AN APPROACH TO HEMIBERLESIA PROBLEM (HOMOPTERA : COCCOIDEA)

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AN APPROACH TO THE HEMIBERLESIA PROBLEM
(HOMOPTERA : COCCOIDEA)

By Sadao Takagi

Abstract


The Japanese species of Diaspidiotus and Quadraspidiotus are critically revised together with some other species, and three species-groups are formed: one group is composed of Quadraspidiotus cryptoxanthus, Diaspidiotus humanai and D. naracola, another of Diaspidiotus mabii, Abgrallaspis momicola and Hemiberlesia pitysophila, and the remain of Quadraspidiotus perniciosus, Q. macroporanus and Q. paraphyses; the last group is accepted as a genus, for which the name Comstockaspis is available. It is suggested that closely related species are allocated to different genera or that the genera concerned are polyphyletic. It is noted that further trials for possible regroupment of species may be useful for the approach to generic difficulties in the taxonomy of Hemiberlesia and allied. In connection with Comstockaspis, the genus Clavaaspidotus is revised, and C. apicalis n. sp. is described from Southeastern Asia and Egypt. Diaspidiotus hydrangeae n. sp. is described from Japan.

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INTRODUCTION

The old genus *Aspidiotus* was split in 1921 into a number of genera by means of mechanical dichotomy. In reducing them to reasonable groups one has found that some genera, quite distinct so far as their nuclei are concerned, grade into each other through intermediate species. This is the case especially with *Hemiberlesia* and its allied genera (*Diaspidiotus*, *Clavaspis*, *Quadraspidiotus*, etc.), and their limits have remained more or less arbitrary. Yet, their union in an enlarged genus has been supposed untenable, resulting in the inclusion of diverse characters adoptable as of generic value. Recent efforts are centred around *Abgrallaspis*, a comparatively later segregation from *Hemiberlesia*, and to justify it. But, even after accepting *Abgrallaspis* as a valid genus, Komosińska (1969) admits that there are “aberrant species scattered on the periphery.”

We may here be concerned with “a question of personal opinion and interpretation” (Komosińska l.c.) in dividing the primarily continuous nature. However, Stannard (1965) shows that the matter is complicated. After him, three forms long accepted as distinct species in two different genera belong, in reality, to a single species and are produced primarily by different feeding sites: one (*ancylus*, the type-species of *Diaspidiotus*) is a bark-form, occurring on the bark of the branches of the host, and the other two (*howardi* and *comstocki*, both referred to *Hemiberlesia* and later to *Abgrallaspis*) are leaf-forms different from each other in host. They were divided into the different genera on the basis of their characters of the second lobes, but Stannard shows that the supposed generic difference is merely a phenotypic modification caused by different feeding sites on a single plant. His study necessarily results in the inclusion of part of *Abgrallaspis* within *Diaspidiotus* and creates a grave doubt as to the genus *Abgrallaspis* itself. Nevertheless, his study seems to have not received a proper appreciation from taxonomists in their recent revisional works. In 1969 I presented a possible extreme argument in uniting *Hemiberlesia*, *Diaspidiotus*, *Quadraspidiotus* and *Abgrallaspis* in a single genus — the enlarged *Hemiberlesia*. This trial will not be justified unless further evidences are obtained concerning the invalidity of the generic separations.

This paper is but a short step to approach the ‘*Hemiberlesia* problem’, giving a trial to put interpretations other than currently adopted on certain Japanese species with expectation of finding light which may lead us to an exit from the dilemma we are in.

In connection with the present study I have examined several other species including two new species. The results of these examinations should also be given in the present paper.
A REVIEW OF JAPANESE SPECIES OF DIASPIDIOTUS AND QUADRASPIDIOTUS

The known Japanese fauna is poor and rather simple as regards the Hemi­berlesia complex, the native forms mainly belonging to Diaspidiotus and Quadraspidiottus. So far as I am aware, four species have been referred to Diaspidiotus and five, including one introduced, to Quadraspidiottus in Japan. In the following lines a trial is given to overlook these species from another viewpoint and as free as possible from the generic evaluation accepted by recent authors. In this procedure the following three groups are formed:

i. Group comprising Quadraspidiottus cryptoxanthus, Diaspidiotus kuwanai and Diaspidiotus naracola.

ii. Diaspidiotus makii is grouped together with Abgrallaspis momicola and the Taiwanese Hemiberlesia pityosiphila.

iii. Group composed of Quadraspidiottus perniciosus, Quadraspidiottus macro­porans and Quadraspidiottus paraphyses.

The remaining Diaspidiotus spiraspinae and Quadraspidiottus williamsi, as well as a new Diaspidiotus-species described hereinafter, are isolated in Japan and adjacent areas.

1. Quadraspidiottus cryptoxanthus, Diaspidiotus kuwanai and Diaspidiotus naracola (Figs. 1 & 2)

These three species are associated with Quercus serrata (=Q. glandulifera) in Japan; the first-named was recorded also from Castanea crenata and from the continent of East Asia. So far, Q. cryptoxanthus and D. naracola have been found on the bark of the host, whereas D. kuwanai on the leaves. Since the host plant is deciduous, D. kuwanai must occur on the bark at least in winter.

Q. cryptoxanthus falls within the limits of Quadraspidiottus adopted by authors, being provided with developed and strongly convergent median and second lobes. D. kuwanai, known only from the leaf-form, is very similar to the bark-form of D. ancylius, the type-species of Diaspidiotus, having ill-sclerotized second lobes. D. naracola, in which the second lobes are practically obsolete, is undubitably a Diaspidiotus-species in authors’ sense (Fig. 1).

These three species agree not only in host plant but also in some structural characters, and are distinguishable from each other by the numbers of dorsal macroducts and perivulvar disc pores in addition to the minor details of the median lobes, which are convergent in all these species, and the state of the second lobes. Except for the second lobes, adopted by authors as the distinguishing feature between Diaspidiotus and Quadraspidiottus, none of the differences found among them may be adoptable as a generic one.
Fig. 1. Pygidial apex. A: Quadraspisidiotus cryptoxanthus. B: Diaspidiotus naracola. C: Diaspidiotus kuwanai (second lobe of one side is unusually developed).

The dorsal macroducts* decrease in number in the sequence: cryptoxanthus — naracola — kuwanai (Fig. 2). Clustered submarginal macroducts are present on the third and fourth abdominal segments in Q. cryptoxanthus, absent on the third but present on the fourth in D. naracola, and absent on both the segments in D. kuwanai except for the occasional presence of one duct (possibly the remnant of a cluster) on the fourth.

The sequence in the number of perivulvar disc pores is identical with that in the dorsal macroducts (Fig. 2). In Q. cryptoxanthus the median group is

* To give an exact number of dorsal macroducts is not always easy, depending on conditions of prepared specimens; so, the numbers calculated in the present study may include some small miscounts. Prepygidial macroducts scattered along the body margin do not count.
usually present, having three to six disc pores, whereas in *D. naracola* and *D. kuwanai* often absent and if present quite small, usually with only one or two disc pores.

The three species seem to differ considerably in the ultimate body size and to form a sequence from the largest *Q. cryptoxanthus* through *D. naracola* to the smallest *D. kuwanai*. Exact measures of individual specimens may be rather meaningless owing to the expected variation caused by a large amount of growth during the adult stage. Measures for the tentorial length also vary widely in each species, but the means may be indicative of the relative body size of the three species (Table 1).

Table 1. Tentorial length in micra in *Quadraspidiotus cryptoxanthus*, *Diaspidiotus naracola* and *D. kuwanai*.

<table>
<thead>
<tr>
<th>Species</th>
<th>n</th>
<th>X</th>
<th>σ</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Q. cryptoxanthus</em></td>
<td>9</td>
<td>178</td>
<td></td>
</tr>
<tr>
<td><em>D. naracola</em></td>
<td>28</td>
<td>155</td>
<td>7.0</td>
</tr>
<tr>
<td><em>D. kuwanai</em></td>
<td>24</td>
<td>133</td>
<td>14.0</td>
</tr>
</tbody>
</table>

Then, the sequences agree in the numbers of dorsal macroducts and perivulvar disc pores and perhaps also in the size of body, showing a decrease in the manner *cryptoxanthus*→*naracola*→*kuwanai* or vice versa an increase. And at the extreme for the increase *Q. cryptoxanthus* shows strong second lobes, whereas in the other species these lobes are much reduced.

The second lobes are a little more developed in *D. kuwanai* than in *D. naracola*, though ill-sclerotized in both; the plates are more developed in *D. kuwanai* than in the other two and reduced to small spiniform processes in *D. naracola*. These features, then, do not exactly follow the decreasing sequence *cryptoxanthus*→*naracola*→*kuwanai*. The female scales are very similar between *Q. cryptoxanthus* and *D. naracola*, being convex and dark grey in both, whereas that of *D. kuwanai* is flat and whitish. However, it deserves attention that a comparison is here made between the bark-forms of *Q. cryptoxanthus* and *D. naracola* and the leaf-form of *D. kuwanai*. In *Diaspidiotus ancyclus* the leaf-form is characterized in comparison with the bark-form by a smaller body size, larger second lobes, more branched plates, and less numerous perivulvar disc pores and dorsal macroducts; the scale is lighter in colour and less convex in shape (Stannard l.c.).

Further discussion should, therefore, be avoided until the bark-form of *D. kuwanai* has been found. It is little probable that *D. naracola* or even *Q. cryptoxanthus* is further present in *D. naracola* and *D. kuwanai*. The dice-grams include some specimens other than shown in the scatter diagram.

Fig. 2. Number of dorsal macroducts (X1) against number of perivulvar disc pores (X2). 
cryptoxanthus is the bark-form of D. kuwanai, because these three species differ in the presence or absence of macroduct-clusters on the third and fourth abdominal segments — this character may, so far as judged from Stannard's study, be little affected by the difference of feeding sites.

The purpose of the account given above is to suggest another possible interpretation as to the relationship of the three species, which occur in the Japanese faunal area on the same plant species, and which have been divided into the two genera on the basis of the single feature. They may in reality be closely allied, and the supposed generic characters may merely reflect different parts of a trend of characters commonly held by them.

As generally accepted, Diaspidiotus is characterized by lacking distinct or well-developed second lobes, whereas Quadraspidiotus by having well-sclerotized and convergent ones. There are, however, transitional species with reduced second lobes. The pygidial lobes are not meristic, so that the number of these lobes cannot definitely behave as a unit character. It seems possible to me that some Diaspidiotus-forms have derived from Quadraspidiotus-forms through reductive change of the second lobes. I believe that this idea has been held by taxonomists of scale insects. For example, in their discussion on the nomenclature of Diaspidiotus, Morrison & Morrison say:

"We believe that the zoological distinction between Diaspidiotus and Quadraspidiotus, as they are now constituted (i.e., each with the type-species indicated and each with numerous included species), can be maintained on present knowledge only with considerable uncertainty. In our view much more critical study of included species would be needed to confirm the zoological separation of these two generic units.... Perhaps this synonymy [Diaspidiotus = Quadraspidiotus] is valid zoologically as well, even if the currently accepted concept of Diaspidiotus rests on the occurrence of a reduced number of pygidial marginal lobes as compared with Quadraspidiotus." — Morrison, H. & Morrison, E. R. 1966. An annotated list of generic names of the scale insects (Homoptera: Coccoidea). USDA Misc. Publ. 1015: 59.

In conclusion, a noteworthy variation found in D. kuwanai should be put on record. I have examined 33 specimens of D. kuwanai from several localities in central Japan. In these specimens the second lobes are low, broad prominences; often terminating in a point, and wholly membranous or narrowly sclerotized along the margin. In one specimen from the type-series, collected at Takao, Tôkyô, the second lobe of one side is developed into an elongate process, well sclerotized along the margin, and parallel to the longitudinal axis of the body, whereas that of the other side is usual for the species (Fig. 1C). The usual and unusual second lobes of D. kuwanai resemble the bark- and leaf-form variations of D. ancyclus. This unusual specimem was, however, collected on the leaf as well as all the other specimens. The unusual second lobe is similar to the state of the corresponding lobes in Abgrallaspis rather than in Quadraspidiotus. However, it should again be emphasized that this variation is associated with the
leaf-form and also that the bark-form of *D. kuwanai* is unknown, so that the meaning conveyed by this variation is not determined.

ii. *Diaspidiotus makii* and its group  
(Fig. 3; Pl. I, Figs. 8 & 9; Pl. II, Fig. 10)

When *makii* was transferred from the old and large *Aspidiotus* to *Diaspidiotus*, it was taken as a relative of the North American *D. coniferarum*, another conifer-feeding scale, and its new generic position seemed to be justified (Takagi 1958). The discovery of *Hemiberlesia pitysophila* threw doubt on its position and, further, its resemblance to *Abgrallaspis momicola* was pointed out (Takagi 1969). The distributions of these three species are known only fragmentarily; the published records and material at hand involve localities in southern Japan (including Ryūkyū), Taiwan and Korea. All these species feed on conifers, *D. makii* and *H. pitysophila* occurring on the needles of *Pinus*, and *A. momicola* on the branches of *Abies*. *D. makii* was also recorded on *Podocarpus* in Korea.

![Fig. 3. Pygidial apex. A: Diaspidiotus makii, Hukuoka, Kyūshū. B: Hemiberlesia pitysophila, from the type-material. C: Abgrallaspis momicola, from the type-series.](image)
The resemblance between *D. makii* from Japan and Korea and *H. pitysophila* from Taiwan is very close: they agree exactly or nearly so in the median lobes, anal opening, dorsal macroducts, patterns of sclerotization on the pygidium, and so on. They differ:

1) In *pitysophila* the second lobes are distinct and well sclerotized, though small, whereas in *makii* quite low, ending in a point.

2) In *pitysophila* three or so plates are present laterally to the position of the third lobe, whereas in *makii* none in the corresponding position except for the occasional presence of irregular small ones.

3) In *pitysophila* one marginal macroduct occurs between the median lobes, and one just laterad of the second lobe, whereas in *makii* none of them.

The discriminating characters are reductive on the side of *D. makii*, which shows a pattern derivable directly from *H. pitysophila* on the supposition of reductive changes in the lateral lobes, the exterior plates and the marginal macroducts. In other features, for example in the body size and the number of dorsal ducts, associated obvious reductive changes are not found in *D. makii* in comparison with *H. pitysophila*. The reductive changes are primarily unrelated to each other and may not be the result of a single undivisible process.

*A. momicola* disagrees rather remarkably with *D. makii* and *H. pitysophila* in the median lobes appearing more robust, and in the dorsal macroducts a little more complicated in arrangement on the pygidium and lacking on the fourth abdominal segment. It agrees with *D. makii* by the absence of the marginal macroduct between the median lobes, and with *H. pitysophila* by the distinct second lobes and by having plates laterally to the third lobes. Here again, a comparison is made between the bark-form of *A. momicola* and the leaf-forms of *D. makii* and *H. pitysophila*, so that the difference between them may be a little exaggerated for their real relationship. In fact, it is no doubt that *A. momicola* and *H. pitysophila* are congeneric and so should be referred together to *Abgrallaspis* if this genus is valid.

I have little doubt that these three species are really close. Then, where should this group be placed generically? *Diaspidiotus* can not accept it any longer; *makii* may be retained in that genus, but the other two species are inconsistent with the genus. It may be referred to *Abgrallaspis*, but then *makii* will make an exception.

iii. A revival of *Comstockaspis*

*Clavaspidiotus* and *Comstockaspis*

Takagi & Kawai (1966) erected the genus *Clavaspidiotus* for their species *C. abietis* and included within that genus *Aspidiotus tayabanus* and *Quadraspidiotus cryptus*. They suggested that *Quadraspidiotus perniciosus, Q. macroporanus*
and *Q. paraphyses* have "unmistakable similarities" to the *Clavaspidiotus*-species, the difference between these groups lying on the presence of one more pair of lobes (the fourth lobes) in the latter group. In 1969, taking a trial to unite *Quadraspidiotus* with *Hemiberlesia*, I wrote: "It should be added here that some species, *perniciosus* and allies, which are referred to *Quadraspidiotus* by recent authors, have a certain peculiar character in common and so can not be easily thrown into the enlarged genus *Hemiberlesia* together with the other *Quadraspidiotus*-species." The allied species of *perniciosus* are *macroporanus* and *paraphyses* as mentioned, and for this group the name *Comstockaspis* (type-species: *Q. perniciosus*) is available. "A certain peculiar character" means the bifurcate plates occurring laterally to the third lobes in this group. These plates, quite distinct in shape from the other plates occurring in the posterior segments, are rather suggestive of the chelate plates of the Furchaspidina, though still different therefrom remarkably. I have not encountered with forms having such plates in the remain of *Quadraspidiotus*, and in its allied genera except for *Clavaspidiotus*, so that the separation of *Comstockaspis* from *Quadraspidiotus* is possible.

*Comstockaspis* and *Clavaspidiotus* are not only common in the bifurcate plates but also similar in other features. In one species of *Comstockaspis* and two authentic species of *Clavaspidiotus* one paraphysis is much elongate and ends in a prominent knob on each side of the pygidium, but the knobbed paraphyses do not correspond between the two genera. In *Comstockaspis* the knobbed one is the outer of the pair between the seventh and eighth abdominal segments, whereas in *Clavaspidiotus* it is, as in *Clavaspis*, the inner of the corresponding pair. Combinations of characters of the lobes and paraphyses in the two genera are given in Table 2. As shown here, the generic separation is based primarily on the presence or absence of the fourth lobes. The number of the pygidial lobes can not be essential in generic division (see p. 8), yet may reflect a difference in evolutionary stage. Knobbed paraphyses are sporadic in various groups of the

<table>
<thead>
<tr>
<th>Outer paraphysis</th>
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<th>paraphyses</th>
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<tr>
<td>Knobbed between</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Abd. vii &amp; viii</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Inner paraphysis</td>
<td>abietis</td>
<td>Apicalis (n. sp.)</td>
</tr>
<tr>
<td>Knobbed between</td>
<td>—</td>
<td>(quadriloba)</td>
</tr>
<tr>
<td>Abd. vii &amp; viii</td>
<td>—</td>
<td>layabanus</td>
</tr>
<tr>
<td>Both paraphyses</td>
<td>cryptus</td>
<td>Macroporana</td>
</tr>
<tr>
<td>Fusiform between</td>
<td>—</td>
<td>Perniciosus</td>
</tr>
<tr>
<td>Abd. vii &amp; viii</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Fourth lobes</td>
<td><em>Clavaspidiotus</em></td>
<td><em>Clavaspis</em></td>
</tr>
<tr>
<td>Present</td>
<td>Fourth lobes absent</td>
<td>—</td>
</tr>
</tbody>
</table>

**Table 2. Characters of lobes and paraphyses in *Clavaspidiotus* and *Comstockaspis*.**
Diaspididae; this character is presumed to be a specialization. The fact that the patterns of this specialization are heterogeneous between Comstockaspis and Clavaspidiotus suggests that the two do not merely correspond to different evolutionary stages. By this reason both the genera may be better kept in spite of all other similarities between them.

Comstockaspis, as here taken, comprises three known species. The widely distributed C. perniciosa is generally supposed to be of Chinese origin. C. macroporana occurs throughout Japan. C. paraphyses is distributed in southern half of Japan and unlike the preceding two restricted to Castanopsis and Quercus. The latter two species suggest that the genus is East Asiatic and, so, support the view that C. perniciosa was originated somewhere in that region.

Clavaspidiotus definitely comprises three described species. C. tayabanus (originally an Aspidiotus) was recorded from the Philippines and Taiwan; I have examined specimens supposedly belonging to this species and collected in Java, Singapore, Taiwan and Okinawa on various plants. C. cryptus (originally a Quadraspidiotus) occurs in China on Juniperus. The type-species C. abietis inhabits Abies and is known from central Japan. Further, Clavaspis quadriloba from Queensland, Australia, and another form (Clavaspidiotus apicalis n. sp.) from Southeastern Asia and Egypt may be referred to the genus. If this composition is right, Clavaspidiotus is largely uncoincident with Comstockaspis in distribution.

Comstockaspis perniciosa and C. macroporana
(Fig. 4)

C. perniciosa, the notorious San Jose scale, is distributed over the world, but since Marlatt’s (1906) investigation it has been accepted that the species is a native of north China and has widely spread through human agencies. In Japan the situation may have not essentially changed from Marlatt’s days, the occurrence of perniciosa seeming largely concerned with orchards and other environments under human impact. C. macroporana occurs throughout Japan and has hitherto been unknown from other parts of the world. It is found on some wild plants and also in abundance in such environments as university grounds. In recent years its severe outbreaks on chestnut trees have been reported from some localities of southern Japan, thus proving its perniciousness.* At times this species was confused with perniciosa, and there has been made no systematic investigation on their relation in distribution and host plants. The materials at hand of both species are still insufficient to picture even a rough

* Infestations by this scale on chestnut trees are especially heavy in the Tyūgoku district, west Honsyū, and Ōita-ken, north Kyūshū. Its outbreak in Ōita-ken has been reported in technical circulars by Hirayama (1969—) of the Ōita Prefectural Agricultural Research Center at Usa.
pattern of their ecological interrelation.

When *C. macroporana* was first described from material collected at Sapporo, its distinctness from *C. perniciosa* was clear in the external characters of the adult females. Materials from other localities show broad individual variations extending towards *C. perniciosa*, so that it is now not always easy to refer isolated specimens to either. However, assignment of material to *perniciosa* or *macroporana* has been possible in terms of colonies.

In connection with the present study I have compared in detail adult female specimens of *C. perniciosa* from six colonies collected in USSR and eight in Japan, and those of *C. macroporana* from 13 colonies, besides the type-series, all collected in Japan. The characters examined are: the shape of the anal opening; the number of the pygidial macroducts; the number of the prepygidial macroducts and their distribution; and the shape of the second lobes.

It has been possible to obtain from not all these colonies excellently prepared specimens sufficiently numerous for comparison. In some colonies even all of the available specimens are limited in number. So, parameters of three characters are here given for two selected colonies of each species in the expectation that they may well show specific trends. The differences in these three characters show themselves significant between the species (Fig. 4).

The trends shown by the two species are summarized as follows:

1) The anal opening is orbicular or more or less oblong, but not much elongate, in *C. perniciosa*. In *C. macroporana* it shows a wide range of variations, at one extreme being indistinguishable from an oblong one in *C. perniciosa* and at the other extreme much longer than wide and amygdaloid in outline, with the posterior end pointed. The amygdaloid type is usual in *C. macroporana*.

2) The second lobes are usually once or at times twice notched on the lateral oblique margin in *C. perniciosa*. In *C. macroporana* these lobes have a tendency to be serrate, though at times notched only once or twice. Their shape is, however, often obscured by marginal effacement in full-grown individuals.

3) *C. macroporana* shows an obvious tendency to have more numerous pygidial macroducts. Further, in this species the interspace between the median lobes is often provided with a pair of macroducts; for example, in Colony MS (see Fig. 4) 28 individuals out of a total of 44 obviously have paired ducts in this space, whereas others can not be determined as to this character or seem to have a single duct. To trace the course of a duct to the orifice is not always easy, but some individuals of *C. macroporana* seem to have actually a single macroduct between the median lobes. It should be emphasized that in *C. perniciosa* paired macroducts have never been seen in the median interlobar space, which is provided probably always with a single macroduct.

4) Prepygidial macroducts are absent or present in *C. perniciosa*. They
Fig. 4. Dice-grams for number of prepygidial macroducts on one side of body (a), number of pygidial macroducts (b), and ratio of length to width (length/width) of anal opening. PS: *Comstockaspis perniciosus*, Sochi, Caucasus, ex *Prunus*. PT: C.p., Tokushima-ken, Japan, ex *Pyrus serotina*. MO: *Comstockaspis macroporana*, Ōita-ken, Japan, ex *Castanea crenata*. MS: C.m., Sapporo, Japan, ex *Betula platyphylla*. 
are always present and tend to be more numerous in *C. macroporana*. A fairly stable difference between the two species is found in that in *C. perniciosa* they occur, if present, on the second abdominal and preceding segments and in *C. macroporana* on the third abdominal and preceding segments. The prepygidial macroducts are much shorter than the pygidial macroducts, yet recognized by their larger size in comparison with neighbouring microducts.

The presence or absence of lateral macroducts on the third abdominal segment provides a widely applicable key character in distinguishing the two species, though there are still found rare exceptions. The other differences are found largely in trend, the ranges overlapping between the species, so that no single character can always serve to distinguish the two. However, an identification with *C. macroporana* is often easy on the basis of an amygdaloid anal opening or a large number of pygidial macroducts, too. As far as the present study goes more than several specimens from a single colony may be sufficient for specific identification.

*C. macroporana* is probably native to Japan, corresponding to *C. perniciosa* in China. Evidences at hand, though meagre and indirect, suggest that they are good species. Morphologically they form together continuous variational ranges of characters. One extreme and its narrow adjacent part of each range are occupied by *C. perniciosa*, while the other extreme and a broad intermediate part by *C. macroporana*. In either species, each colony seems to have more or less limited ranges. Thus, through various forms of *C. macroporana* there may occur in each character a morpho-cline towards *C. perniciosa*.

**Clavaspidiotus tayabanus** and *C. abietis*

(Fig. 5; Pl. III, Fig. 12)

The type-specimens of *C. tayabanus* from Luzon are missing (S. Nakahara in litt.), and no material from the Philippines has been available for the present study. The published descriptions are too brief to make a clear identification. The specimens here supposed to belong to this species are as follows:

3) One: Singapore, on *Ficus* sp., G. Compere (Compere Coll. No. 530).
4) Eleven: Java, on “woody shrub or tree”, 7-xii-1901, C. L. Marlatt.

Except for the specimens from Okinawa, all belong to the USNM collection. Only two specimens from Okinawa are comparatively in good condition.

The pygidial lobes are fairly stable in shape among the examined specimens;
median lobes convergent, yet separated by a narrow but distinct space of a uniform width between them, each lobe robust, with one or several notches on outer side; second lobes much smaller, serrate on oblique outer margin, the apex narrow or almost pointed; third and fourth lobes small, pointed apically. The paraphyses show some variations: the paraphysis at the outer basal corner of the median lobe is at times little knobbed, yet always the longest; the one at the inner base of the median lobe is at times somewhat knobbed. Dorsal macroducts long and slender; one between median lobes; two (?) or three between paraphyses in interspace of median and second lobes; 6–10 in a single or irregularly double, oblique row arising at inner base of third lobe; one between third and fourth lobes near margin; 4–8 in a row arising at inner base of fourth lobe and running parallel with the former row, with 1 isolated duct laterally and near margin. Abd. iv lacking dorsal macroducts. Much shorter macroducts occurring along margin in prepygidial segments as far as prothoracic tubercle, few. Several submedian dorsal microducts on abd. i–iii (found only in the specimens from Okinawa and indiscernible in the other specimens perhaps owing to their poor condition).

When *C. abietis* was described from Japan, it was taken for another species almost exclusively owing to its host plant. Specimens at hand, from Tōkyō, Kyōto and Okayama-ken, were all collected on the conifer *Abies firma*. As stated, the identity of *C. tayabanus* still remains uncertain, so that a reliable comparison is not possible between the two species, which are supposed to be very close. So far as based on the present tentative identification of *C. tayabanus*, the two are quite close. I can point out only the following differences (Fig. 5):

![Fig. 5. Pygidial apex. A: Clavaspidiotus tayabanus ?, Taiwan. B: C. abietis, from the type-series.](image-url)
1) In *C. tayabanus* the second lobes are narrow and even pointed, whereas in *C. abietis* broadly rounded and similar in shape to the median lobes.

2) In *C. tayabanus* the third lobes are small and conical in outline, being similar in shape and size to the fourth lobe (at times smaller than the fourth), whereas in *C. abietis* well developed and roundish at the apex.

Takahashi (1933) gives a figure of *C. tayabanus* ("*Chrysomphalus tayabanus*") on the basis of specimens collected in Taiwan on *Pyracantha koidzumii* (Rosaceae). His figure does not agree with my observation concerning the differences given above, but the question of minute exactness may not be excluded from it. It should again be emphasized that the present specimens of *tayabanus* are uniform in the pygidial fringe in spite of a diversity in their localities.

*Clavaspidiotus apicalis* n. sp.

(Fig. 6; Pl. III, Fig. 13)

Diagnosis. Body broadly pyriform, a little longer than wide, derm remaining membraneous throughout prepygidial region. Pygidium broad, triangular, with free margin little rounded, abd. iv lowly convex laterally. Median lobes set close, connected through a narrowly sclerotized margin between them, each lobe rounded apically, deeply notched once on outer margin, which is much longer than the inner. Second lobes rounded apically, paucidentate on long, oblique outer margin. Interspace between median and second lobes sclerotized on margin. Third lobes smaller than the second, blunt or narrowly rounded apically. Fourth lobes rather prominent, conical, sharply pointed apically. Laterally to the fourth lobe there are usually found one or two prominences, which are as large as or smaller than the fourth lobe, more or less conical, and little or weakly sclerotized. Plates absent between median lobes and between median and second lobes; two between second and third lobes, not extending beyond level of apex of second lobe, the inner divided into two slender processes, the outer simple; three bifurcate plates well developed between third and fourth lobes. A prominent paraphysis at inner basal angle of median lobe, extending anteriorly near to anal opening (which is subapical in position), clavate; another larger paraphysis between median and second lobes, terminating in a knob; a pair of much smaller paraphyses between second and third lobes. Dorsal setae on median and second lobes much shortened. Anal opening oblong, 1.4–1.8 times as long as wide, removed from bases of median lobes by about twice its length. Perivulvar disc pores absent. Dorsal macroducts long and slender, not discernible between median lobes; two or three between abd. vii and viii just laterally to the paraphysis or partly superimposed on it; 8–11 in a single oblique row originating between second and third lobes; 8–11 in another single row originating near base of fourth lobe and running parallel with and extending further than the former row, at times with other one or two just outside; 3–6 in a single
Fig. 6. *Clavaspidiotus apicalis* n. sp. Pygidium and pygidial apex, based on the holotype.

oblique row on abd. iv; 2–5 at posterolateral corner of abd. iii; at times 1–3 at posterolateral corner of abd. ii. Much shorter macroducts scattered along lateral margin of prepygidial region, few in number (in some specimens two on abd. iii, 2–4 on ii, two or three on i, three on metathorax, and one or two on mesothorax). Ventral microducts along free margin of pygidium laterally to fourth lobe (on abd. iv and v). Dorsal microducts scattered submarginally on abd. iii and preceding segments, and submedially on abd. i–iii; the submarginal microducts
are quite short, being about as long as the longest diameter of the orifice (the
dorsal microducts are variable in number, and may at times be absent). Pro-
somatic tubercle much smaller than antennal tubercle. Pygidium with mediobasal
and laterobasal scleroses dorsally and perivulvar and apical scleroses ventrally,
all well shown.

Second instar female with median lobes separated from each other; with
interspace between median and second lobes not sclerotized on margin, and with
plates between median lobes and between median and second lobes; otherwise
similar to adult female in pygidial fringe and paraphyses.

Material. Three adult females mounted on one slide (one the holotype),
"on shaddock tree/Java: at n. 4./Hodson, et al. Colrs/March 9, 1938/n. 4–
76159"; one adult female, "on Cyllicodaphne sebifera/Buitenzorg, Java/R. S.
Woglung Coll./# 142/Jan. 1911"; one adult female, "On Citrus/Java/R. S. Woglung
Jan. 1911"; two adult females, "Buitenzorg, Java/E. Jacobson, Coll./Jan. 1915/
# 3"; one adult female, "On Pangium leaves/Buitenzorg, Java/at Quar. D. C./
Java at Phila./Wm J. Ehinger/July 11. 1933/Phila. # 18194"; one adult female,
"Philippines/ex Citrus paradisi/III–28-47/San Pedro 5296/L. Hart (47-1199)"
; five adult females, "On Pomelos/Singapore, S.S.: at Boston/J. T. Beauchamp Colr./
July 15 1936/Boston no. 118 67"; 3 adult females, "On Pomelos/Penang, S. E.
Indies: at Boston/A. O. Hardy, Coll./March 14, 1937/Boston–12913"; eight adult
females, one second instar female, "On Lemon/Egypt: at Phila./J. A. Ramos,
Coll./Oct. 20, 1935/Phila.–28709."

The slides are all deposited in the collection of USNM.

The holotype is comparatively in good condition, but part of its prepygidial
region is lost. The other specimens, except the one from the Philippines, are
in poor condition. They well agree, however, in the pygidial characters. One
paratype from Java, which is well expanded on the slide and has some eggs
within the body, measures 1.3 mm in length and 1.1 mm in width; its pygidium
measures 300 micra in length and 500 micra in width (width = distance between
the anterolateral bases of the fourth abdominal segment). Anal opening is 13–
14 micra long in some specimens measured.

Remarks. In comparison with the nucleus of the genus, represented by C.
abietis or by C. tayabanus as here understood, the present species is peculiar as
follows:

1) The interspace between the median lobes and also that between the
median and second lobes are sclerotized along the margin, so that the pygidial
apex is sclerotized in a broad, continuous region. This region lacks plates, and
the setae in it are much shortened.

2) The interspace between the median and second lobes is provided with
only one strong paraphysis. This paraphysis is probably homologous with the inner component of the pair expected to be found at that position, because it is accompanied by dorsal macродucts just on its outer side. A small, slender sclerosis is found at the inner base of the second lobe; it is, then, the reduced outer paraphysis of the pair expected there.

All this suggests a much derived condition of the present species from the nucleus of Clavaspioïdotus. Characteristics of the genus nevertheless persist in the bifurcate plates, knobbed paraphyses, fourth pygidial lobes, etc., so that the inclusion of the present species in the genus is possible.

So far as judged from the present material, domesticated forms of Citrus are main host plants of this scale insect. Its wide distribution in the Old World tropics may partly be due to human agency.

iv. Isolated species

In the original descriptions the Japanese species Diaspidiotus spiraspinae and Quadraspidiotus williamsi were compared with certain Central Asian species on the basis of published descriptions of the Central Asian ones. Even if their resemblances are really close, their distant connections in distribution leave doubt whether the Japanese species are really closely related phylogenetically with the Central Asian ones. In the present situation that faunal investigations are obviously far from exhaustive in Japan and adjacent areas it is fruitless to proceed further with the “isolated” species. Another species given below also has no closely related species known in East Asia.

Diaspidiotus hydrangeae n. sp.
(Fig. 7; Pl. II, Fig. 11)

Diagnosis. Body broadly pyriform, a little longer than wide; derm remaining membraneous in prepygidial region. Pygidium broad, roundish on free margin, abd. iv lowly convex laterally. Median lobes well sclerotized, set close, leaving a slender space between them, each lobe about as long as wide, with a deep subapical notch on mesal side, and with one or two deep notches on outer side a little basally to the level of the mesal notch, the apex flatly rounded. Second and third lobes practically obsolete. Plates slender, not surpassing apices of median lobes, little fimbriate between median lobes; two between median and second lobes and three between the second and third, spiniform or a little branched on lateral side; none laterally to third lobe, but several microducts are often produced beyond margin on abd. v and vi. Anal opening elliptical, ca. 1.3–2.3 times as long as wide, as long as or longer than median lobe, removed from bases of median lobes by ca. 0.8–1.7 times its length. Perivulvar disc pores present, 3–13 in anterolateral group, and 4–9 in posterolateral; median group present or absent, if present with 1–3 disc pores and often dislocated towards one side.
Fig. 7. *Diaspidiotus hydrangeae* n. sp. Pygidium and pygidial apex, based mainly on the holotype.

Dorsal macroducts somewhat reduced in size, yet obviously larger than ventral microducts; one between median lobes, not extending anteriorly beyond anal opening; 2–4 between median and second lobes, enclosed by a pair of strong paraphyses; one on margin on abd. vii just laterally to second lobe, rarely one submarginal on this segment; one marginal between strong paraphyses, leading to a short oblique row of 2–4 submarginal ducts between supposed abd. vi and vii; one marginal and 1–3 submarginal on abd. vi, the submarginal ducts situated anteriorly to the level of the intersegmental row between abd. vi and vii and at times on extension line of that row; 5–11 in an oblique row between abd. v and vi, the row single or nearly so, often attaining or passing laterobasal sclerosis of pygidium; 1–3 on abd. v; 7–12 forming more or less of a row, sometimes with other one or two laterally to the row, on abd. iv; 4–8 submarginal, with other one or two marginal, on abd. iii; metathorax and abd. i and ii each with two or three marginal macroducts, and mesothorax usually with one. Antennal tuber-
cles rather large, pointed apically. Prosomatic tubercles much smaller than antennal tubercle, rounded.

Material. Holotype and more than 40 adult females, collected at Masutomi, Yamanasi-ken, central Honshū, Japan, on the stems of *Hydrangea paniculata*, 16-vi-1966, S. Takagi. Found under the thin surface layer of the stems. The holotype is deposited in the collection of the Entomological Institute, Hokkaidō University.

The holotype is a young adult female; most paratypes are full-grown, and in many of them the median lobes are effaced apically.

Some full-grown specimens well expanded on slide measure ca. 1.3–1.7 mm. in length; in 12 specimens the ratio of the pygidial width (distance between laterobasal corners of abd. iv) to the pygidial length (width/length) ranges between 1.6–2.0, mean 1.8. In 41 specimens the total of perivulvar disc pores ranges from 22 to 36, mean 27.4; out of the 41 specimens 15 are provided with the median group, which is represented by a single disc pore in six specimens, by two in other six and by three in the remaining three. Based on about 10 specimens, the marginal macroduct occurring between the median lobes measures 35–42 micra in length; and the antennal tubercles 11–18 micra in height.

Remarks. The new species resembles none of the other known Japanese species of *Diaspidiotus*, but is rather similar to several European and North American ones. Its resemblance to the North American *D. hunteri* may be closest, but in the latter the prosoma is somewhat sclerotized at maturity, the anal opening is removed more interiorly, the dorsal macroducts in the mesal two intersegmental rows and the perivulvar disc pores are more numerous, and the median lobes are set rather apart. This comparison is based mainly on Kosztarab's (1963) redescription of *D. hunteri*.

The anal opening is noteworthy of the present species; it is remarkably elongate, often surpassing the median lobe in length and reducing the relative length of the postanal distance.

**NOTES ON THE HEMIBERLESIA PROBLEM**

The same as the preceding section the present notes are notes only, and not by any intention the last word on the problem. In fact, the available information is too meagre, and further evidences are necessary to rouse helpful discussion. The purpose of the present notes is to suggest a possible approach to the problem.

There may be other approaches, of which some are as follows:

1) Colonizing experiments are undoubtedly necessary and the results are decisive as to leaf- and bark-form relations. Leaf-forms on deciduous trees are promising, even if bark-forms are unknown from the trees. After being scrutinized,
host trees, preferably potted and insulated, should be infected in autumn with crawlers hatched from leaves. All adult females found on the leaves from which the crawlers emerged should be mounted for examination.

2) Field observations, combined with serial collections, will also clearly reveal ecophenotypic polymorphism if this takes place. Even arbitrarily collected material, when carefully examined, may at times be fully suggestive.

Experimental and field studies, however important they are, will be limited to a comparatively small number of species, because many species may be obligatory bark-feeders and others seem to be restricted to the leaves of evergreen trees. We do not know to what extent the polymorphism takes place in the genera concerned, and so whether a knowledge of the polymorphism alone will be capable of settling the problem.

3) Adult males are undoubtedly important in scale insect taxonomy and will contribute much to the problem. Our present knowledge on this subject, however, is limited and its rapid growth is not expected.

I think that a critical reconstruction of groups, based on routine adult female characters, is readily feasible and worthy of trial for a considerable number of species now allocated to the genera concerned. Resemblances in external structures other than those hitherto evaluated as of generic value must be taken in consideration in forming species-groups. A group thus formed should not be abandoned when support is found to it in biogeographical pattern, in host association, in character-trend, in supposed ancestral-descendant relation, etc. A practical way is to try out the possibility of regroupment for species with a particular host association or with distributions falling in an appropriate geographical extent, or preferably with both.

The procedure suggested above is followed in the preceding section of this paper and three groups are formed: one group comprises species from *Diaspidiotus* and *Quadraspispidiotus*, another from *Diaspidiotus* and *Abgrallaspis* or *Hemiberlesia* s. lat., and the last is composed of species hitherto referred to *Quadraspispidiotus*, from which it is supposed to be distinct. It is suggested, then, that on the generic side these genera would be polyphyletic in their current compositions and that on the specific side supposedly close species are allocated to different genera. This does not immediately mean the invalidity of these genera themselves, but gives rise to doubt as to other parts of their compositions.

On the assumption that the reduced state of the lateral lobes of the pygidium is a derived character, a *Diaspidiotus*-type can be derived either from a *Quadraspispidiotus*-type or an *Abgrallaspis*-type. When the bifurcate plates are ignored and the knobbed paraphyses of *Comstockaspis paraphyses* or that species itself is not counted, *Comstockaspis* can be included within *Quadraspispidiotus*. The Japanese *Diaspidiotus spiraspinae*, *D. hydrangeae* (n. sp.) and *Quadraspispidiotus*
*williamsi* are isolated in Japan and adjacent areas, so that they are compared with species from remote parts of the world. There may be some truth in the question whether these Japanese species are related in phylogeny with the Central Asian or North American species brought to comparison. Thus, parallelism and convergence are presumably involved in the problem. The North American *Hemiberlesia querocola* is outside of *Hemiberlesia* even if the genus is enlarged to tolerable limits; its resemblance to *Hemiberlesia*-species is possibly in convergence. It is necessary first to remove such species. But certain monotypic genera, e.g. *Borchseniaspis* for *Hemiberlesia palmae* and the revived *Chemnaspidiotus* for *Hemiberlesia liquidambaris*, seem to be products merely of a procedure to give too strict a definition to *Abgrallaspis* or *Hemiberlesia*.

A reasonable generic definition may be possible for the united *Hemiberlesia, Abgrallaspis, Diaspidiotus* and *Quadraspidiotus* as once tried (Takagi 1969), and the enlarged genus *Hemiberlesia* thus defined seems to be comparatively discrete from other aspidiotines. *Clavaspis* is one of a few which still have connection, but it should be taken in consideration that this genus is restricted to America, with possible expansions to Africa, Madagascar and Australia.

**Concluding remarks**

Having struggled across the discussion I am under the impression that we have, after all, little of phylogenetic basis to build up working hypotheses in the problem. It was practically the only way for me to try to look at the taxa in question with 'open mind'! Indeed, classification of organisms is basically formed not by individual characters but by our cognition of each taxon as a whole — cognition by pattern in other words. Taxonomy is primarily the expression of our pattern cognition by means of characters. In *The Coccidae* MacGillivray (1921) went about taxonomy in the wrong way, basing his genera on disconnected characters. His system has received much criticism from authors, and evaluation has been tried out on his generic characters. It is now established that some characters, e.g. the presence or absence of perivulvar disc pores, have no generic value by themselves. But other characters are employed by authors in accepting genera about which I am very dubious. Perhaps, the *Hemiberlesia* problem will be completely settled only after phylogenetic evaluation of characters has succeeded. And this may not be possible without comparative studies throughout the ontogeny of various groups of the family.

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**Scale insect taxa mentioned**


*Abgrallaspis howardi* (Cockerell, 1895). Stannard, L.J. Jr., l.c. [leaf-form of *Diaspidiotus ancylius*, on *Ulmus*].


*Chemnaspidiotus* MacGillivray, 1921. Type-species: *Cryptophyllaspis liquidambaris* Kotinsky. Borhzenius, N.S., 1966, Catalogue p. 312 [the genus is accepted as valid].


*Comstockaspis* MacGillivray, 1921. Type-species: *Aspidiotus perniciosus* Comstock. Ferris, G.F., 1937, Microent. 2: 53, 55, 56 [suppressed as a synonym of *Quadraspidiotus*].


*Diaspidiotus* Leonardi, 1898. Type-species: *Diaspis ancylius* Putnam. Balachowsky, A., 1950, Les Cochenilles V: 488-534 [Palaearctic spp.]. — Remarks: The nomenclature of this genus is confused, and I am in no position to discuss about it. For
a while, exclusively for convenience of discussion on the taxonomic problem, I prefer to credit the genus to Leonardi (1898) and with a distinct fixation of the type-species.


PLATES
Pygidium:

Fig. 8. *Diaspidiotus maki*, Hukuoka, Kyūsyū.
Fig. 9. *Hemiberlesia pilysophila*, from the type-material.
Pygidium:

Fig. 10. *Abgrallaspis momicola*, from the type-series.
Fig. 11. *Diaspidiotus hydrangeae* n. sp., one of the paratypes.
Pygidium:

Fig. 12. Clavaspidiotus tayabanus ?, Yohana-dake, Okinawa.
Fig. 13. Clavaspidiotus apicalis n. sp., holotype.