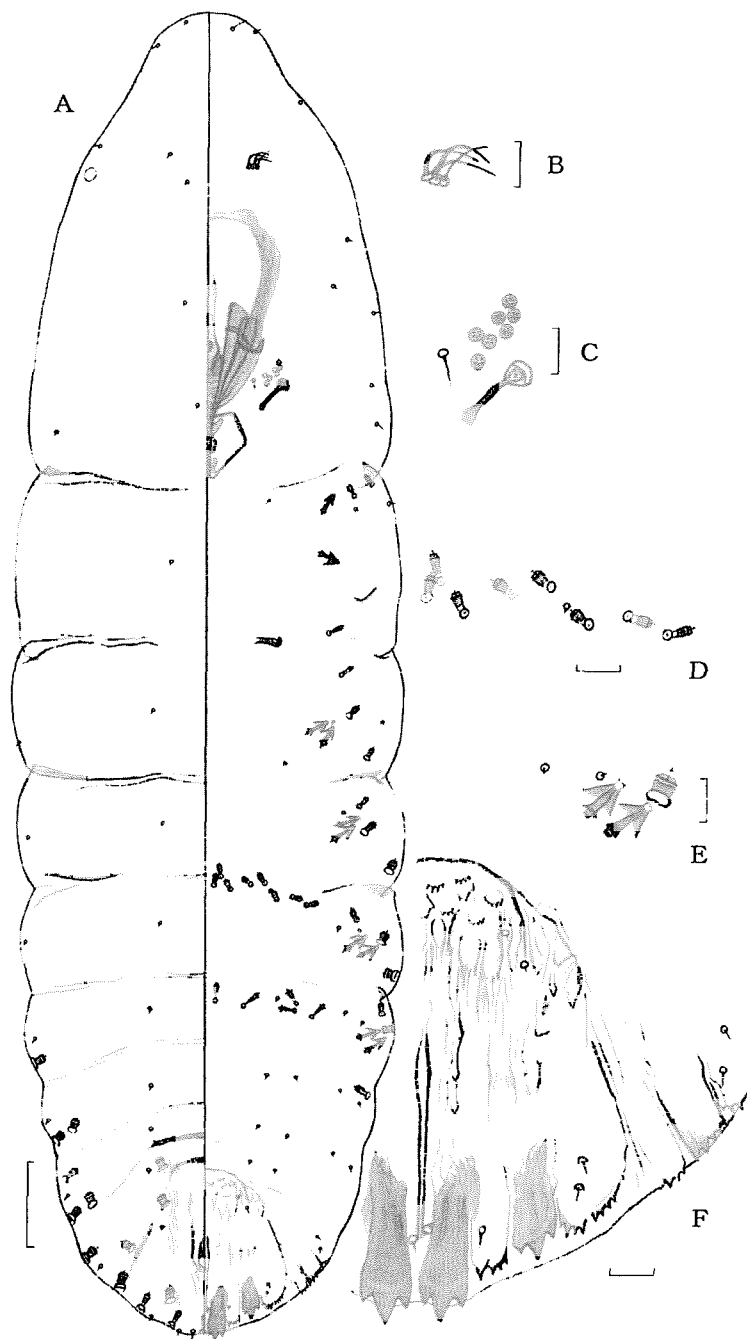


Fig. 8. *Mongrovaspis quadrispinosa*, second instar female. B: antenna; C: anterior spiracle; D: row of ducts across ventral surface of abd II; E: gland tubercles on abd II; F: pygidium, ventral surface. Scales: A, 50 μ m; B-F, 10 μ m. 94PL-68.



Fig. 9. *Mongrovaspis quadrispinosa*, second instar male. B: part of head, ventral surface; C: anterior spiracle; D: pygidium, ventral surface. Scales: A, 50 μ m; B-D, 10 μ m. 94PL-68.



Fig. 10. *Mongrovaspis quadrispinosa*, first instar nymph. Scale: 50 μ m. 94PL-68.

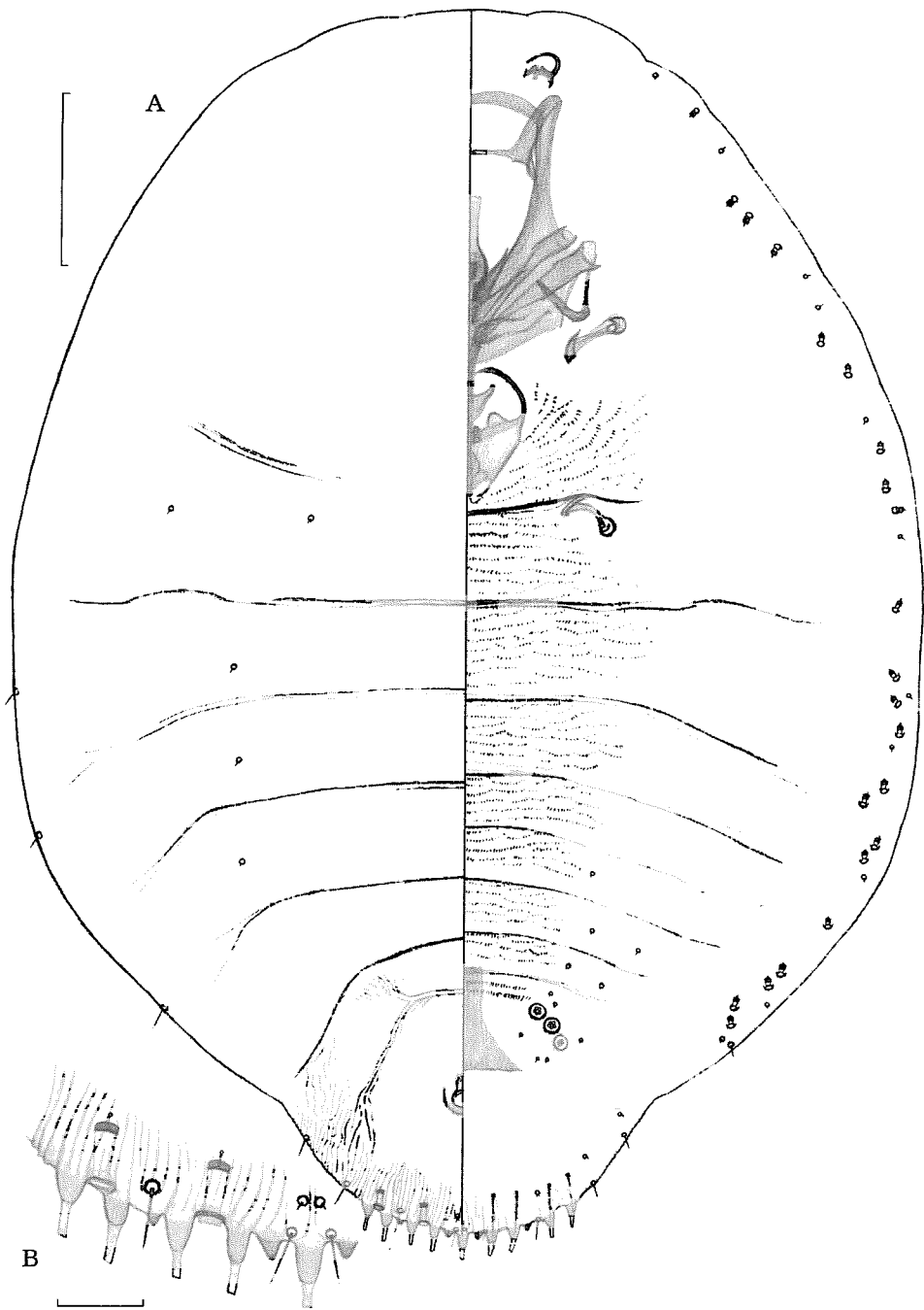


Fig. 11. *Ligaspis maculata*, adult female. B: pygidial margin, dorsal surface. Scales: A, 50 μ m; B, 10 μ m. 94PL-10.

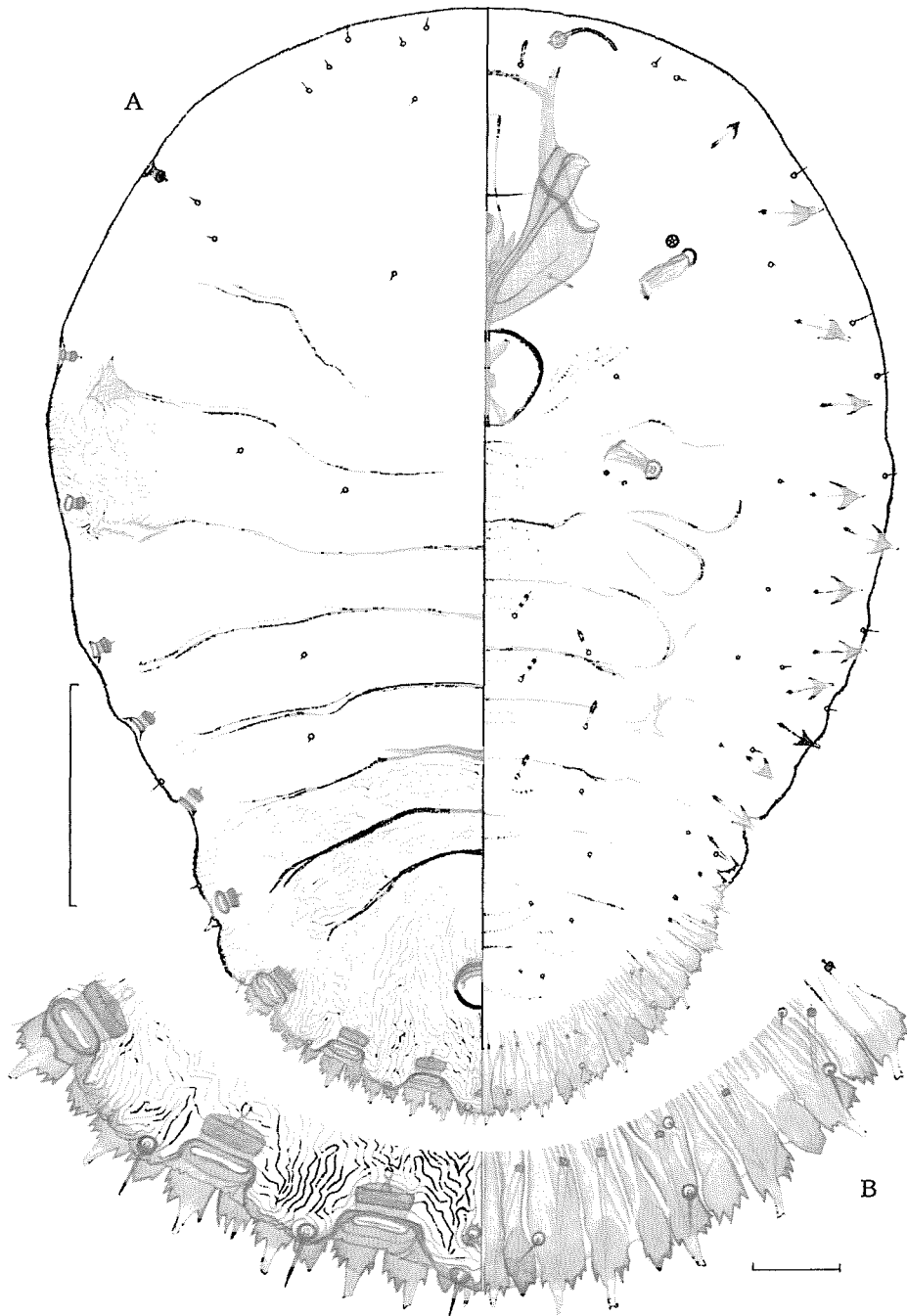


Fig. 12. *Ligaspis maculata*, second instar female. B: pygidial margin. Scales: A, 50 μ m; B, 10 μ m. 94PL-10.

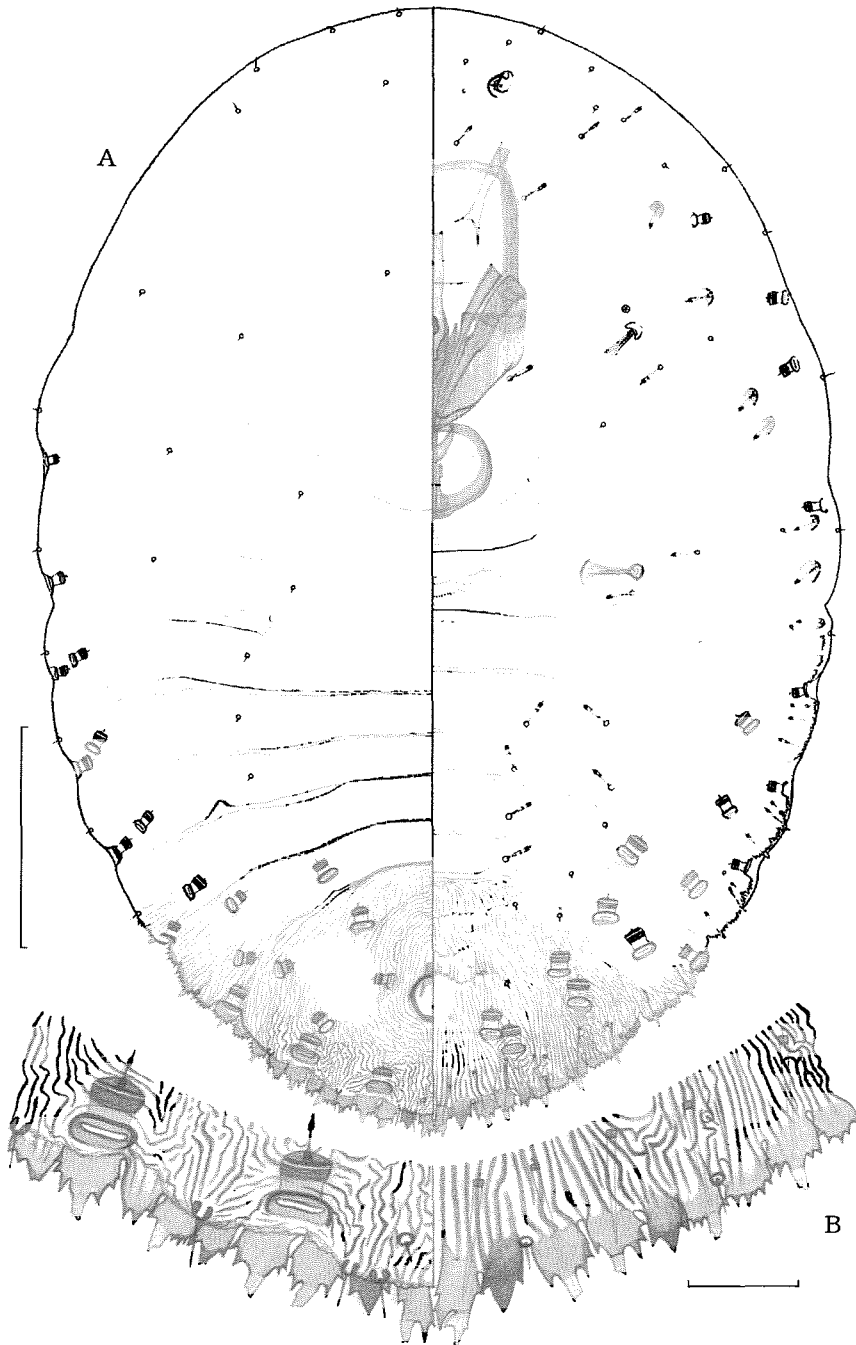


Fig. 13. *Ligaspis maculata*, second instar male. B: pygidial margin. Scales: A, 50 μ m; B, 10 μ m.
94PL-10.

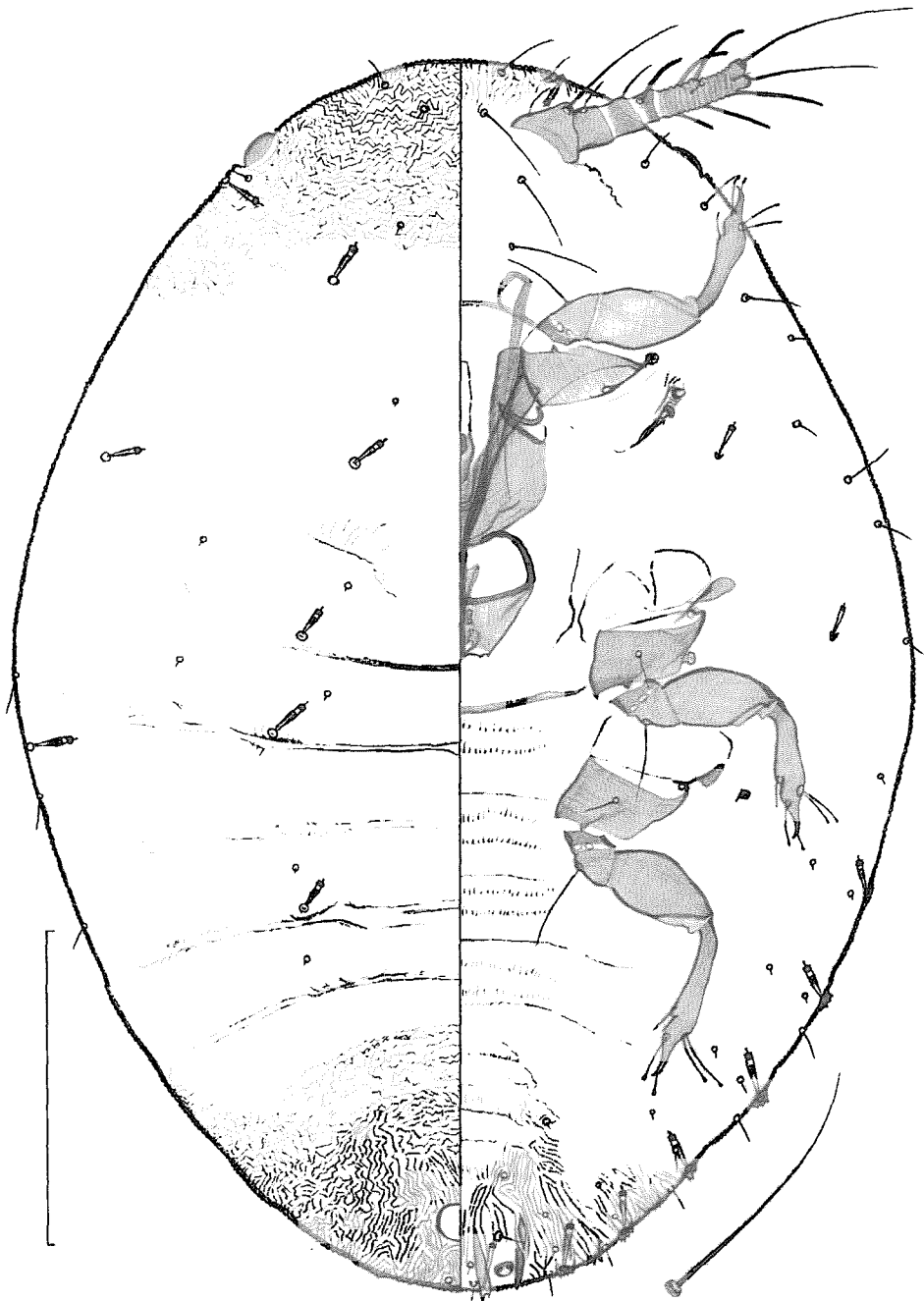


Fig. 14. *Ligaspis maculata*, first instar female. Scale: 50 μ m. 94PL-10. (Male with a submedian dorsal seta on abd I and a campaniform sensillum on each tibiotarsus.)

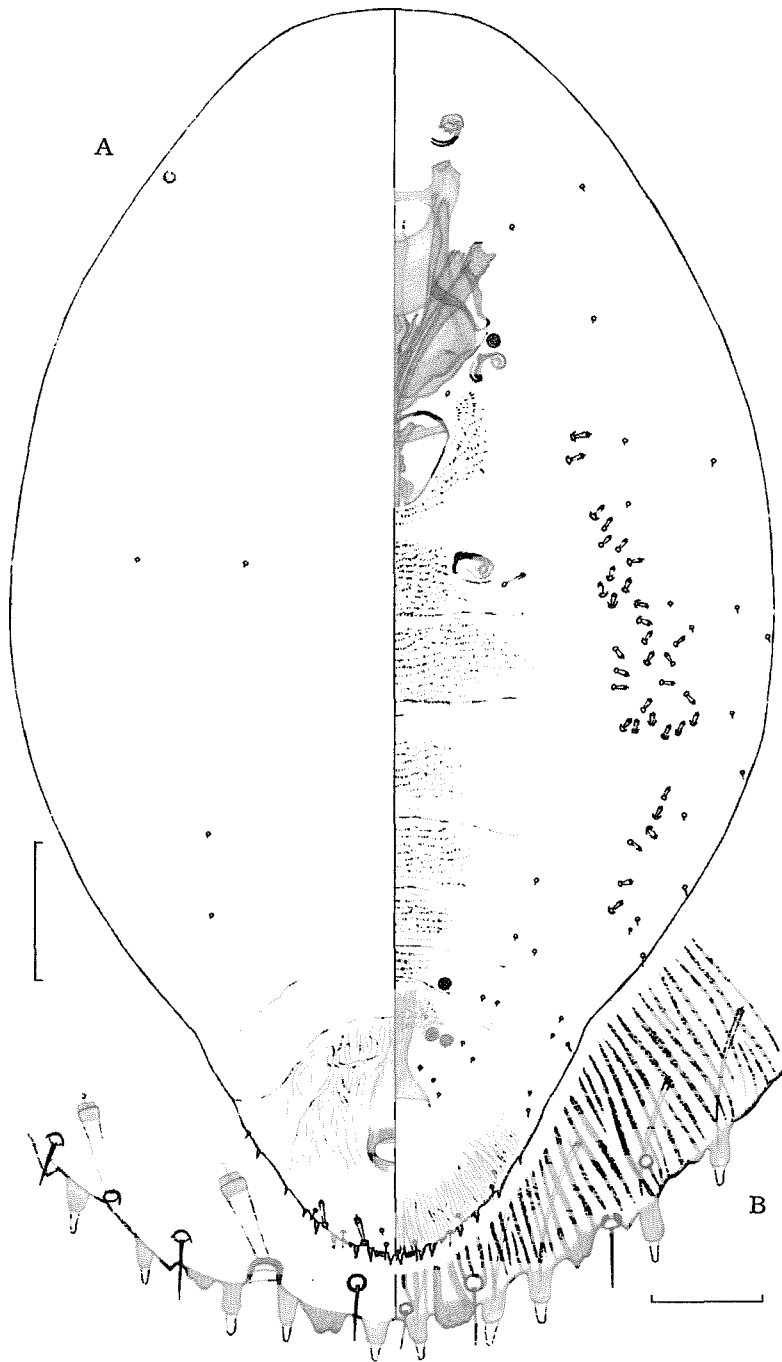


Fig. 15. *Ligaspis pala*, adult female. B: pygidial margin. Scales: A, 50 μ m; B, 10 μ m.



Fig. 16. *Ligaspis pala*, second instar male. B: pygidial margin. Scales: A, 50 μ m; B, 10 μ m.

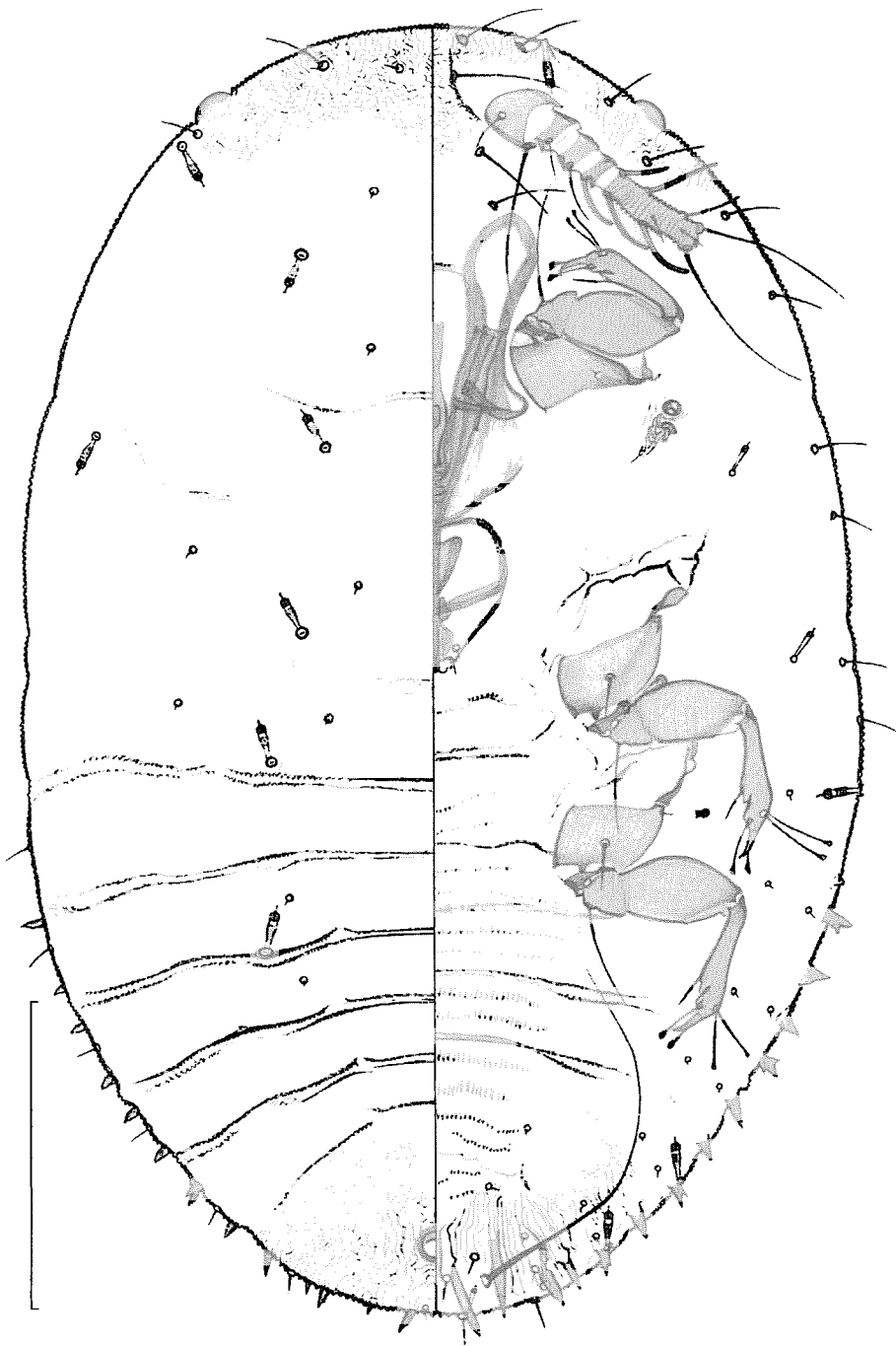


Fig. 17. *Ligaspis pala*, first instar female. Scale: 50 μ m. (Male with a submedian dorsal seta on abd I and a campaniform sensillum on each tibiotarsus.)



Fig. 18. *Smilacicola apicalis*, second instar male. B: antennae; C: rudiments of fore leg; D: pygidial margin. Scales: A, 50 μ m; B–D, 10 μ m.

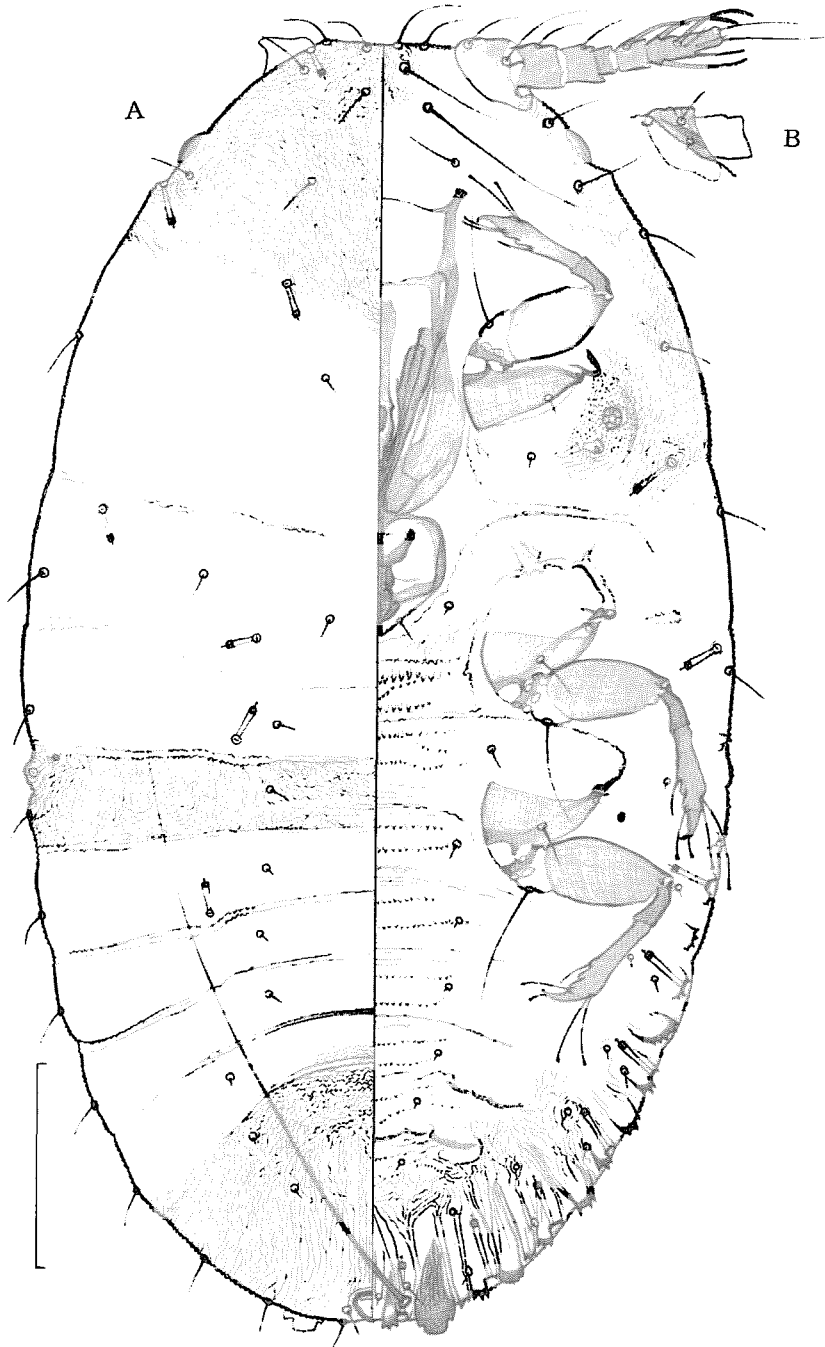


Fig. 19. *Smilacicola crenatus*, first instar nymph. B: basal antennal segment, dorsal surface. Scale: 50 μ m.



Fig. 20. *Odonaspis arcusnotata*, second instar male. B: pygidial margin. Scales: A, 50 μ m; B, 10 μ m. Hi-no-Misaki, Wakayama-ken, Japan, on *Pleioblastus* sp.



Fig. 21. *Odonaspis arcusnotata*, first instar male. B: antenna, dorsal surface; C: pygidial margin; D: hind tibia and tarsus. E: hind tibia and tarsus of first instar female. Scales: A, 50 μ m; B–E, 10 μ m. Hi-no-Misaki, Wakayama-ken, Japan, on *Pleioblastus* sp. (Female lacking submedian dorsal seta on abd I.)



Fig. 22. *Mongrovaspis quadrispinosa*, female exuvial casts. Top: first and second instar casts, dorsal view; middle: pygidium of second instar cast, dorsal surface; bottom: pygidium of second instar cast, ventral surface. 94PL-68.

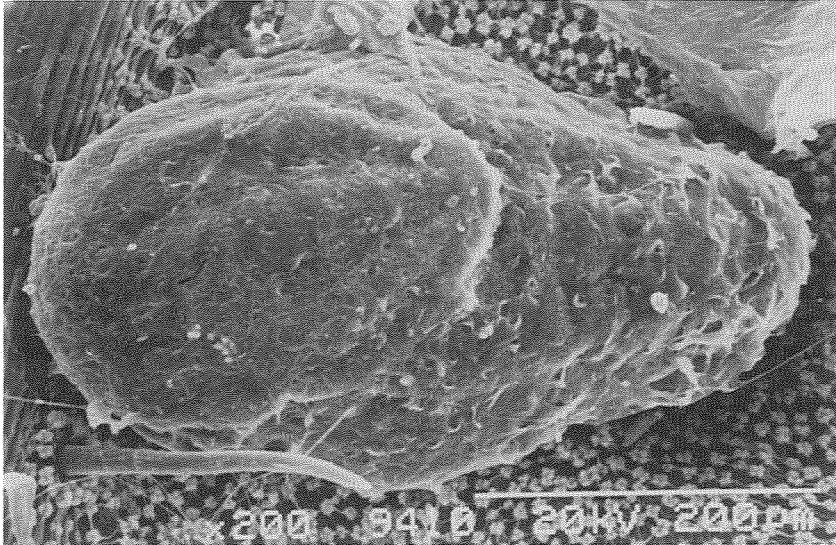


Fig. 23. *Ligaspis maculata*, female exuvial casts. 94PL-10.

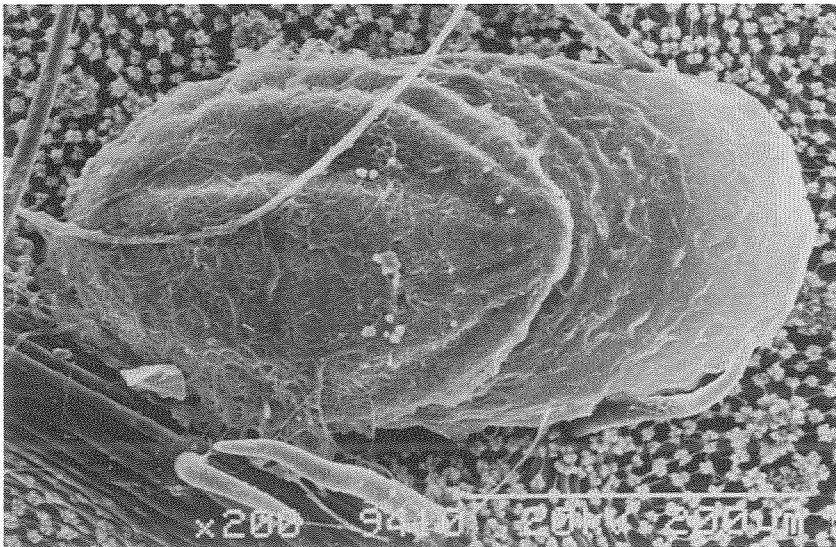


Fig. 24. *Ligaspis maculata*, male test (not yet fully formed). 94PL-10.



Fig. 25. *Ligaspis pala*, female exuvial casts (upper) and male test (lower).

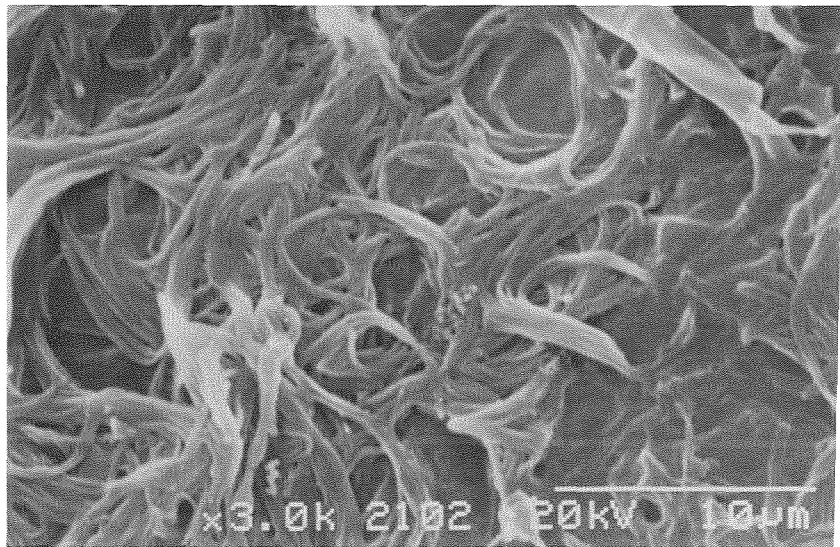


Fig. 26. *Ligaspis pala*, male test. Wax filaments.