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**FURTHER FORMS FOR THE RUGASPIDIOTINI-PROBLEM  
(HOMOPTERA : COCCOIDEA : DIASPIDIDAE)**

By SADAŌ TAKAGI, TANG FANG-TEH, BÜLENT YAŞAR  
and TAKUMASA KONDO

*Abstract*

TAKAGI, S., TANG F.-t., YAŞAR, B. and KONDO, T. 1997. Further forms for the Rugaspidiotini-Problem (Homoptera : Coccoidea: Diaspididae). *Ins. matsum. n. s.* 53 : 81-116, 26 figs.

Four rugaspidiotine-patterned genera are dealt with in 4 parts. Part I. *Adiscodiaspis tamaricicola* Malenotti, *Prodiaspis tamaricicola* Young and *Circodiaspis sinensis* Tang, all associated with tamarisks, belong to the same genus *Prodiaspis* Young [= *Circodiaspis* Tang, new synonymy], and are rearranged to *Prodiaspis sinensis* [= *P. tamaricicola* Young = *C. sinensis*, new synonymy] and *Prodiaspis tamaricicola* (Malenotti) [transferred from *Adiscodiaspis*, new combination]. The 1st instar larvae of these 2 species are remarkably different in the occurrence of ducts, but otherwise closely similar to each other, and appear to be related to the Diaspidini but not definitely. Their female tests show no regular running pattern of wax filaments, suggesting that the females make no regular movements in forming the test. — Part II. *Mangaspis bangalorensis* Takagi and Kondo, gen. et sp. nov., occurring on the twigs of *Mangifera indica*, is described from India. It is similar to *Rugaspidiotinus* and *Smilacicola* in the adult female, but distinct in the 1st instar, in which it shows characters common to the Parlatoriini-Odonaspidiini group. It usually occurs beneath leaf buds, and, thus, it may afford another example of the emergence of the rugaspidiotine pattern in a habitat where the adult female is impeded in making regular movements during the formation of the test. — Part III. *Pygalataspis miscanthi*, occurring on *Miscanthus* and inhabiting the inner surface of the leaf-sheath, has been disputable as to its taxonomic position. It agrees with the Diaspidini in some characters of the 1st instar, and is assumed to have originated from an advanced form of Diaspidini with lobes, which are replaced by pectinae in *P. miscanthi*. The test surface shows no evidence of horizontal movements of the adult female, and the disappearance of sclerotized lobes is probably associated with the suppression of horizontal movements in the cryptic habitat. — Part IV. *Roureaspis dungunensis* Takagi, gen. et sp. nov., is described from Malaya as occurring on *Rourea rugosa*. It is similar to odonaspidiines rather than to rugaspidiotines in the adult female. In some characters of the 1st instar it is related to the Diaspidini. It occurs on the midvein of the leaflet among dense erect hairs, which apparently constitute an obstacle to the horizontal movements of the adult female in the formation of the test. Thus it is analogous to rugaspidiotines in its supposed evolution in the confined space of the habitat. In Concluding remarks it is stated that rugaspidiotine forms have arisen from diverse groups of diaspidids and that atavism can be involved in their emergence. In Appendix the method adopted in mounting specimens of the 1st instar is described.

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\* Systematic and Ecological Surveys on Some Plant-parasitic Microarthropods in South-east Asia, Scientific Report.

FURTHER FORMS FOR THE RUGASPIDIOTINI-PROBLEM I:  
THE GENUS PRODIASPIS  
(HOMOPTERA : COCCOIDEA : DIASPIDIDAE)

By SADAŌ TAKAGI, TANG FANG-TEH and BÜLENT YAŞAR

Three forms of diaspidids associated with tamarisks, *Adiscodiaspis tamaricicola*, *Prodiaspis tamaricicola* and *Circodiaspis sinensis*, appear very close to one another in the adult female, while they have been treated not unanimously as to their taxonomic relationships. *Adiscodiaspis tamaricicola* was referred to the subtribe Rugaspidiotina, the tribe Odonaspidini, by Balachowsky (1953), who recognized it as a species of *Rugaspidiotus*. It was also placed in the Rugaspidiotina by Borchsenius (1966), who, however, removed the subtribe to the Diaspidini. It was referred to the Diaspidini by Danzig (1993) on the basis of the 1st instar, but its relationship to other Diaspidini remained unknown. *Prodiaspis tamaricicola* was described by Young in Young and Wang (1984) as a form of the subfamily Xanthophthalminae. *Circodiaspis sinensis* was described by Tang (1986) as belonging to the Rugaspidiotini. The genus *Circodiaspis*, which was erected for *Adiscodiaspis tamaricicola* and *Circodiaspis sinensis*, was not adopted by Danzig (1993), who referred both these species to *Adiscodiaspis*, which is nomenclatorially based on the *Erica*-associated *A. ericicola*.

According to the views we adopt here, these forms should be rearranged both generically and specifically. First of all, the material of *Prodiaspis tamaricicola* studied by Young and Wang and part of Tang's material of *Circodiaspis sinensis* came from the same area — Ningxia, China. Although no material of *P. tamaricicola* has been available for our study, we are strongly inclined to believe that *P. tamaricicola* and *C. sinensis* represent the same species. Secondly, we agree with Danzig (1993) in the view that this species is congeneric with *Adiscodiaspis tamaricicola*, but, thirdly, we do not adopt the view that they belong to *Adiscodiaspis*. All this requires nomenclatorial changes as follows :

Genus *Prodiaspis* Young, 1984

Name-bearing species [type-species] : *Prodiaspis sinensis* (Tang, 1986) [= *Prodiaspis tamaricicola* Young, 1984].

*Circodiaspis* Tang, 1986 [Name-bearing species: *Adiscodiaspis tamaricicola* Malenotti, 1916 (designated by the name '*Adiscodiaspis tamaricicola*' by Tang)], new synonymy.

*Prodiaspis sinensis* (Tang, 1986), new combination

*Prodiaspis tamaricicola* Young, 1984 [preoccupied by *Prodiaspis tamaricicola* (Malenotti, 1916), which is transferred from *Adiscodiaspis*], new synonymy.

*Circodiaspis sinensis* Tang, 1986.

*Prodiaspis tamaricicola* (Malenotti, 1916), new combination

*Adiscodiaspis tamaricicola* Malenotti, 1916.

*Rugaspidiotus tamaricicola* : Balachowsky, 1953.

*Circodiaspis tamaricicola* : Tang, 1986 [*sic*].

The revised *Prodiaspis* is assignable to the Rugaspidiotini, the Diaspidini, or the Xanthophthalminae according to the authors mentioned above. Thus it is a genus to be examined in connection with the 'Rugaspidiotini-problem' posed by Howell (1992) and Takagi (1995). So far, the examination of the 1st instar has been indispensable for the problem. Danzig (1993) examined the 1st instar of *Adiscodiaspis tamaricicola*, but our material does not agree with her observation.

#### DESCRIPTIONS OF THE FIRST INSTAR LARVAE

*Prodiaspis sinensis* (Fig. I-1)

Material. Collected in Ningxia, China, on *Myricaria dahurica* [Tamaricaceae], July 15, 1982 [part of the type-material of *Circodiaspis sinensis*; material no.: Tang 3301].

Body, especially dorsal surface, densely with wrinkles running predominantly longitudinally. Three somewhat enlarged dorsal ducts on each side of thorax submedially; 10 small ducts on each side of body, opening on margin or ventrally near margin; no other ducts. Anterior spiracle with 1 disc pore, which is 3-locular. Submedian dorsal setae on all of 1st-7th abdominal segments; no submedian ventral setae on abdominal segments anterior to 7th segment. Anus surrounded by a thick sclerotized ring except posteriorly. No trace of marginal appendages. Antennae 6-segmented; 3rd segment about twice as long as the 4th; 6th segment nearly as long as the 3rd, not annulate; 2 setae on basal segment and 1 on the 2nd slender, 1 on the 5th and 4 on the 6th fleshy, 6th segment also with 1 slender, long apical seta; 1 invaginated minute seta on apex of 6th segment. Legs with a distinct tibiotarsal articulation; tarsus a little longer than tibia, with a well-developed seta ventrally; claws elongate; tarsal and unguis digitules little knobbed apically. A small, sclerotized patch of derm is found laterally to the hind coxa, irregular in outline.

*Prodiaspis tamaricicola* (Fig. I-2)

Material. Collected at Ankara, Turkey, on *Tamarix* sp. [Tamaricaceae], Oct. 1, 1995.

As compared with *P. sinensis* the body is roughly wrinkled. A small duct is found laterally to the fore coxa near the body margin; there are no other ducts dorsally and ventrally. Otherwise very similar to *P. sinensis*.

The 1st instar of *Adiscodiaspis tamaricicola* studied by Danzig (1993, Fig. 10) has, on each side of the body, 3 submedian dorsal ducts on the thorax and 10 marginal ducts on the thorax and abdomen, and thus agrees with *P. sinensis* but not with our *P. tamaricicola*. The identification of the Ankara material follows Yaşar (1995). *P. tamaricicola* thus identified and *P. sinensis* are surprisingly similar in the adult females, which may be distinguished by trifling differences in the antennae (Figs. I-3 and -4) and other features. Their 1st instar larvae are remarkably different in the occurrence of ducts, and suggest that the forms under study are distinct species, apart from the question whether the Ankara form is rightly identified or not. All this seems to require a careful study of both the adult female and the larval stages on the basis of material collected extensively in Eurasia and North Africa.

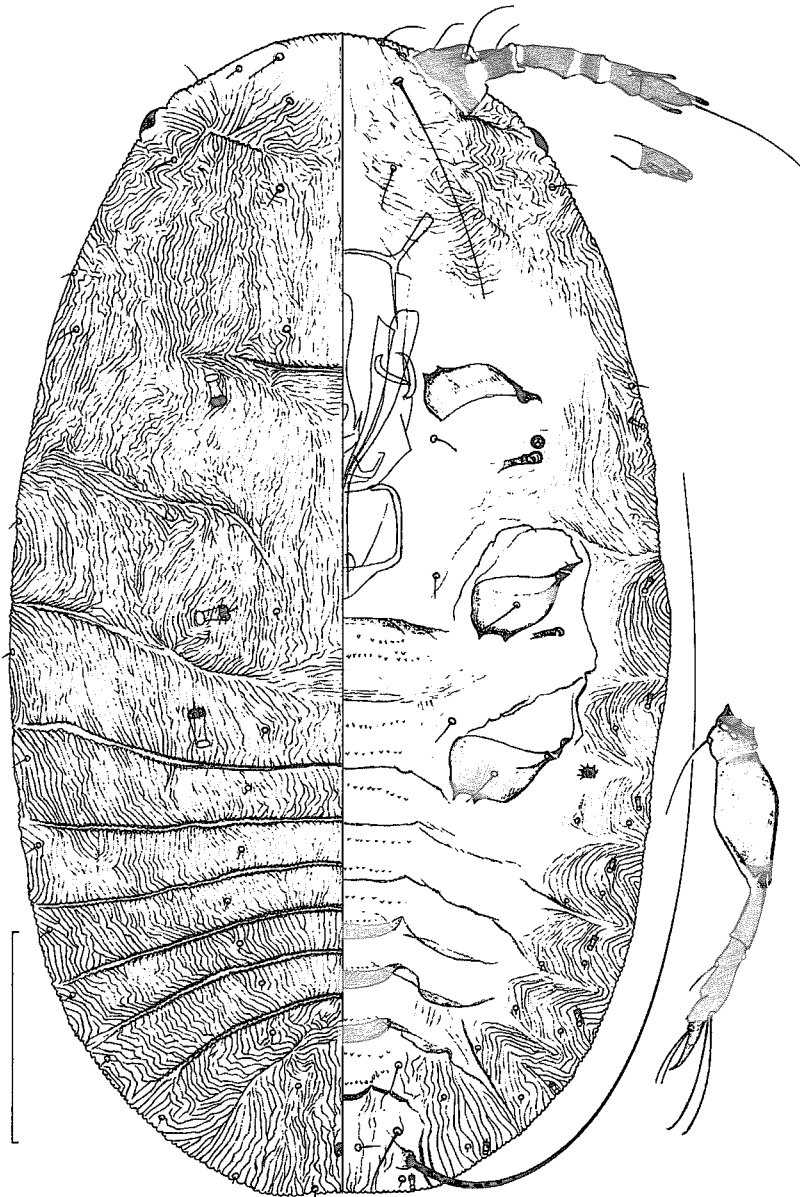


Fig. I-1. *Prodiaspis sinensis*, 1st instar. Scale: 50  $\mu$ m. Figure inserted below the antenna: terminal segment of antenna in dorsal view.

#### TAXONOMIC POSITION

Our recent knowledge of the 1st instar of the family Diaspididae owes much to Howell, Howell and Tippins, and a few others. Accurate observations are still limited. The 1st instar may be expected to have phylogenetically stable characters

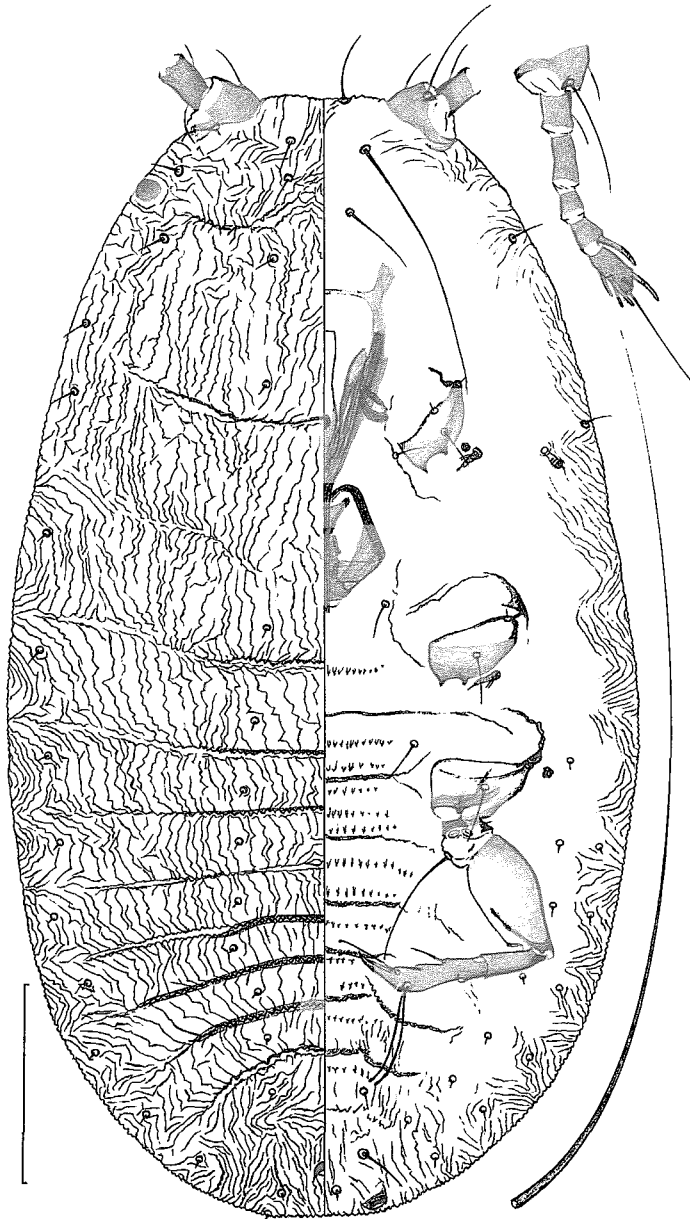


Fig. 1-2. *Prodiaspis tamaricicola*, 1st instar. Scale: 50  $\mu$ m.

relative to the succeeding stages. However, cases are known where characters in the 1st instar are noticeably changed between species which are closely related to each other in all other respects. It would be misleading, therefore, to form a general pattern of 1st instar characters for a genus, a subtribe, a tribe or a subfamily on the basis of a limited number of species.

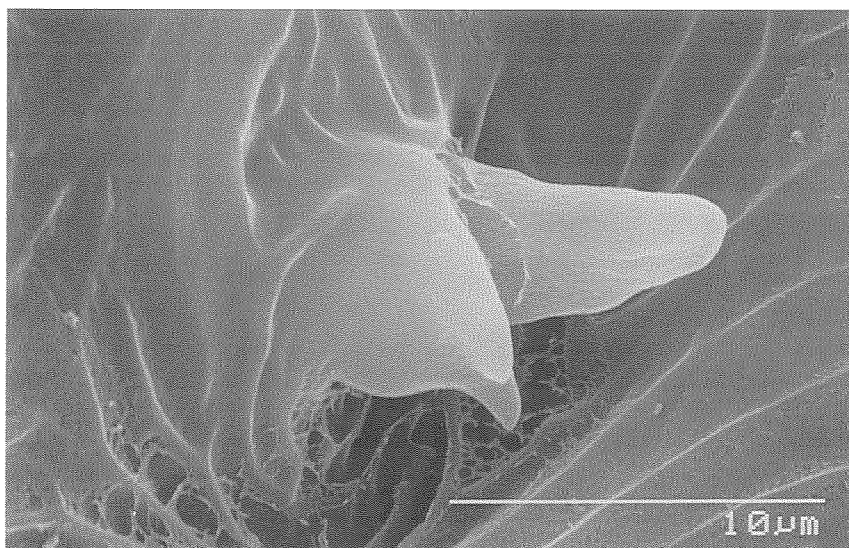


Fig. I-3. *Prodiaspis sinensis*, adult female: antenna.

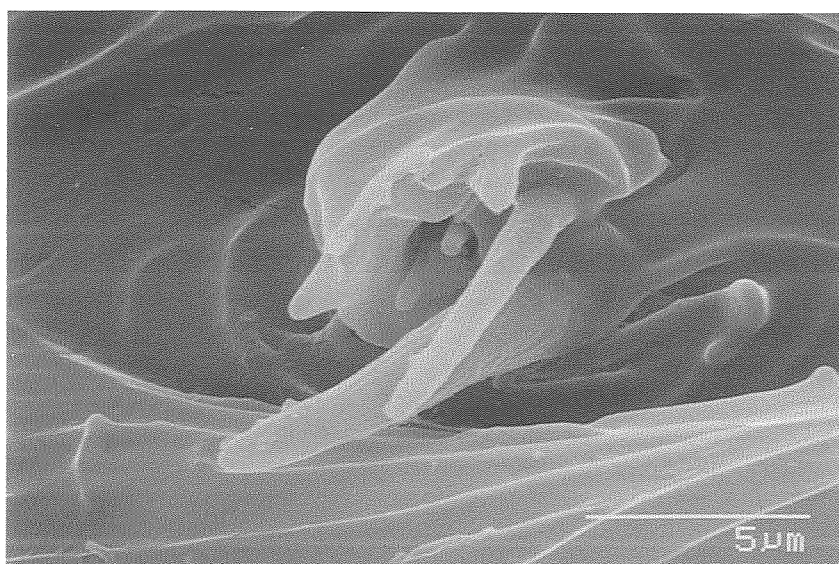


Fig. I-4. *Prodiaspis tamaricicola*, adult female: antenna.

The 1st instar larvae of *Prodiaspis sinensis* and *P. tamaricicola* afford another example of the instability of characters, remarkably differing in the presence or absence of submedian dorsal ducts on the thorax and marginal ducts on the thorax and abdomen. In spite of these differences they well agree in the other characters, and we have no doubt that they are closely related.

No trace of pygidial appendages has been found in *P. sinensis* and *P. tamar-*

*icicola* in the 1st instar as well as in the adult female. If this state is primary, *Prodiaspis* should be a primitive genus of the family, assignable to Level O in the scheme presented by Takagi (1995). Young and Wang (1984) supposed their *Prodiaspis tamaricicola* (= *P. sinensis*) to be very primitive and referable to the Xanthophthalminae, because 'the posterior abdominal segments of the adult female are not fused to form a pygidium' (translated from the Chinese text).

However, no other characters support the view that *Prodiaspis* is very primitive. Except for the segmentation there are no particular characters common to *Prodiaspis* and *Xanthophthalma* (this genus was studied by Stickney, 1934a) in both the adult female and the 1st instar, either. The macroducts of the adult female belong to the 2-barred type, and are not of the geminate-pore type as in certain forms that are supposed to be very primitive diaspidids. The antennae of the adult females of both the species (Figs. I-3 and -4) are not multisetose as in some primitive forms.

As in certain forms of the 'Rugaspidiotini' discussed by Takagi (1995) the absence of pygidial appendages in *Prodiaspis* may be secondary and the genus may have some relationship to an ordinary group of the family. It is certain that *Prodiaspis* has nothing to do with the Aspidiotinae so far as based on the combination of some characters of the 1st instar — 1) the terminal segment of the antenna is not particularly elongate and not annulate, with 1 apical seta; 2) submedian dorsal ducts are present on the thorax (in *P. sinensis*) but not on the abdomen; 3) submedian setae are present dorsally on all of the 1st to 7th abdominal segments, but absent ventrally on the abdominal segments anterior to the 7th. In these characters it agrees with some well-studied forms of the Diaspidini. However, it noticeably differs from the latter in having a well-developed seta on the tarsus. This character has been found in the Aspidiotinae and the Lepidosaphedini. So far as known, it is rare in the Diaspidini.

The putative ancestral form with pygidial appendages may have been a species of the Diaspidini. But, when emphasis is laid on the well-developed tarsal seta of the 1st instar, the possibility that it was a lepidosaphedine cannot be excluded. In this connection the 2nd instar male is worthy of study, because in the Diaspidini, in general, sexual dimorphism is remarkable in the 2nd instar, in which some odd types of the male are known.

Ghuri (1962) studied the adult males of some Diaspididae and discussed their relationships. According to his analysis, *P. tamaricicola* (*Rugaspidiotus tamaricicola* in his study) is close to the Diaspidini and the Lepidosaphedini (Diaspidina + Chionaspida and Lepidosaphedina, all under the Diaspidini, in his study), but is referable to neither of them. Davis and Boratyński (1979) made a quantitative comparison of adult male diaspidids belonging to 24 species. According to them, *P. tamaricicola* (*Adiscodiaspis tamaricicola* in their study) forms the nucleus of a separate group, with remote affinities to the Lepidosaphedini, Diaspidini and Parlatoriini in that order.

After all, *Prodiaspis* has nothing to do with *Rugaspidiotus arizonicus*, *Xanthophthalma* and any well-studied forms of the Aspidiotinae; it is referable to the Diaspidinae (Diaspidini + Lepidosaphedini), but in this subfamily its taxonomic position is still not exactly decided.

The 1st instar of *Adiscodiaspis ericicola* has not been examined in connection

with the present study. So far as their adult females are concerned, however, *Adiscodiaspis* and *Prodiaspis* appear distinct, *Adiscodiaspis ericicola* differing from the *Prodiaspis* species, above all, in having a well-formed pygidium (based on the redescription given by Balachowsky, 1953: *Rugaspidiotus ericicola*). Compared with *Adiscodiaspis*, the *Prodiaspis* adult female is characterized as follows: 1) inter-segmental furrows of the abdomen are distinct as posteriorly as between the 6th and 7th segments; 2) the macroducts of the abdomen are divided into a marginal-submarginal and a submedian zone; 3) the anus is surrounded by a thick sclerotized ring, which is often incomplete posteriorly and, thus, shaped like a horseshoe.

#### OBSERVATIONS ON THE FEMALE TESTS

Female tests of *P. sinensis* formed on branches have been examined. They are nearly circular, with the exuvial casts situated on or near the margin, and, in scanning electron microscopy, show many ribs on the dorsal surface (Fig. I-5), which run in arcs subtending the exuvial casts. In gross appearance they are similar to the tests of certain advanced diaspidids that make horizontal movements when forming the test. The tests of *P. sinensis*, however, show no regular pattern of wax filaments, which run disorderly between the ribs (Fig. I-6). It does not seem, therefore, that the females make regular horizontal movements in forming the test.

Female tests of *P. tamaricicola* collected at Van, Turkey, on slender twigs of *Tamarix tetrandra* have been examined. They are elongate globular, with the exuvial casts at the anterior end, and broader than the thickness of the twigs (Figs. I-7, -8, -9). The surface shows many transverse wrinkles (rather than well-shaped ribs) but no distinct running pattern of wax filaments between transverse wrinkles (Figs. I-10 and -11). Obviously the test is formed around the fixed body of the

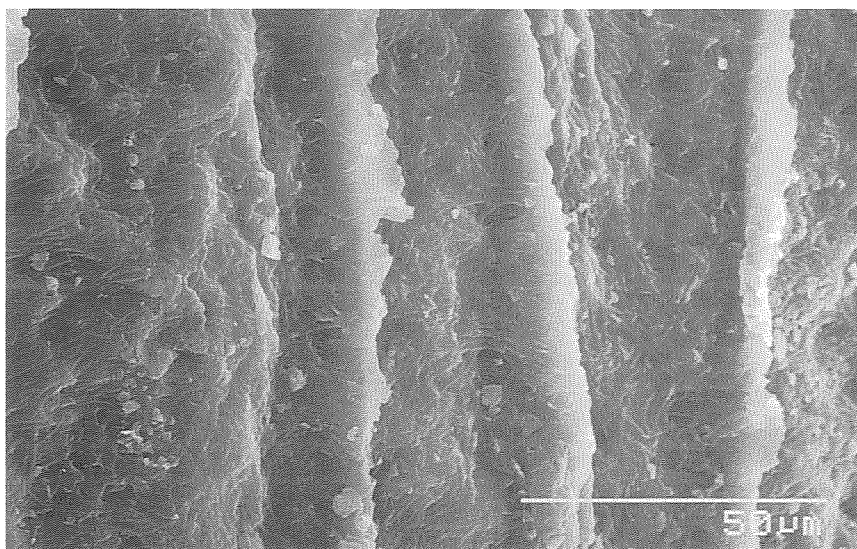


Fig. I-5. *Prodiaspis sinensis*, female test: part of dorsal surface (left side: anterior direction).

insect, the parts secreted earlier being successively pushed up by the growing insect body, which becomes not only larger but also globular. At full growth the adult female is thickly sclerotized on the anterior half of the body (the cephalothorax and the base of the abdomen), into which the membranous segments of the abdomen are, along with the deposition of offspring, retracted to form a space behind to accommodate the deposited offspring (Fig. I-12).

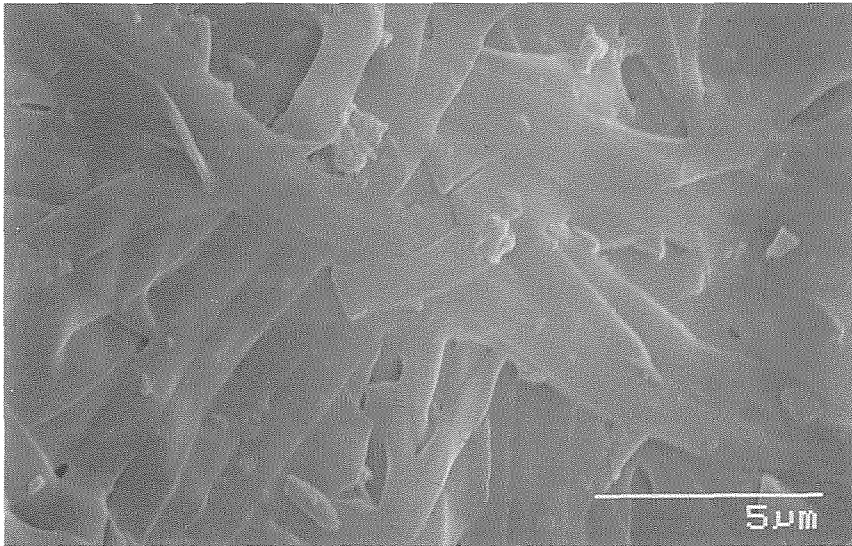


Fig. I-6. Part of Fig. I-5, showing wax filaments.

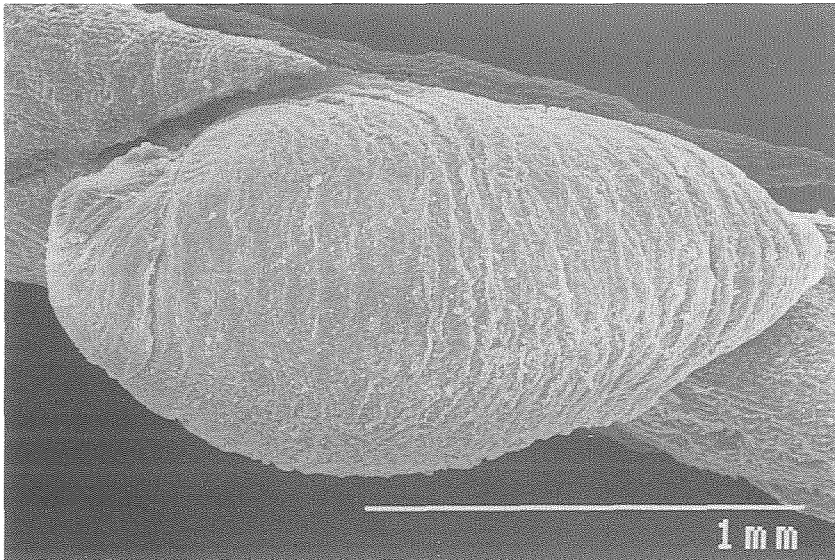


Fig. I-7. *Prodiaspis tamaricicola*, female test : dorsal view.

Takagi (1995) argues that the rugaspidiotine pattern of characters will evolve in habitats where the adult female is impeded in making horizontal (rotative or oscillatory) movements during the formation of the test. Tamarisks, with minute scalelike leaves, produce clusters of slender green twigs, which perform the functions of leaves. In the case of the material from Van the adult females apparently find

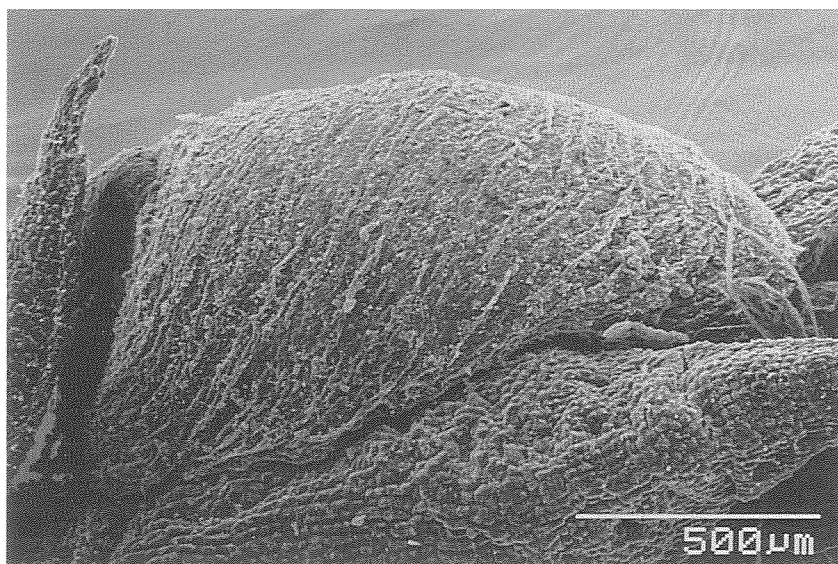


Fig. I-8. *Prodiaspis tamaricicola*, female test : lateral view.

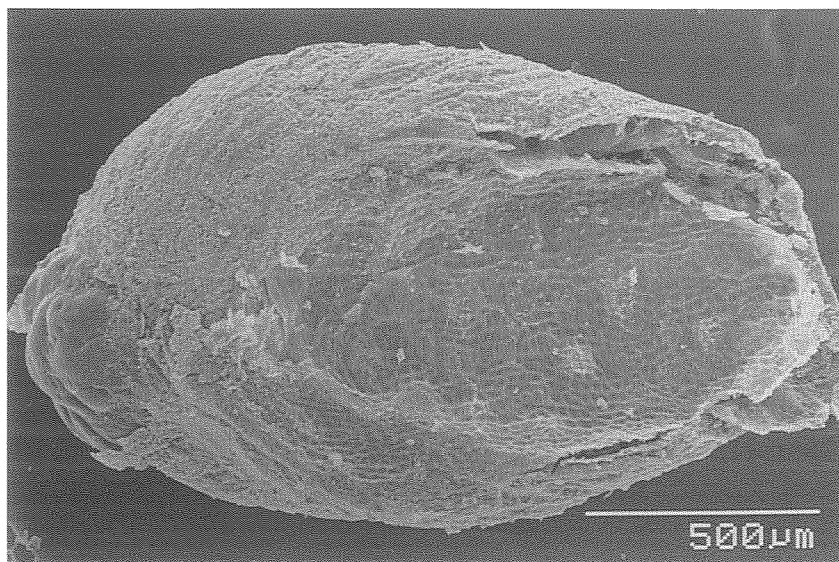


Fig. I-9. *Prodiaspis tamaricicola*, female test : ventral view.

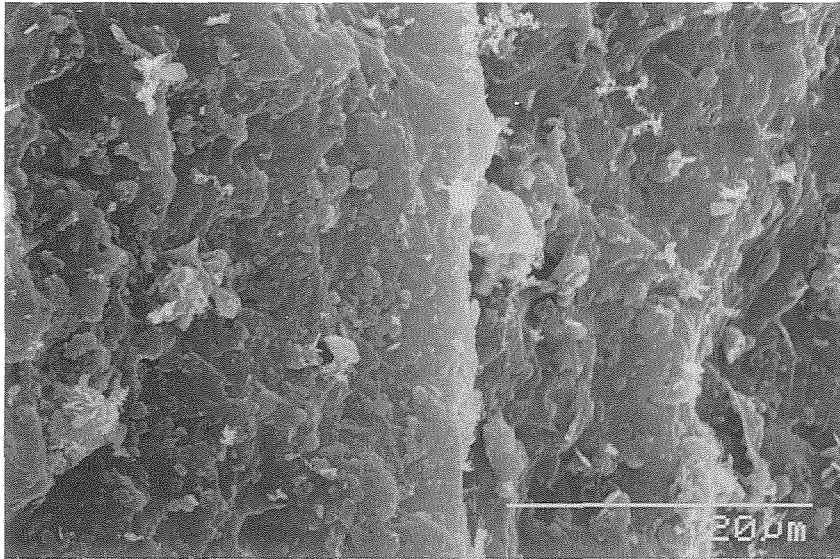


Fig. I-10. *Prodiaspis tamaricicola*, female test : part of dorsal surface (left side : anterior direction).

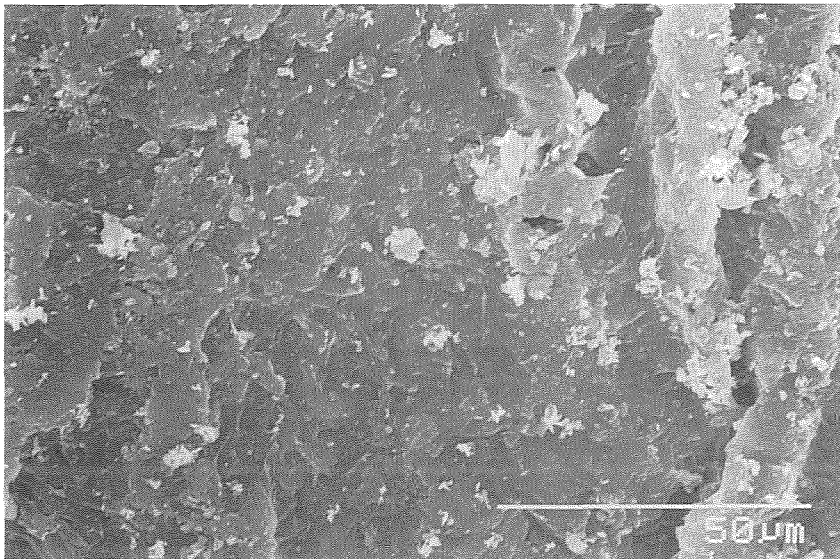


Fig. I-11. Same as Fig. I-10, another part.

no space for making horizontal movements on the slender twigs. But *Prodiaspis* females are not restricted to slender twigs, thus contradicting Takagi's supposition. The point here may be whether or not the green twig is the primary habitat of the *Prodiaspis* species.

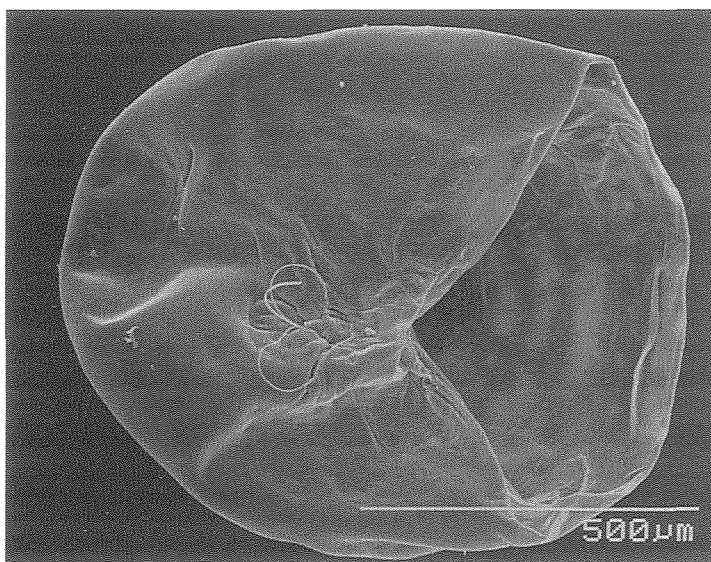


Fig. I-12. *Prodiaspis tamaricicola*, adult female : eventual state of body in ventral view.

FURTHER FORMS FOR THE RUGASPIDIOTINI-PROBLEM II :  
A NEW SCALE INSECT ASSOCIATED WITH MANGO-TREE IN INDIA  
(HOMOPTERA : COCCOIDEA : DIASPIDIDAE)

By SADAO TAKAGI and TAKUMASA KONDO

In 1991 to 1995 the junior author made surveys on coccoids occurring on mango-trees in southern Japan, Thailand, India, Indonesia, and Colombia. Samples from Cambodia and Nepal were also examined. Eighty species of coccoids belonging to 52 genera in 6 families have been recognized in his study, and 21 of them, including some unidentified ones, are new to our knowledge of the pest fauna of mango-trees.

In this paper, one of the unidentified forms is described from India as a new species representing a new genus. Apparently even in India, where coccoid pests have been studied for a century, the fauna associated with *Mangifera indica*, the fruit *par excellence* of India, is not yet fully known. The new diaspidid is also interesting in that the adult female represents the rugaspidotine pattern of characters. According to Takagi (1995), this pattern can be manifested by unrelated diaspidids living in some habitats where the regular, horizontal movements of the adult female are restricted or impeded by a confined space during the formation of the test. The new form may adduce another case in support of his supposition.

The junior author expresses his sincere thanks to all persons who helped him in his surveys. The material of the new species was collected with the cooperation of Dr P.L. Tandon, Indian Institute of Horticultural Research, Bangalore.

*Mangaspis bangalorensis* Takagi and Kondo, sp. nov.

Material. Collected at Bangalore, Karnataka, India, on *Mangifera indica*, June 26, 1995. Occurring on twigs, usually beneath leaf buds, where males and females are crowded together. Adult females also occur under the epidermis, being entirely hidden inside the twig, with the posterior end of the body directed outwards, and are detectable by the presence of a very small white powdery patch on the twig surface (thus suggesting the formation of a pit gall). Adult females (about 20 specimens), 2nd instar females (about 10), 2nd instar males (7), and 1st instar larvae (including embryonic ones) have been examined. Name-bearing specimen [holotype]: adult female, deposited in the collection of the Laboratory of Systematic Entomology, Hokkaidô University.

Adult female (Fig. II-1). Body obovoid, growing elongate and inversely pyriform; at full maturity, the cephalothorax is swollen and, together with the base of the abdomen, strongly sclerotized, and a broad apical region of the pygidium is also heavily sclerotized. Segmentation rather indistinct, but it seems that the pygidium is composed of the 5th and succeeding abdominal segments. Pygidial margin nearly smooth, with slight undulations and indentations, but with no trace of marginal appendages. A number of ducts strewn on both surfaces, all small, but those occurring on the posterior area of the pygidium with the orifice surrounded by a thick sclerotized rim. Anus situated in the bottom of the pygidium, surrounded by a thick sclerotized ring. Antennae situated between the anteriormost arms of the frame of mouth-parts, set rather close together; each antenna is a small sclerotized tubercle, with a single seta, but is rather complicated in structure, having several ducts incorporated. Spiracular disc pores 5-locular; 7-23 associated with anterior spiracle, and 7-29 with the posterior.

Second instar female. Similar to adult female, being obovoid, with small ducts on both surfaces, and with no trace of marginal appendages on pygidium. Anus with a conspicuous ring as in adult female, but situated about the centre (not in the bottom) of the pygidium. Anterior spiracle with 2-8 disc pores and the posterior with 4-10.

Second instar male (Fig. II-2). Body oblong or ovoid. Pygidium well sclerotized, marginally with low prominences but with no distinct appendages. Ducts rather abundant on both surfaces, moderate in size and with a thickened rim around the orifice on pygidium, becoming smaller on anterior segments. Slender ducts occurring at intervals along the margin of the abdomen. Anus situated about the centre of the pygidium, surrounded by a thick sclerotized ring. Antennae situated between frontal margin and mouth-parts, separated from each other by a space as broad as mouth-parts; each antenna is a sclerotized tubercle with spinous projections and bears a single seta. Anterior spiracle with 1-4 disc pores and the posterior with 0-3.

First instar larva (Fig. II-3). Six submedian dorsal ducts on each side, occurring on head, pro-, meso- and metathorax, and 2nd and 3rd abdominal segments; 1 duct occurring just posteriorly to eye and another dorsal duct in anterolateral corner of mesothorax; 3 ventral ducts laterally to coxae. No enlarged dorsal ducts on head. Pygidium with 2 pairs of enlarged ducts marginally, and just laterally to the caudal setae with a pair of sclerotized, apically dentate processes; caudal setae short. Abdomen ventrally with submedian setae, but dorsally without submedian

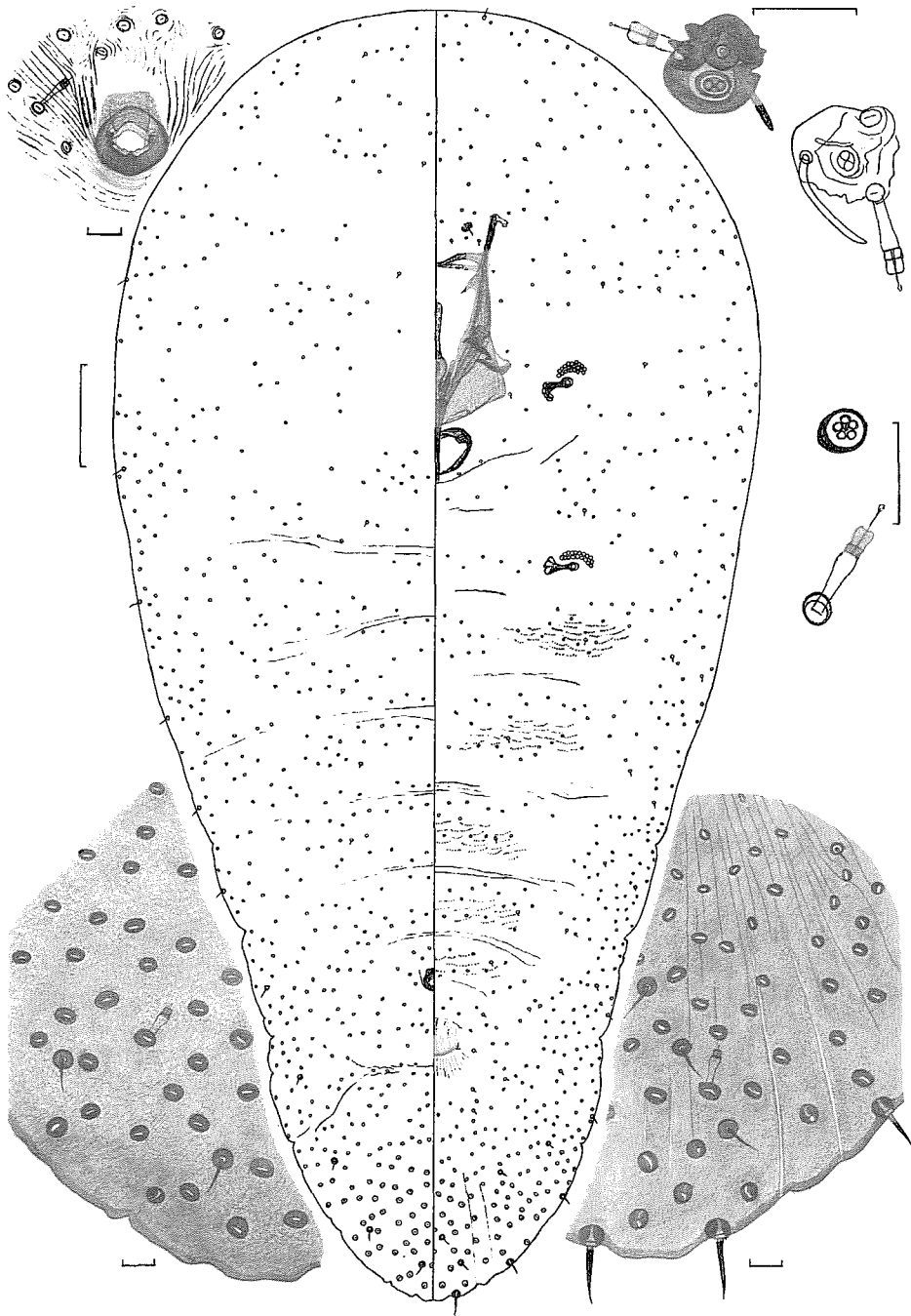


Fig. II-1. *Mangaspis bangalorensis*, adult female. Parts around body : anus (left upper) ; part of pygidium in dorsal view (left lower) ; antennae (right upper ; the lower figure was drawn from the antenna on the opposite side of the body) ; spiracular disc pore and duct (right middle) ; part of pygidium in ventral view (right lower). Scales : 100  $\mu\text{m}$  for body, 10  $\mu\text{m}$  for parts.



Fig. II-2. *Mangaspis bangalorensis*, 2nd instar male. Scale : 100  $\mu$ m.

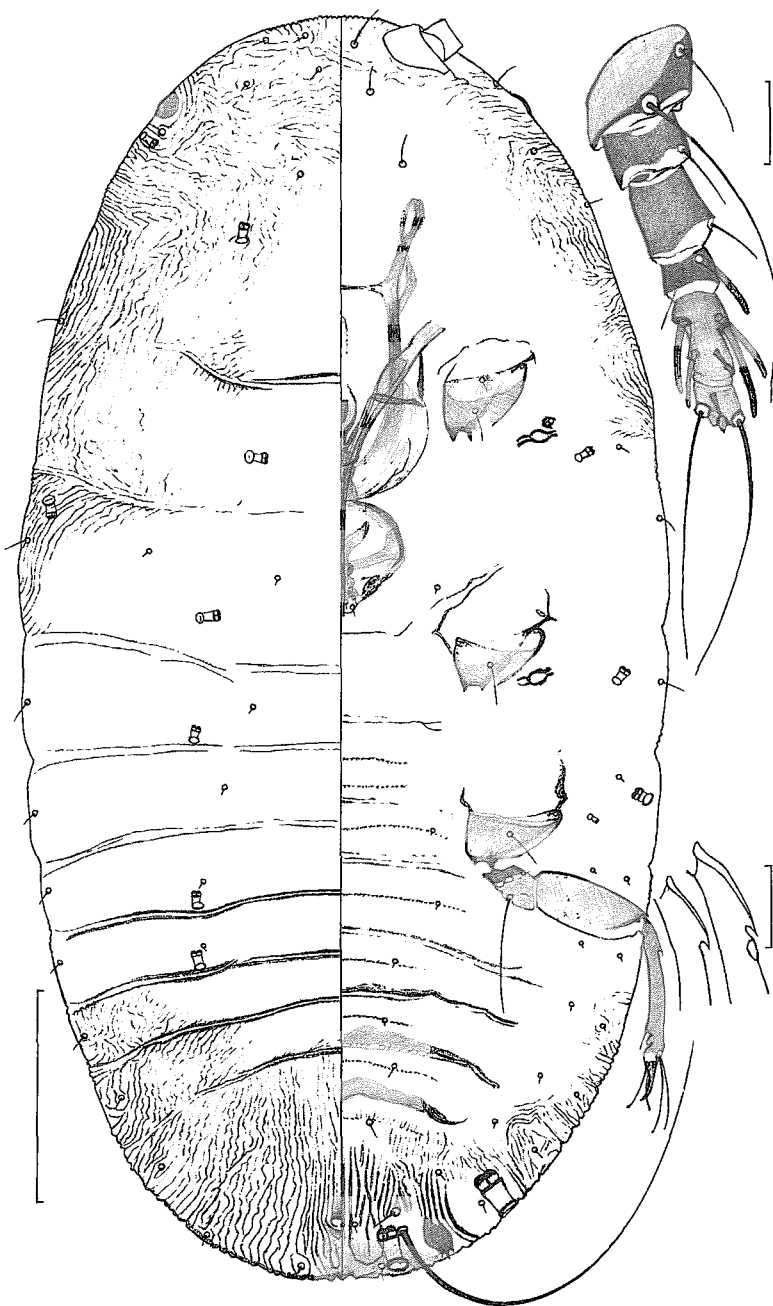


Fig. II-3. *Mangaspiis bangalorensis*, 1st instar. Scale: 50  $\mu$ m for body; 10  $\mu$ m for parts.

setae on 4th and succeeding segments. Anterior spiracle with 1 disc pore, which appears to be 3-locular. Antennae 5-segmented; 5th segment about as long as the 3rd and 4th combined, not annulate; 3rd segment about twice as long as the 4th; 1 long apical seta, 1 long subapical seta, 4 fleshy setae, and 2 invaginated minute setae on 5th segment; 1 fleshy and 1 slender seta on the 4th; 1 slender seta on the 2nd and 3rd each; 2 slender setae on basal segment, one of them is very long, attaining the apex of the antenna. Tibia and tarsus completely fused together, the supposed tibia and tarsus being 1:3 in length; claws elongate; tarsal and unguis little expanded apically. Campaniform sensillum of the tibia clearly visible in some specimens, while indiscernible in others (it is possible that this difference is sexual and that the specimens with the sensillum are male larvae). An unidentified minute structure is found laterally to the hind coxa, trifold or irregularly shaped, sometimes appearing like a duct.

*Mangaspis* Takagi and Kondo, gen. nov.

Name-bearing species [type-species]: *Mangaspis bangalorensis*, sp. nov.

In the adult female this genus is very similar to some 'rugaspidiotines', especially *Rugaspidiotinus* and *Smilacicola*. It is distinguishable from the latter two in the position of the anus: in *Mangaspis* the anus is situated more anteriorly and appears to occur on the 5th abdominal segment. It is also characterized in the antennae, which are situated close to the mouth-parts, beset with several microducts, and provided with a single seta. Furthermore, the ducts are all small in *Mangaspis*.

In the 1st instar, however, *Mangaspis* is remarkably different from *Rugaspidiotinus* and *Smilacicola*. It differs from *Rugaspidiotinus* (studied by Howell, 1992) as follows: 1) the antennae end in 2 long setae (in *Rugaspidiotinus*, in a single long seta); 2) the tibia and tarsus are completely fused together, the supposed tibia and tarsus being 1:3 in length (the tibiotarsal articulation is distinct and the tibia and tarsus are subequal in length); 3) no submedian dorsal setae occur on the abdominal segments posterior to the 3rd (submedian dorsal setae occur as posteriorly as the 7th abdominal segment); 4) 6 submedian dorsal ducts occur on each side (no submedian dorsal ducts on the thorax and abdomen); 5) 2 pairs of enlarged ducts occur marginally on the pygidium (marginal ducts all slender).

No specimens of the 1st instar of *Smilacicola* prepared in good condition have been available for the present study. The drawing of the 1st instar of *S. heimi* in Takagi (1983) is not accurate in all features depicted (Takagi, 1995). Yet *Mangaspis* and *Smilacicola* are quite distinct as follows: 1) in *Mangaspis* the antennae are 5-segmented (in *Smilacicola*, 6-segmented); 2) the tibia and tarsus are completely fused together (the articulation is distinct); 3) no submedian dorsal setae occur on the abdominal segments posterior to the 3rd (the posterior segments also possess submedian dorsal setae); 4) 2 pairs of enlarged ducts occur marginally on the pygidium (marginal ducts all slender).

#### TAXONOMIC POSITION

In spite of the close resemblance in the adult female the 3 genera mentioned above are remarkably different in the 1st instar, so that they should belong to different groups. Based on the 1st instar larvae studied by Howell (1992),

*Rugaspidiotinus* was supposed to be related and referable to the Lepidosaphedini [Diaspidinae] (Takagi, 1995). *Smilacicola* is related to the Parlatoriini [Aspidiotinae], having parlatoriine-patterned forms in the 2nd instar, but differs from the latter in having multisetose antennae in the adult female and the 2nd instar. In this respect it is apparently primitive in comparison with the Parlatoriini, and was supposed to have derived not from the Parlatoriini but from a more primitive group that is also ancestral to the Parlatoriini (Takagi, 1983).

*Mangaspis* is referable to the Aspidiotinae in the combination of the following characters of the 1st instar: 1) presence of 2 terminal setae on the antennae; 2) presence of a strong seta on the tarsus; 3) absence of submedian dorsal setae on the abdomen posterior to the 3rd segment; 4) presence of submedian dorsal ducts on the abdomen (especially on the 2nd segment). It is also characterized by the complete fusion of the tibia and tarsus. This character has been known in some other diaspidids: well-studied examples are *Xanthophthalma* (studied by Stickney, 1934a), *Parlatoria* (Stickney, 1934b; Howell and Tippins, 1977), *Praecocaspis* (Howell and Tippins, 1975), *Xerophilaspis* (Howell, Beshear and Tippins, 1986), and *Odonaspis* (Howell and Tippins, 1977, 1983). *Xanthophthalma* is generally regarded as a primitive form of the Diaspididae. *Praecocaspis* and *Xerophilaspis* are supposed by Howell *et al.* to be related or referable to the Diaspidini [Diaspidinae], but apparently have no relation to each other. *Parlatoria* and *Odonaspis* belong to the Aspidiotinae. Their tribes, Parlatoriini and Odonaspidini, are evidently related to each other phylogenetically, parlatoriine-patterned 2nd instar males having been found in some Odonaspidini; it is assumed that the tribe Odonaspidini originated from the Parlatoriini. Obviously the tibiotarsal fusion has arisen polyphyletically, and, therefore, is not always significant phylogenetically. However, there seems to be no positive reason against supposing a relationship between *Mangaspis* and the Parlatoriini-Odonaspidini group. Indeed *Mangaspis* may be peculiar in the occurrence of 2 pairs of enlarged marginal ducts on the pygidium and of a submedian dorsal duct on the 3rd abdominal segment, but, because accurate observations are still scanty in the 1st instar of the family, further discussion is obviously pointless.

According to Takagi (1995), the absence of lobes in the adult female of a diaspidid coupled with the presence in the 1st instar suggests the disappearance of lobes once developed in the adult stage. *M. bangalorensis*, with well-sclerotized lobes in the 1st instar, may have originated from a parlatoriine form with developed pygidial appendages. Occurring in a confined space beneath the leaf bud, it may afford another example of the emergence of the rugaspidiotine pattern in a habitat where the adult female is impeded in making regular, horizontal movements during the formation of the test. Further, the female may occasionally induce a pit gall on the twig (see Material), but this habit has not been ascertained.

FURTHER FORMS FOR THE RUGASPIDIOTINI-PROBLEM III :  
PYGALATASPIS MISCANTHI  
(HOMOPTERA : COCCOIDEA : DIASPIDIDAE)

By SADAO TAKAGI

Ferris (1921) established the genus *Pygalataspis* on the basis of *P. miscanthi*, a species collected in Taiwan on *Miscanthus sinensis* [Poaceae]. In 1937 he reillustrated the species, and in 1955 he recorded it from Hong Kong. Tang (1986) recorded it from Fujian and Guangdong Provinces, China. Thus the known localities of the species have been limited to Taiwan and part of the Continental China opposite Taiwan.

*Pygalataspis miscanthi* finds no close relatives, having large lobelike processes bearing peculiarly shaped pectinae. Ferris (1921 and 1955) mentioned that this extraordinary form was apparently referable to the *Odonaspis* group. Borchsenius (1966) placed it in the Rugaspidiotina, which he segregated from the Odonaspidini and removed into the Diaspidini. Thus, *P. miscanthi* is involved in the 'Rugaspidiotini-problem' posed by Howell (1992) and Takagi (1995). However, it is odd for a 'rugaspidiotine' due to the presence of well-developed pectinae. Takagi (1981) supposed the genus to be a primitive form comparable with *Megacanthaspis* and *Thysanaspis*, because all these genera are commonly characterized by having pectinae while having no lobes. Tang (1986) referred it to the Kuwanaspidina because of the pectinae and the marginal macroducts with the orifice thickly rimmed and not vertical to the pygidial margin.

DESCRIPTION OF THE FIRST INSTAR (Fig. III-1)

Material. Collected in the Kowloon Peninsula, Hong Kong, on *Miscanthus* sp. (*M. sinensis* ?), 21 IV 1965.

Newly hatched larva elongate elliptical. No ducts dorsally. Nine enlarged ducts occurring along margin on ventral surface on each side of body. Submedian dorsal setae occurring as posteriorly as 7th abdominal segment; submedian ventral setae absent on abdominal segments anterior to the 7th. The seta situated just anteriorly to the caudal seta is unusually long. A pair of elongate sclerotized processes between caudal setae; another pair of sclerotized processes laterally to caudal setae, similar in size to the inner pair but with a developed basal extension. One or 2 small triangular processes just anteriorly to the posteriormost marginal duct; 1 similar but smaller process on 2 preceding segments each (not always discernible). Anterior spiracle with 1 disc pore, which is 3-locular. Antennae 5-segmented; 5th segment about twice as long as the 4th, not annulate, 3rd and 4th segments deeply constricted at about basal 1/3; 5th segment with 4 setae, of which the one occurring at the base is fleshy, in addition to a long apical seta, and with 2 invaginated minute setae; 4th segment with a strong seta; 2 setae on basal segment and 1 on the 2nd slender. Tibiotarsal articulation distinct and oblique; tarsus twice as long as tibia, with oblique sutures dorsally, without strong seta, with a minute process ventrally near base; claw elongate; tarsal and unguis digitules only a little



Fig. III-1. *Pygalataspis miscanthi*, 1st instar larva. Scales: 50  $\mu\text{m}$  for body; 10  $\mu\text{m}$  for antenna.

swollen apically. An unidentified minute structure is found laterally to the hind coxa ; it is so minute and obscure that it could easily be overlooked.

#### TAXONOMIC POSITION

In the combination of the following characters of the 1st instar *Pygalataspis miscanthi* has nothing to do with *Rugaspidiotus arizonicus* and does not belong to the Aspidiotinae, either, but is related to the Diaspidinae and the Diaspidini : 1) presence of submedian dorsal setae on the abdomen as posteriorly as the 7th segment ; 2) absence of submedian ventral setae on the abdomen anterior to the 7th segment ; 3) terminal segment of antenna with a single apical seta ; 4) tarsus without strong seta ; 5) 3-locular spiracular disc pore. It may provisionally be referred to the Diaspidini.

The disc pores of the adult female have been observed in scanning electron microscopy. The spiracular disc pores are 3-locular, with the septa a little produced (Fig. III-2). The perivulvar disc pores are of the capitate type (Fig. III-3). Thus the characters of these pores do not contradict the assignment of *Pygalataspis* to the Diaspidini.

In the Diaspidini some odd types of the 2nd instar male have been known. However, the 2nd instar male of *Pygalataspis miscanthi* is of the same type as the adult female. Pectinae are well developed in the 2nd instar as in the adult female : in the 2nd instar male they are remarkable especially in the mesal 2 pairs, and in the 2nd instar female are well represented in the median pair alone. The 2nd instar female also differs from the adult female and the 2nd instar male in having macroducts of the geminate pore type — a primitive feature as compared with the 1- and 2-barred types of macroducts.

The sclerotized processes occurring laterally to the caudal setae in the 1st instar

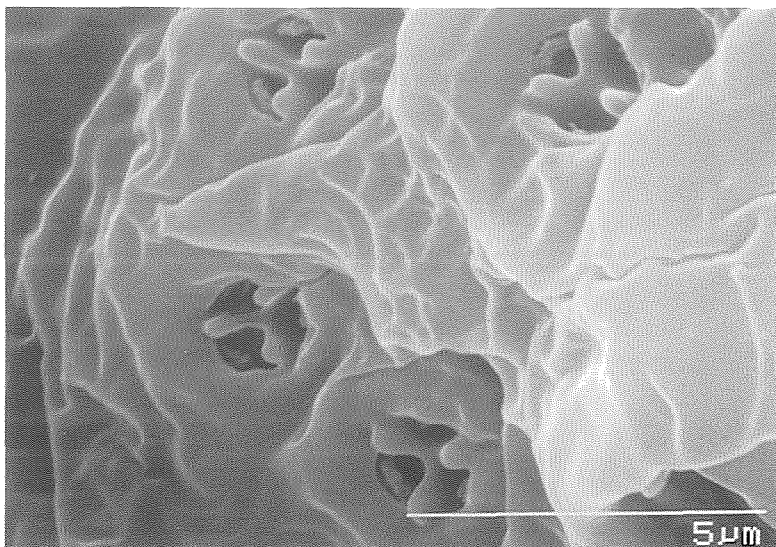


Fig. III-2. *Pygalataspis miscanthi*, adult female : spiracular disc pores.

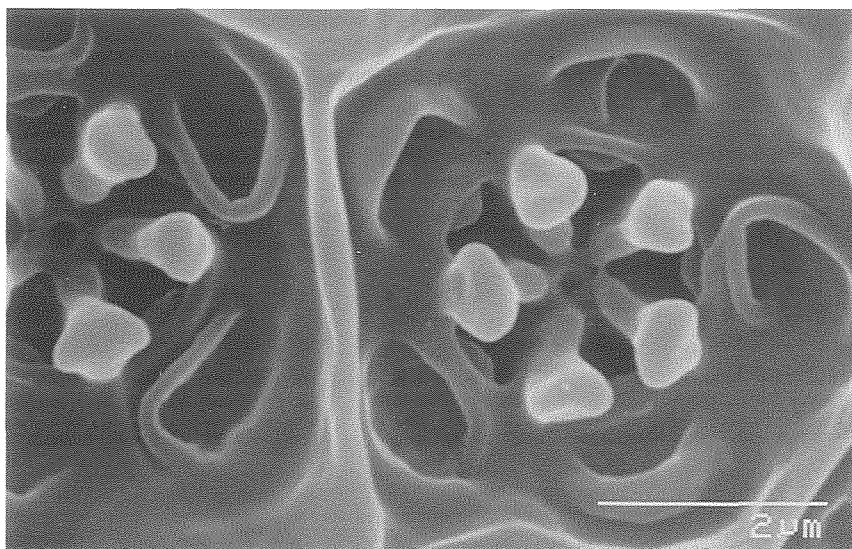


Fig. III-3. *Pygalataspis miscanthi*, adult female : perivulvar disc pores.

can be lobes, having a sclerotized basal extension. According to Takagi (1995), the absence of lobes in the adult female of a diaspidid coupled with the presence in the 1st instar suggests the disappearance of once developed lobes in the adult female. Based on this premise, *Pygalataspis* should have originated from a form with sclerotized lobes in the adult female. Takagi's (1981) supposition that the genus is a primitive form is rejected now, and the apparently primitive characters should be atavistic.

The 1st instar of *Pygalataspis* affords no positive evidence for the supposed relationship to the Kuwanaspidina (immature stages of *K. howardi* were studied by Howell and Tippins, 1973). The genus may be related to a more advanced form of the Diaspidini. It is interesting that *Pygalataspis* agrees, in the 1st instar, with *Diaspis* and *Fiorinia* in having a minute ventral process near the base of the tarsus (the 1st instar larvae of *Diaspis* and *Fiorinia* species were examined by Howell, 1977, and Howell and Tippins, 1977). However, accurate studies of the 1st instar are still too few to evaluate this character.

It is noticeable that in the 1st instar of *Pygalataspis* the seta occurring just anteriorly to the caudal seta — here called subcaudal seta — is unusually long for a diaspidine. Long subcaudal setae are found in the palm-associated genera *Phoenicococcus*, *Palmaricoccus*, *Halimococcus*, *Platycoccus* and *Thysanococcus* (all studied by Stickney, 1934a). These genera have been classified in the families Phoenicococcidae and Halimococcidae (or all referred to the Phoenicococcidae) by recent authors, but they are apparently related to the Diaspididae and may tentatively be placed in the Level 0 group of the Diaspididae in the scheme presented by Takagi (1995). In this disposal the long subcaudal seta in the 1st instar is a primitive feature in the Diaspididae, principally associated with the primary absence of marginal appendages in the adult female. According to the conclusion adopted above, *Pygalataspis* originated from an advanced diaspidine with well-developed

lobes. In this context the long subcaudal seta should be an atavistic feature in *Pygalataspis*. It should be added that somewhat long subcaudal setae are occasionally found in other diaspidids, too. It is also noticeable that *Limacoccus* (= *Canceraspis*), another palm-associated genus, possesses '2 pairs of long caudal setae' (Foldi, 1995), which may be homologous with the caudal seta and the subcaudal seta as

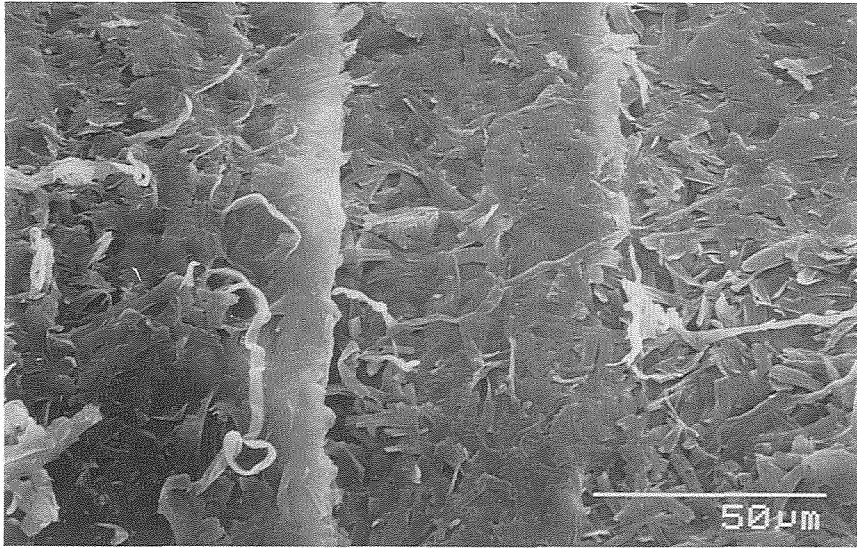


Fig. III-4. *Pygalataspis miscanthi*, test of adult female : part of dorsal surface.

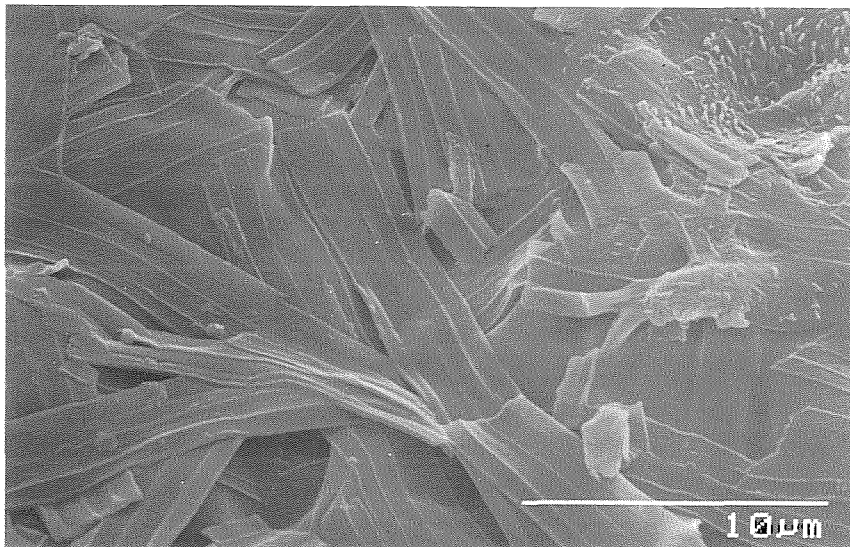


Fig. III-5. Part of Fig. III-4, showing irregularly laid wax filaments.

designated above. (Foldi referred *Limacoccus* to the Beesoniidae on the basis of a cladistic analysis. The taxonomic position of this genus is, however, beyond the scope of the present paper.)

*Pygalataspis miscanthi* inhabits the inner surface of the leaf-sheath of the host plant, where male and female tests are crowded together. Scanning electron microscopy of the female test gives no evidence of regular, horizontal movements of the insect body (Figs. III-4 and -5). Apparently, *Pygalataspis* affords another case of the disappearance of sclerotized lobes associated with the suppression of horizontal movements during the formation of the test. Why the pectinae of the peculiar type have developed instead is, however, unexplainable in the present state of our knowledge.

FURTHER FORMS FOR THE RUGASPIDIOTINI-PROBLEM IV :  
AN ODONASPIDINE-PATTERNED FORM FROM MALAYA  
(HOMOPTERA : COCCOIDEA : DIASPIDIDAE)

By SADAO TAKAGI

The new form described below may represent the 'Odonaspidini-problem' rather than the Rugaspidiotini-problem, because it is more similar to odonaspidines than to rugaspidiotines in the ducts all minute and, especially, in having intersegmental scleroses on the pygidium. However, the odonaspidines and many rugaspidiotines, while almost or completely lacking pygidial appendages in the adult female, are assumed to have derived from forms with well-developed appendages. They pose, therefore, common questions as to the cause and conditions for their evolution.

DESCRIPTION OF THE NEW FORM

*Roureaspis dungunensis* Takagi, sp. nov.

Material. Collected at Kuala Dungun, Terengganu, Malaya, on *Rourea rugosa* [Connaraceae] (det. K.L. Kochummen), July 22, 1990 [90ML-294]. Occurring on the undersurface of the leaflet, on the lateral side of the midvein, which is densely grown with long erect hairs (Fig. IV-1). Male and female tests are crowded together in a mass. Adult females (8 specimens), 2nd instar females (6), 2nd instar males (about 30), and 1st instar larvae were examined. Name-bearing specimen [holotype], adult female, deposited in the collection of the Entomology Division, Forest Research Institute of Malaysia, Kepong, Selangor, Malaysia.

Adult female (Fig. IV-2 and -3). Body obovoid or inversely pyriform. Pygidium composed of 5th and succeeding abdominal segments dorsally; supposed posterior angles of 6th segment produced; margin between the produced angles nearly flat and irregularly crenulate; sclerotized except basally; dorsal surface with 5 longitudinal intersegmental scleroses on about apical 2/3 and with some sclerotized patches subbasally; ventral surface with many small, circular, obscure patches densely strewn apically to subapically. Minute ducts strewn on both surfaces. Antennae situated laterally to mouth-parts, each in a dermal invagination, with a seta, which is divided basally (thus it may be composed of 2 setae united

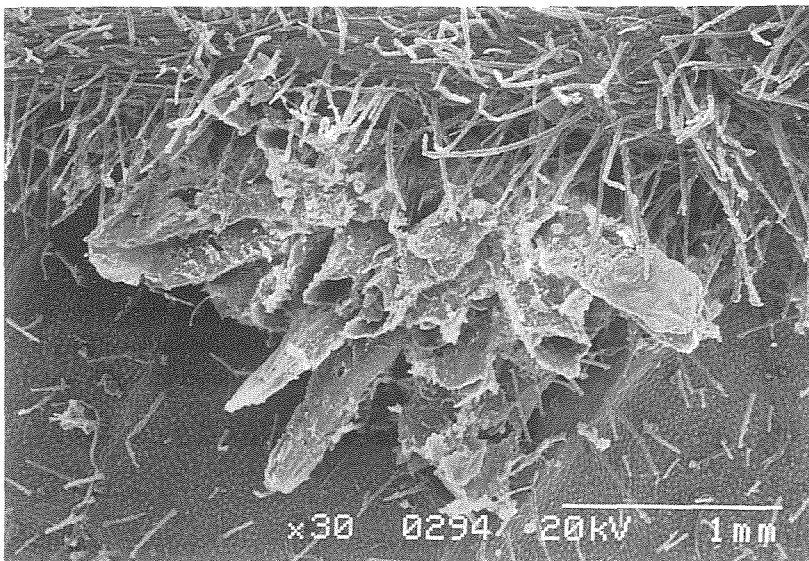


Fig. IV-1. *Roureaspis dungunensis* on the host plant.

together except basally). Spiracular disc pores 3-locular, 9-16 associated with anterior spiracle, none with posterior spiracle. Anus situated not within pygidium but on the preceding segment (4th abdominal segment), thickly sclerotized around. Vulva situated near the base of the pygidium.

Second instar female (Fig. IV-4). Body obovoid. Pygidium composed of 5th and succeeding abdominal segments dorsally, with a pair of marginal processes arising at the supposed posterior angles of 7th segment, each followed laterally by 2 smaller processes. Slender ducts strewn on both surfaces. Antennae as in adult female. Anterior spiracle with 4-7 disc pores. Anus situated in the bottom of the pygidium, thickly sclerotized around.

Second instar male (Fig. IV-5). Body oblong. Pygidium composed of 5th and succeeding abdominal segments dorsally. Four pairs of triangular marginal processes occurring on 4th-7th abdominal segments. Very short ducts occurring along margin on 3rd-7th abdominal segments, forming a dorsoventral cluster on each segment, each with the orifice slender and surrounded by a thick rim; 2 (or occasionally 3) such ducts and 1 minute duct are joined together to form a peculiar set in each cluster. Two-barred ducts strewn on dorsal surface in prepygidial region as anteriorly as the posterior angle of the prothorax, and arranged on ventral surface in a transverse or oblique row laterally to each spiracle and also submarginally on each of 1st and 2nd abdominal segments. Much smaller ducts on ventral surface posteriorly to spiracles and on prepygidial abdomen. Antennae situated between frontal margin and mouth-parts, each composed of a flat disc and 3 (at times 2?) setae. Anterior spiracle with 0-2 disc pores (usually 1). Anus situated in the bottom of the pygidium.

First instar larva (Fig. IV-6). Head with a pair of enlarged ducts; a pair of similar ducts at the caudal end of the body posterolaterally to anus; 9 slender ducts

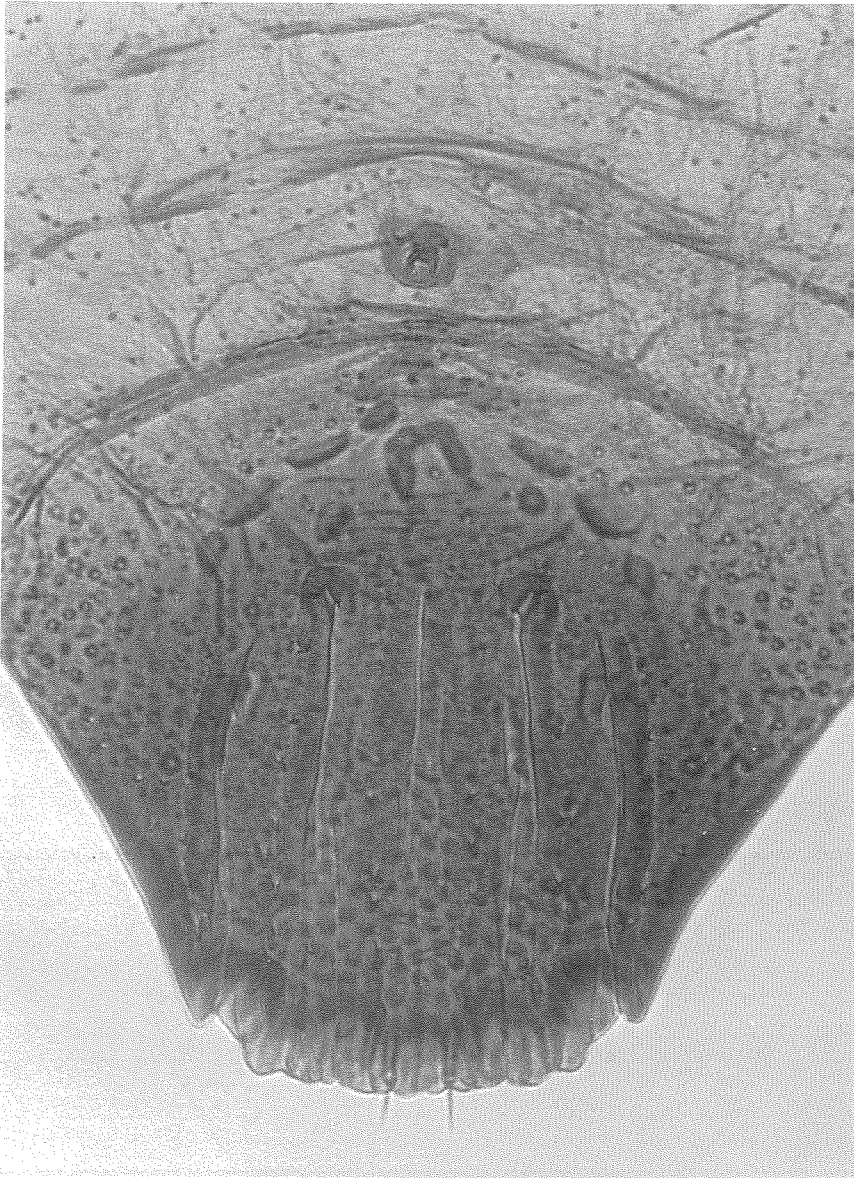


Fig. IV-2. *Roureaspis dungunensis*, adult female : pygidium.

occurring ventrally along body margin on each side. Submedian dorsal setae occurring as posteriorly as 7th abdominal segment ; no submedian ventral setae on abdomen anterior to 7th segment. A pair of small pointed processes between caudal setae ; a sclerotized, tricuspid process laterally to caudal seta, with a basal extension, accompanied by 2 pointed processes just laterally ; similar pointed processes occurring on 3 preceding segments. Anterior spiracle with 1 disc pore. Antenna 6-segmented ; 6th segment as long as the 3rd-5th combined, little annulate, with 1

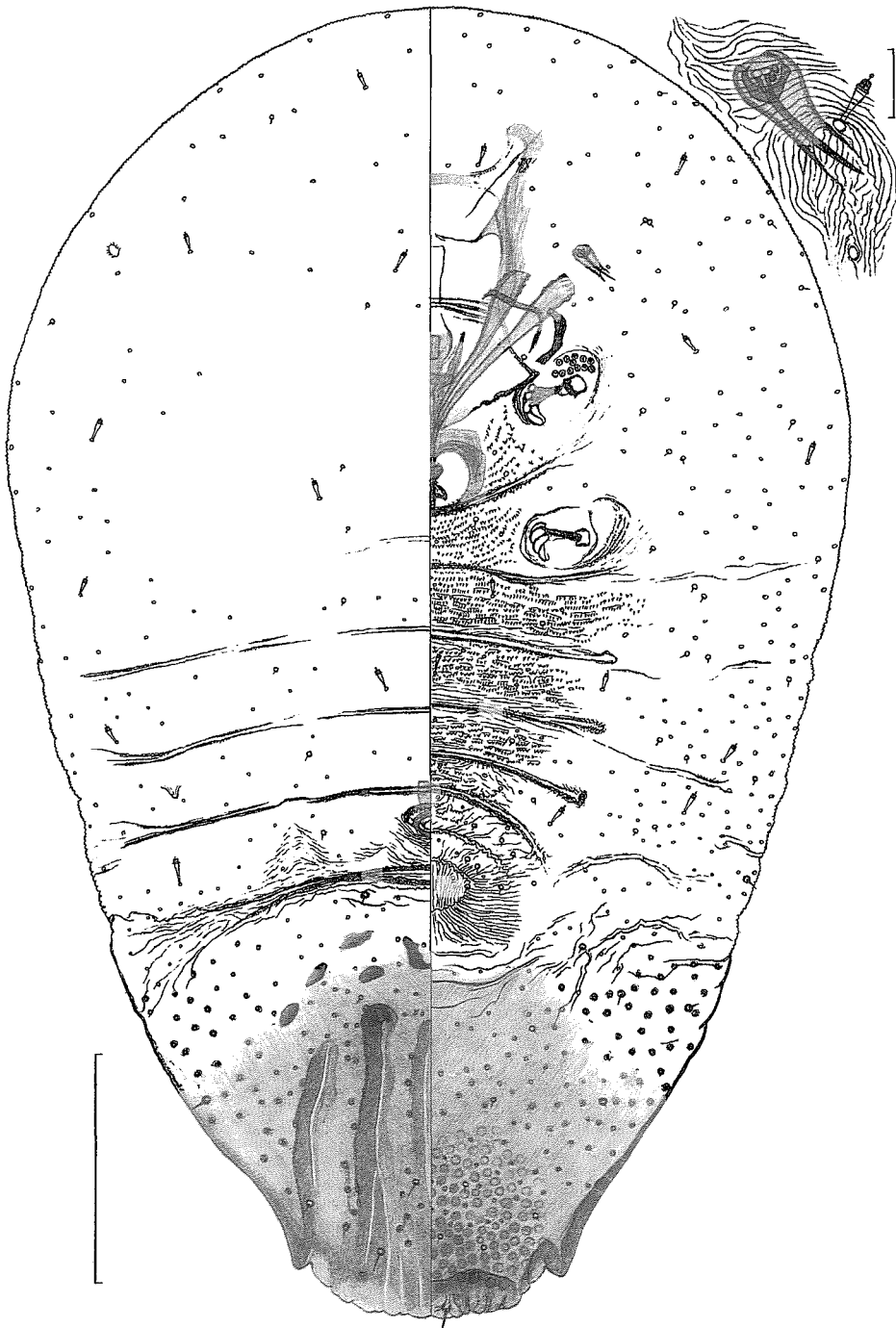


Fig. IV-3. *Roureaspis dungunensis*, adult female. Scales: 100  $\mu\text{m}$  for body; 10  $\mu\text{m}$  for antenna.

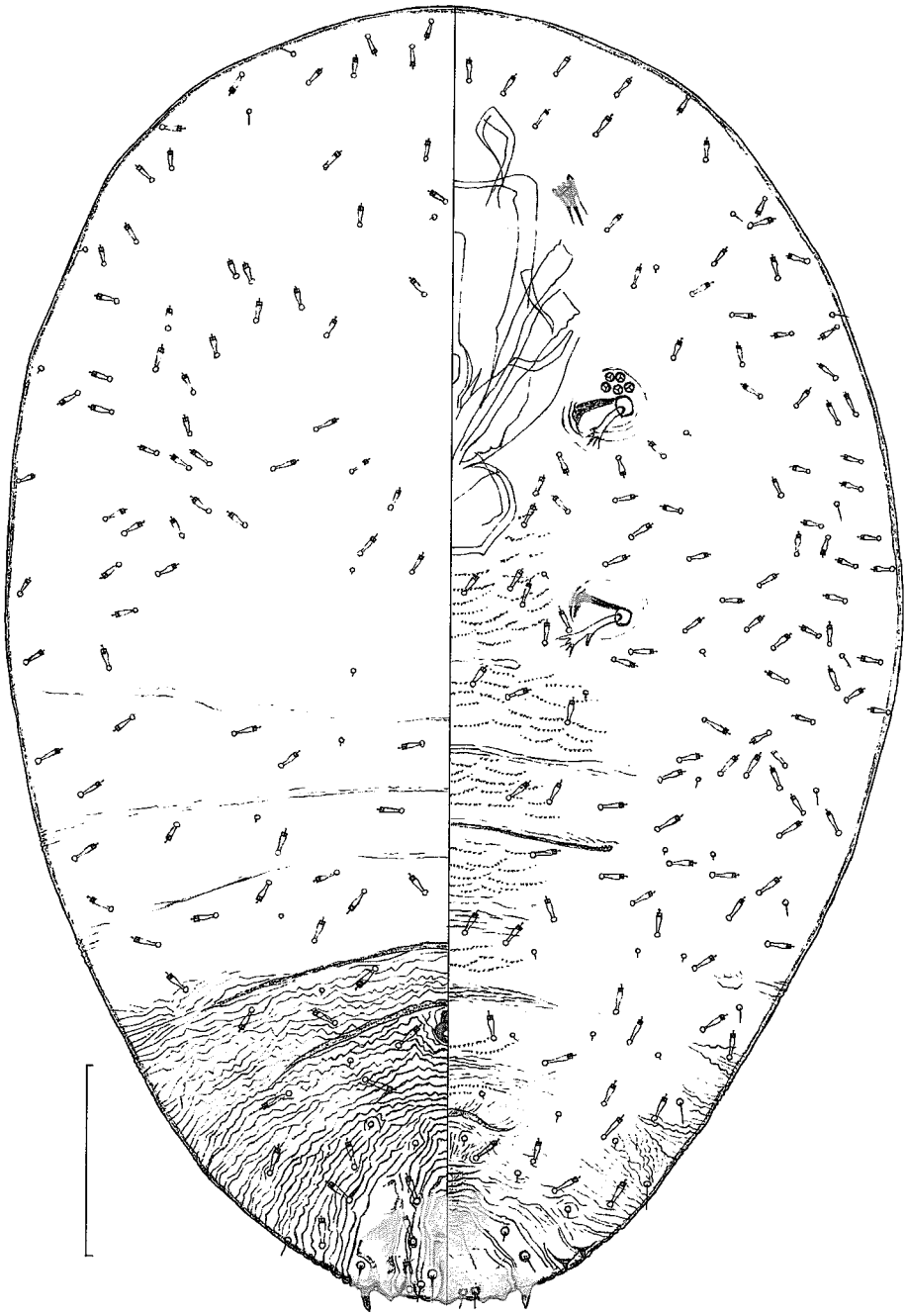


Fig. IV-4. *Roureaspis dungunensis*, 2nd instar female. Scale: 50  $\mu$ m.

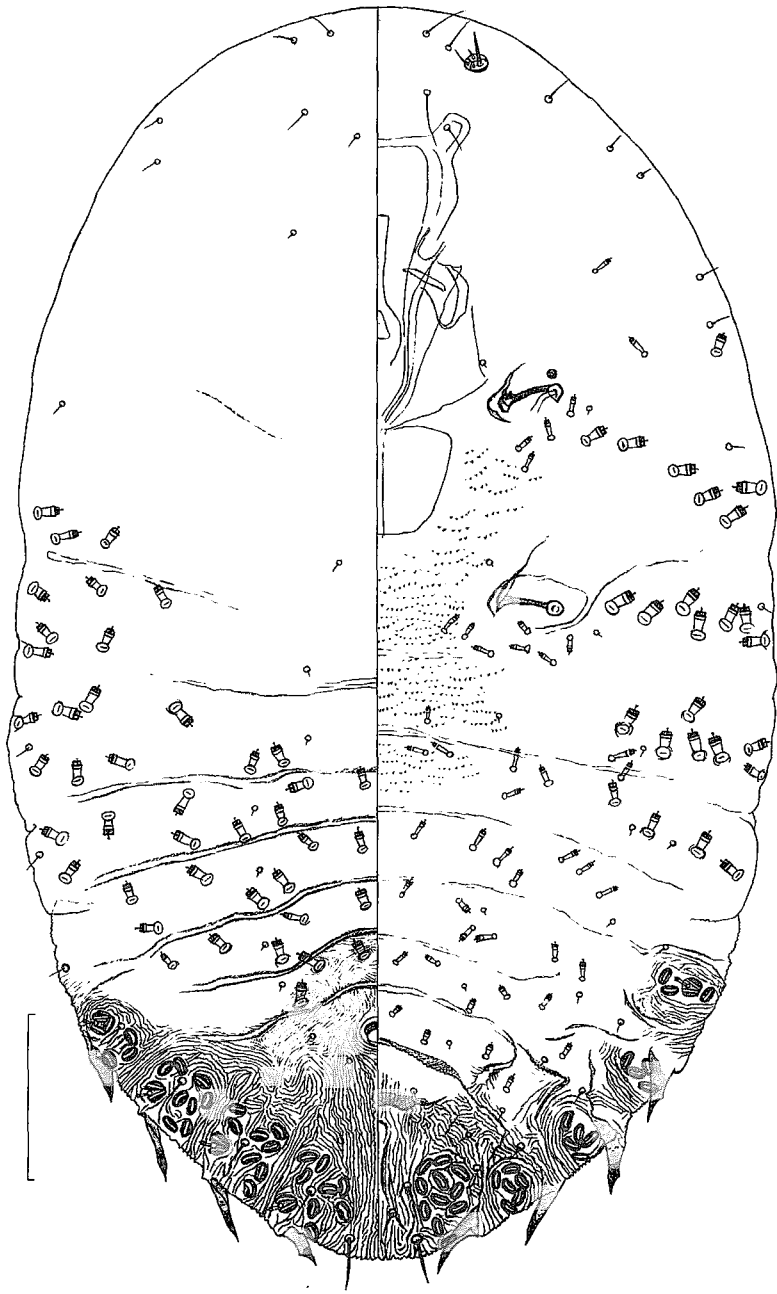


Fig. IV-5. *Roureaspis dungunensis*, 2nd instar male. Scale: 50  $\mu$ m.



Fig. IV-6. *Roureaspis dungunensis*, 1st instar larva. Scale: 50  $\mu\text{m}$  for body; 10  $\mu\text{m}$  for antenna.

apical seta, 5 fleshy setae, and 2 invaginated minute setae ; 5th segment with 1 fleshy seta ; 2 setae on the 1st segment and 1 on the 2nd slender. Tibiotarsal articulation distinct, tarsus nearly twice as long as tibia, obliquely striate dorsally, without strong seta ventrally ; tarsal and unguis digitules little expanded apically. An unidentified minute structure is seen laterally to the hind coxa ; it is often obscure and hardly discernible.

*Roureaspis* Takagi, gen. nov.

Name-bearing species [type-species] : *Roureaspis dungunensis*, sp. nov.

This genus is somewhat similar to odonaspidines in the adult female, but peculiarly characterized by the anus, which is situated not within the pygidium but on the segment anterior to the pygidium, and by the antennae, which are situated laterally to the mouth-parts in a pocket of the derm. In the 1st instar it is quite different from *Odonaspis secreta*, studied by Howell and Tippins (1977), as follows : 1) terminal segment of antenna little annulate and with 1 apical seta ; 2) tibiotarsal articulation distinct ; 3) tarsus without strong seta ; 3) submedian dorsal setae occurring as posteriorly as 7th abdominal segment ; 4) submedian ventral setae absent on abdomen anterior to the 7th segment.

#### TAXONOMIC POSITION

In spite of the similarity to odonaspidines in the gross appearance of the adult female, *Roureaspis dungunensis* is not referable to the Odonaspidini [Aspidiotinae] so far as based on the 1st instar. It agrees with some well-studied species of the Diaspidini [Diaspidinae] in the combination of 1st instar characters mentioned above, and may be referred to this tribe. This disposal is not contradicted by the spiracular disc pores, which are 3-locular in all the examined instars. *R. dungunensis* is unique in the 'joined ducts' of the 2nd instar male. Various Diaspidini show modified ducts of various types in the 2nd instar male, and *R. dungunensis*, understood as belonging to the tribe, may add another type to the duct polymorphism.

The 1st instar larva possesses sclerotized lobes and a series of marginal processes. Based on the premise that in a diaspidid the absence of lobes in the adult female coupled with the presence in the 1st instar suggests the disappearance of once developed lobes in the adult female (Takagi, 1995), *R. dungunensis* is assumed to have originated from an advanced form possessing well-developed marginal appendages in the adult female. The 2nd instar male supports this assumption, possessing remarkable marginal processes, which are comparable with the prominent pectinae in the 2nd instar male of *Pygalataspis miscanthi*, a 'rugaspidiotine' referable to the Diaspidini. *R. dungunensis* and *P. miscanthi* also agree in the obliquely striate tarsi of the 1st instar (as to *P. miscanthi*, see Part III of this series). It is still unknown, however, whether this character has any phylogenetic significance.

*R. dungunensis* inhabits the hairy midvein of the leaflet, where male and female tests are crowded together in a mass (Fig. IV-1). In this respect it is comparable with *Amphisoma erectum* — an 'incipient rugaspidiotine' (Takagi, 1995) — which occurs among hairs on the twig and petiole. In either case the dense, long, and erect hairs of the host plant apparently constitute an obstacle to the horizontal movements of the adult female in the formation of the test. The evolution of *R. dungunensis*,

therefore, may be analogous to the emergence of many rugaspidiotines, which are associated with narrow, confined, or hidden spaces in some particular habitats.

#### CONCLUDING REMARKS (for Part I-IV)

The tribe Rugaspidiotini (or the subtribe Rugaspidiotina under the Odonaspidini or the Diaspidini) has been composed of forms which are similar principally in lacking pygidial lobes and other marginal appendages and in having numerous small ducts strewn on both surfaces of the pygidium. Studies on the 1st instar larva — Howell, Beshear and Tippins (1986), Howell (1992), Takagi (1995), and the present series of papers — have shown that the tribe includes unrelated genera, and we may reasonably conclude that the tribe as composed by authors is an artefact. Many of the rugaspidiotine genera seem to have arisen from advanced Diaspidini, while others from Lepidosaphedini or Aspidiotinae. Apparently their similarity in the adult female is superficial from the viewpoint of phylogeny.

These diaspidids are principally associated with some particular habitats, where the adult female may be impeded in making regular, horizontal movements during the formation of the test. Thus their similarity may have been caused by convergence. In the general usage of the term, convergence means the independent acquisition of similar attributes through the process of mutations and selections in unrelated taxa exposed to the same or similar environmental conditions. On this understanding, convergence alone cannot explain the emergence of *Nimbaspis*, in which the macroducts are all of the geminate-pore type. This type of duct is deemed to be primitive in comparison with the 1- and 2-barred ones. Takagi (1995) interpreted the occurrence of this primitive feature, coupled with the presence of well-sclerotized lobes in the 1st instar, as an atavistic character in *Nimbaspis*. He further suggested that, in general, atavism should be involved in the arising of rugaspidiotine-patterned forms, especially in the disappearance of marginal appendages and the appearance of many ducts on both surfaces of the pygidium, and that convergence involving atavism should have made the appearance of the rugaspidiotine pattern so frequent. If his suggestion is correct, the similarity among rugaspidiotines is not superficial, but requires deeper insight into their phenotypic manifestation.

Atavism (reversion; reversal; recall) as generally understood is 'the reappearance of a lost character (morphology or behaviour) typical of remote ancestors and not seen in the parents or recent ancestors of the organisms displaying the atavistic character' (Hall, 1984). Usually it means an occasional — teratological rather than normal — reappearance of such a character in a limited number of individuals within a population or in experimental organisms. However, when selected for, an atavistic variation will be an attribute of a whole population as shown by Kurtén (1963) in the dentition of fossil and Recent felid forms, thus having an evolutionary significance.

The rugaspidiotini-problem appears more complicated than some well-known cases of atavism, because it concerns whole organisms rather than single features, and patterns of characters rather than individual characters. The supposition that atavism is involved in the arising of the rugaspidiotine pattern from other patterns of diaspidids may not be accepted without some postulations concerning genetic

mechanisms underlying varying phenotypic patterns in general.

The basic postulation here may be that a change in a phenotypic pattern should be attributed to expression of genes rather than to genes themselves. An ancestral phenotypic pattern achieved millions of years ago could reappear in accordance with a reversed change in the integrating regulation of gene expression so far as the functional homologies of the genes concerned have been maintained since that time in spite of accumulated base substitutions. In fact, genes themselves have proved to be conservative. Corresponding genes have been found between protozoans and humans, between bacteria and humans, and even between plants and humans: 'their basic molecular organization and the products formed have been maintained for billions of years' (Lima-de-Faria, 1983). Genes may remain silenced without mutational inactivation of the encoded protein for 'a surprisingly long time' (Raff, 1996).

Britten and Davidson (1969) constructed a model for the genomic regulation system of higher organisms on the supposition that repetitive nucleotide sequences perform the integrated activation of noncontiguous genes. Sibley and Ahlquist (1990) reviewed studies on repeated sequences and showed that their possible functions were still in dispute but not wholly negated. Other regulatory systems were also discovered. Recently, Jablonka and Lamb (1995) have developed the concept of the epigenetic inheritance systems, which are composed of information carriers additional to DNA. According to them, a change in chromatin acquired during epigenetic process, for example, can be passed to progeny cell, and the changed pattern of chromatin structure thus inherited — an epiallele in their terminology — may alter the expression of the associated gene in the progeny. What seems especially relevant to our problem is that the epigenetic inheritance systems, being sensitive to environmental conditions, may bring about frequent parallelism and convergence. The essential point for our problem is, however, whether changes in repeated sequences, epialleles or any other regulatory elements can be reversed in such a way as to result in the reappearance of ancestral phenotypic patterns. 'The reactivation of a complex morphogenetic pathway seems intuitively unlikely... Nevertheless, evolutionary reactivation of morphogenetic processes has been observed' (Raff, 1996).

The idea of convergence involving atavism may sound fantastic, but it can be harmonious with some hypotheses proposed in other fields of biology, of which a few are mentioned above. It is still difficult to understand this idea and also some general notions relevant to it, such as prepattern, phenotypic potential, and 'principle of preformation' (Lima-de-Faria, 1983), in terms of mechanisms. But 'In constructing a phylogeny, if we reject the possibility of reversals exceeding a certain magnitude, our phylogeny will be of little value in the detection of such reversals' (Blackburn, 1984). The arising of rugaspidiotini-patterned forms from a wide range of diaspidids may suggest that phenotypic reversals of considerable magnitude are not unusual.

#### APPENDIX : MOUNTING METHOD OF FIRST INSTAR DIASPIDIDS

The examination of the 1st instar is essential and indispensable for the Rugaspidiotini-problem as shown above. It requires careful preparation of speci-

mens as well as a powerful microscope. There are numerous methods for mounting scale insects. Below is given the method adopted for mounting the 1st instar larvae used in the present series of study.

1. Put material in 10% KOH, leave at room temperature for 24-48 hr.
2. Check whether specimens are well cleared. If not, leave for some more time. When necessary, gently press by the use of a tip-bent micropin (fixed at the apex of a stick) to tease out body contents (press so as to make specimens flat dorsoventrally).
3. Transfer to staining solution [acid fuchsin 1-2 gr and azophloxin 1-2 gr dissolved in lactic acid or Essig's aphid fluid (lactic acid 20 parts, melted phenol 2 parts, and glacial acetic acid 4 parts) 500 cc], heat at 60°C for 1 hr.
4. Transfer to acetosalicylate [glacial acetic acid 1 part and methyl salicylate 1 part], heat at 60°C for 10-20 minutes.
5. Check whether specimens are properly stained. When stained too dark, transfer to lactic acid or Essig's aphid fluid and then to acetosalicylate, heat at 60°C for 10-20 minutes in each. (Better stain dark and then remove excess stain in lactic acid or Essig's aphid fluid.)
6. Transfer to carboxylol [xylol 3-5 parts and melted phenol 1 part].
7. Mount in Canada balsam.
8. Heat finished slides at 60°C for 10-20 minutes, and then cure at 40-45°C for 3-4 weeks (label before starting to cure).

This method can be applied to other stages of diaspidids and other families of coccoids, especially to small membranous specimens. Other steps (making a cut on the body wall, heating in KOH solution, etc.) may be added for preparing larger specimens. Sclerotized specimens may be stained by azophloxin alone. [Azophloxin (=pontacyl carmine) has the same composition as lignin pink, slightly differing from the latter in structure. Wilkey (1990) recommended lignin pink for a double staining with acid fuchsin. Azophloxin is adopted here only because it is readily available in Japan (producer: Tokyo Kasei).]

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