DISC PORES OF DIASPIDIDAE: MICROSTRUCTURE
AND TAXONOMIC VALUE
(HOMOPTERA: COCCOIDEA)

By Sadao Takagi

Abstract


Disc pores of some diaspids were observed in a scanning electron microscope. Perivulvar disc pores are quinquelocular and, in most of the species observed, provided with eminent processes, which are capitate, sulcate or spatulate. Simpler abdominal disc pores are found in primitive forms. Spiracular disc pores are tri- or quinquelocular, and subdivided into some types. Disc pores are distinguished into 2 groups according to the manner of secretion. So far as the species examined are concerned, the types of disc pores well correspond with taxonomic groups. In structure the spiracular and perivulvar disc pores of the Diaspididae are supposed to have a common origin.

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INTRODUCTION

In 1979 Miller and Kosztarab presented in their review SEM photomicrographs of the perivulvar disc pores of 2 diaspidid species and suggested that highly magnified features of disc pores have "considerable potential as taxonomic characters". One decade has passed since that time, but, so far as I am aware, no attempt has yet been made to realize the supposed potential. My SEM observations are still limited to a small number of species, but afford some outlook on the taxonomic significance of the microstructure of disc pores in the Diaspididae. The 2 types of perivulvar disc pores presented by Miller and Kosztarab seem prevailing in the family and little or only a little variable as will be shown. Simpler types of abdominal disc pores have been found in more or less primitive forms. Spiracular disc pores (or, to be more exact, perispiracular disc pores) are also represented by some types. Disc pores are different not only in structure but also in secreting manner. The recently discovered *Ulucoccus danumensis* affords a clue to the evolutionary interpretation of the various types of disc pores, and the spiracular and perivulvar disc pores are supposed to have a common origin in structure.

MATERIAL

In this paper SEM photomicrographs are presented for the following 19 species ([P] in the list stands for the perivulvar (or abdominal) disc pore, and [S] for the spiracular disc pore). For methods adopted see Takagi (1990: this issue, p. 17).

*Spiracular disc pores are usually, and perivulvar disc pores often, covered by their own secretion. Sometimes material was treated with chloroform for several days or in an ultrasonic cleaner.*

*U*lu*coccus danumensis*. [PS]. Malaysia (Sabah), on *Dinocloia scabrida*. Figs. 1, 21 and 26.

*Megacanthaspis langtangana*. [PS]. Nepal (Langtang Valley), on *Persea duthiei*. Figs. 2 and 27.

*Nikkoaspis shiranensis*. [P]. Japan (Kyoto·hu), on *Sasa sp.* Fig. 3.

*Chionaspis alnus*. [PS]. Japan (Sapporo), on *Alnus japonica*. Figs. 4, 23 and 28.

*Pinnaspis boehmeriae*. [P]. Japan (Kyoto·hu), on *Boehmeria spicata*. Fig. 5.

*Avulicaspis distylii*. [P]. Japan (Okinawa), on *Distylum racemosum*. Figs. 24 and 25.

*Pseudaonidas prunicola*. [PS]. Japan (Sapporo), on *Prunus lannesiana*. Figs. 6, 29 and 30.

*Fiorinia pinicola*. [P]. Japan (Kyoto), on *Pittosporum tobira*. Fig. 7.

*Lepidosaphes pallidula*. [P]. Japan (Amami·Osima), on *Euonymus japonicus*. Figs. 8 and 34.

*Lepidosaphes ulmi*. [PS]. Japan (Sapporo), on *Crataegus jozana*. Figs. 9, 31 and 32.

*Andaspis crawii*. [PS]. Japan (Tokuno·Simia), on *Castanoposis cuspidata*. Figs. 10 and 33.

*Thysanaspis perkensi*. [P]. Taiwan (Kuan·tzu·ling), on *Litsea akoensis*. Figs. 11 and 22.

*Lopholeucaspis japonica*. [PS]. Japan (Sapporo), on *Betula platyphylla*; Japan (Toyama), on *Enkianthus perulatus*. Figs. 12, 19, 20 and 37 (Sapporo); Figs. 35 and 36 (Toyama).

*Parlatoria camelliae*. [PS]. Japan (Osaka), on *Camellia sasanqua*. Figs. 13 and 38.


*Cryptoparatorea leucaspis*. [P]. Japan (Hukuoka·ken), on *Chamaecyparis obtusa*. Fig. 15.

*Odonaspis greeni*. [PS]. Japan (Hyogo·ken), on *Miscanthus sinensis*. Figs. 16, 40 and 41.

*Pseudaonidas paonae*. [PS]. Japan (Osaka), on *Camellia sasanqua*. Figs. 17 and 42.
Aspidiotus cryptomeriae. [P]. Japan (Sapporo), on Taxus cuspidata. Fig. 18.

**Observations**

Abdominal disc pores

The adult female of *Ulucoccus danumensis* is provided with tri- or quadrilocular disc pores on the ventral surface of the abdomen. These pores are not perivulvar but submarginal in position, occurring on the 6th and 7th abdominal segments. The trilocular type has been observed in the present study (Fig. 1). The pore is raised on a tubercle, and is partitioned by 3 walls or 'septa', which are united at the centre of the pore.

In the adult females of the other species examined the abdominal disc pores are perivulvar in position (but with supernumerary disc pores in *Lopholeucaspis japonica*). Each pore is not raised but depressed, and is quinquelocular, being partitioned by 5 septa, which are disconnected with each other at the centre of the pore. There is a secretory aperture between adjacent septa on the surrounding wall. Each pore, therefore, has 5 apertures. There is a pit on the bottom at the centre of the pore (except in *Thysanaspis perkinsi*).

In *Thysanaspis perkinsi* the septa appear a little swollen as compared with those in *Ulucoccus danumensis* (Fig. 11). In the other 17 species each septum is expanded to form an eminence. In a pore the septal processes are arranged like petals of an opened or half-opened flower, so that they may be called petals. Three types of petals may be recognized as follows.

1. Spatulate type. In *Lopholeucaspis japonica* (Fig. 12) the petals are flat on the inner surface and broadened toward the apex, which is truncate and scarcely or only slightly swollen.

2. Capitate type. The petals are swollen apically to form a cap. This type is represented by *Megacanthaspis langtangana* (Fig. 2), *Nikkoaspis shiranensis* (Fig. 3), *Chionaspis alnus* (Fig. 4), *Pinnaspis boehmeriae* (Fig. 5), *Aulacaspis distylii* (Figs. 24 and 25), *Pseudaulacaspis prunicola* (Fig. 6) and *Fiorinia pinicola* (Fig. 7). The perivulvar disc pores of *Lepidosaphes pallidula* (Fig. 8), *Lepidosaphes ulmi* (Fig. 9), and *Andaspis crawii* (Fig. 10) are also referable to this type, though the caps of the petals often appear less distinct and a little constricted medially.

3. Sulcate type. The petals are grooved longitudinally on the inner surface. This type has been seen in *Parlatoria camelliae* (Fig. 13), *Microparlatoria itabicola* (Fig. 14), *Cryptoparlatoria leucaspis* (Fig. 15), *Odonaspis greeni* (Fig. 16), *Pseudaonidia paeoniae* (Fig. 17), and *Aspidiotus cryptomeriae* (Fig. 18).

Abdominal disc pores in the 2nd instar

The 2nd instar male of *Lopholeucaspis japonica* is provided with disc pores on the ventral surface of the abdomen. These pores are located submarginally on the 6th and 5th segments (Fig. 19). In structure they are not much different from the perivulvar disc pores of the adult female, with the petals, however, apparently less developed (Fig. 20).

Spiracular disc pores

In *Ulucoccus danumensis* the spiracular disc pores (Fig. 26) are trilocular and do
not appear to be different in structure from the abdominal disc pores. Trilocular spiracular disc pores are found also in other diaspidids; examples here are *Megacanthaspis langtangana* (Fig. 27), *Chionaspis alnus* (Fig. 28), *Pseudaulacaspis prunicola* (Figs. 29 and 30), *Lepidosaphes ulmi* (Figs. 31 and 32), *Andaspis crawii* (Fig. 33), and *Microparlatoria itabicola* (Fig. 39). They are simple in structure in the 1st 3 species, with the septa, however, apparently thickened as compared with the disc pores of *U. danumensis*.

In *L. ulmi* and *A. crawii* the septa are even expanded to form processes, which are, however, less developed than in the perivulvar disc pores of the same species, and there is a pit on the bottom at the centre of the pore. In *M. itabicola* the septa are also expanded and even grooved; they are connected with each other around the centre of the pore, and there is no pit on the bottom of the pore. It might be said that in these species the spiracular disc pores are incomplete copies of the perivulvar disc pores.

Quinquelocular spiracular disc pores are found in other species and also variable in detailed structure. In *Lopholeucaspis japonica* the spiracular disc pores of the adult female (Fig. 35) are similar to the perivulvar disc pores, being provided with well-developed septal processes and a central pit; those of the 2nd instar male and female (Fig. 37) are similar to the abdominal disc pores of the 2nd instar male in having ill-developed septal processes. The spiracular disc pores of *Parlatoria camelliae* (Fig. 38) are also similar to the perivulvar disc pores of the same species, having grooved petals, but are different from the latter in having the petals connected with each other around the centre and in lacking a pit on the bottom. *Odonaspis greeni* (Figs. 40 and 41) and *Pseudaonidia paeoniae* (Fig. 42), on the other hand, have simpler spiracular disc pores, which are different from the perivulvar disc pores of these species in having little expanded septa.

**Secretion**

The secretion of the disc pore, when discharged from the secretory aperture, takes the form of a slender cylinder, which is depressed on one side to form a lumen and curved with the depressed side inside. Three cylinders can be produced from a trilocular disc pore, and 5 from a quinquelocular one, at a time. The disc pores may be divided into 2 groups according to the secreting manner as follows.

1. Disc pores producing excurved wax cylinders. The cylinder is secreted with the depressed side faced toward the circumference of the disc pore, and is, therefore, curved toward the circumference ['abduction']. It grows to a long and curled thread. Sometimes the wax thread is strongly coiled and then broken into circular pieces (Fig. 34). In *Ulucoccus danumensis* both the abdominal (Figs. 1 and 21) and the spiracular disc pores (Fig. 26) are abducent. In the present study it has been found that the spiracular disc pores of some other species belong to this group (Figs. 27, 28, 30 and 32).

2. Disc pores producing incurved wax cylinders. The cylinder is discharged with the depressed side faced toward the centre of the disc pore, and is, therefore, curved and led toward the centre ['adduction']. Fig. 25 shows cylinders in different growing stages; it seems that they are held between the septal processes while growing. Eventually the cylinders grow into circular pieces (rings or lunulae), which meet at the centre of the disc pore (Fig. 23) and then are loosened to go out
of the pore (Fig. 24). The perivulvar disc pores of some species definitely belong to this group (Figs. 23–25).

It is to be ascertained whether throughout the family the spiracular disc pores are always abducent, and the perivulvar disc pores adducent, in secretion. Abdominal disc pores also occur in the 2nd instar males of leucaspidines. In the present study, however, no secretion of the larval abdominal disc pores has been observed in *Lopholeucus japonica*.

**CORRESPONDENCE WITH TAXONOMIC GROUPS**

Knipscher et al. (1976), Miller and Kosztarab (1979), and Ben-Dov (1988) presented SEM photomicrographs of the perivulvar disc pores of *Chionaspis nyssae*, *Hemiberlesia lataniae*, *Pseudaulacaspis pentagona*, and *Odonaspis anneckei*. Even with these added, micrographs available here are limited to 23 species belonging to 19 genera. In Table 1 these species as represented by their genera are located in a scheme formulated for subclassifying the Diaspididae on the basis of the organization of the pygidial margin. This scheme is substantially the same as that proposed by Takagi (1981). Most diaspidids are divided into 2 large groups, Stock I and II, and these are subdivided according to organizational levels, which represent evolutionary stages from primitive (lower) to advanced (upper) ones. Table 2 shows how the types of perivulvar (or abdominal) disc pores fit in with the scheme.

In Stock I the genera except *Ulucoccus* have perivulvar disc pores of the capitate type. In Stock II the 7 genera at the uppermost level exhibit the sulcate type. Below them *Lopholeucus* shows a simpler type of septal process, and further below

<table>
<thead>
<tr>
<th>Stock I</th>
<th>Stock II</th>
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<tbody>
<tr>
<td>Level III</td>
<td>Lu+Pg</td>
</tr>
<tr>
<td>Lb+D+S</td>
<td>Hemiberlesia</td>
</tr>
<tr>
<td>Andaspis</td>
<td>Aspidiotus</td>
</tr>
<tr>
<td>Lepidosaphes</td>
<td>Pseudaulacaspis</td>
</tr>
<tr>
<td>Fiorinia</td>
<td>Pseudaulacaspis</td>
</tr>
<tr>
<td>Pseudaonidia</td>
<td>Pseudaonidia</td>
</tr>
<tr>
<td>Pinnaspis</td>
<td>Pinnaspis</td>
</tr>
<tr>
<td>Chionaspis</td>
<td>Chionaspis</td>
</tr>
<tr>
<td>Level II</td>
<td>Lb+P+P</td>
</tr>
<tr>
<td>Lb+P+P</td>
<td>Lopholeucus</td>
</tr>
<tr>
<td>Nikkoaspis</td>
<td>Lopholeucus</td>
</tr>
<tr>
<td>Level I</td>
<td>P</td>
</tr>
<tr>
<td>P+S</td>
<td>Megacanthaspis</td>
</tr>
<tr>
<td>Thysanaspis</td>
<td></td>
</tr>
<tr>
<td>Level 0</td>
<td>S</td>
</tr>
<tr>
<td>Ulucoccus</td>
<td>Ulucoccus</td>
</tr>
</tbody>
</table>

*Lb*: lobes (lateral lobes bilobulate); *Lu*: lobes (all unilobed); *D*: pore prominences; *S*: gland spines; *P*: plates or plate-like processes (nonglandulous); *Pg*: plates (glandulous).
Table 2. Types of perivulvar (or abdominal) disc pores in the scheme presented in Table 1.

<table>
<thead>
<tr>
<th>Level</th>
<th>Stock I</th>
<th>Stock II</th>
</tr>
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<tbody>
<tr>
<td>III</td>
<td>Capitate type</td>
<td>Sulcate type</td>
</tr>
<tr>
<td>II</td>
<td>Capitate type</td>
<td>Spatulate type</td>
</tr>
<tr>
<td>I</td>
<td>Capitate type</td>
<td><em>Thysanaspis</em> type</td>
</tr>
<tr>
<td>0</td>
<td><em>Ulucoccus</em> type</td>
<td></td>
</tr>
</tbody>
</table>

comes *Thysanaspis*, in which the perivulvar disc pores are devoid of any septal process. *Ulucoccus* represents the lowest level in the scheme. In this form the abdominal disc pores are not perivulvar but submarginal in position, and are not different from the trilocular spiracular disc pores of the same species in structure and secretion.

It was generally believed for a long time that the spiracular disc pores are quinquelocular throughout the family (this may have been due to the limited power of microscopes available in those days). Owing to this misconception not all drawings published in the past are reliable and our knowledge is still inaccurate as to the number of the loculi in many species. As a matter of fact, trilocular and quadrilocular spiracular disc pores occur in the family. In the present study SEM observations of the spiracular disc pore are limited to 11 species. On the basis of light transmission microscopy it may be stated that the spiracular disc pores are usually trilocular and rarely quadrilocular in the Diaspidinae (Diaspidini and Lepidosaphedini) and quinquelocular (and exceptionally trilocular) in the Aspidiotinae (Aspidiotini, Odonaspidiini, Parlatoirini and Leucaspidini). In Table 1 Stock I corresponds to the Diaspidinae (but *Ulucoccus* may not be included within the subfamily) and Stock II to the Aspidiotinae (*Thysanaspis* may tentatively be included in the subfamily).

Thus the subfamily Diaspidinae may be characterized, at least for its large part, by having tri- or quadrilocular (that is, tri- or quadrisepatate) spiracular disc pores and by the perivulvar disc pores belonging to the capitate type. In the subfamily Aspidiotinae the spiracular disc pores are quinquelocular (but trilocular in *Microparlatoria*) and the perivulvar disc pores belong to the sulcate type (except in the Leucaspidini and *Thysanaspis*).

*Megacanthaspis* and *Nikkosaspis* represent comparatively primitive stages of the Diaspidinae in the organization of the pygidial margin. But they cannot be distinguished from the advanced forms (*Chionaspis* up to *Fiorinia* in Table 1) of the tribe Diaspidini in having distinctly capitate septal processes. In this respect they may be included within the tribe. The species examined of the Lepidosaphedini (*Lepidosaphes* and *Andaspis* in Table 1) are also hardly distinguishable from the Diaspidini in the perivulvar disc pores. However, in *L. ulmi* and *A. crawii* the spiracular disc pores are provided with septal processes, thus differing from the simple disc pores of the Diaspidini.

Two species of the tribe Odonaspidiini, *Odonaspis greeni* and *O. anneckeii* (photomicrograph in Ben-Dov, 1988) closely agree with the 3 species examined of the Parlatoirini (*Parlatoria camelliae, Microparlatoria itabicola*, and *Cryptoparlatoria itabicola*).
leucaspis) in the structure of the perivulvar disc pore. *Pseudoaonidia paeoniae*, *Aspidiotus cryptomeriae*, and *Hemiberlesia lataniae* (photomicrograph in Miller and Kosztarab, 1979), all belonging to the tribe Aspidiotini, agree with the 5 species of the Odonaspidini and the Parlatoriini in having sulcate septal processes, but are different from the latter in having a more or less enlarged central pit.

The spiracular disc pores are not uniform in the few species examined of the Aspidiotinae. It is especially strange that the spiracular disc pores of *Microparlatoria itabicola* are trilocular. But they are quite different from the trilocular spiracular disc pores of the Diaspidinae in having sulcate petals. In this feature *M. itabicola* is similar to *Parlatoria camelliae*, in which, however, the spiracular disc pores are quinquelocular as usual in the Aspidiotinae.

Thus the cursory examination carried out in this paper may be sufficient to show that the spiracular and perivulvar disc pores combine to have a considerable taxonomic value.

**EVOLUTIONARY INTERPRETATION**

Needless to say, the information available is too fragmentary to give an interpretation other than a hasty one of the evolution of the spiracular and perivulvar disc pores. Especially it is still deficient in primitive forms. Fortunately, *Ulucoccus*, a very primitive form of the Diaspididae (Takagi et al., 1990: this issue, p. 1), has been available for the present study and provides a starting point for discussion.

**Origin of the spiracular and perivulvar disc pores**

Various types of disc pores are found in other families of the Coccoidea, but it is beyond the scope of the present study to trace the origin of the diaspidid disc pores in them. So far as based on the state in *Ulucoccus danumensis* it may be supposed that the spiracular and abdominal disc pores of the Diaspididae have a common origin in structure and that the original disc pore was trilocular, with the loculi divided by simple septa, and secreted excurved wax cylinders.

In *U. danumensis* the abdominal disc pores are tri- or quadrilocular (in the examined material these 2 types occur nearly with the same frequency). The number of loculi varies also in other taxa. In *Gynandraspis gabonensis* Balachowsky et Matile-Ferrero, 1980, the spiracular disc pores are usually trilocular and occasionally quadrilocular. In *Chionaspis* the spiracular disc pores are usually trilocular, but in *C. arkhola* Takagi, 1985, quadrilocular. So far as known, the quadrilocular disc pores are rare and occur in taxa in which the spiracular disc pores are usually trilocular. (Sometimes apparent malformations of spiracular and perivulvar disc pores are found among normal disc pores. Fig. 36 shows a spiracular disc pore with 3 septa in an adult female of *Lopholeucaspis japonica*. This pore differs from the normal quinquelocular one not only in the number of septa but also in having no pit on the bottom.)

**Spiracular disc pores**

In the Diaspidini the spiracular disc pores are usually trilocular as in *Ulucoccus danumensis* and produce, so far as known, excurved wax cylinders. The septa are thickened as compared with those in *U. danumensis*. In the 2 species examined of
the Lepidosaphedini the septa are expanded to form processes, which are, however, not fully developed as compared with the perivulvar disc pores. These types of spiracular disc pores can easily be related to the original trilocular disc pore in structure. On the other hand, it is by no means certain that the quinquelocular spiracular disc pores of the Aspidiotinae can also be traced back to this supposed original type. They may have an independent origin, but there is no positive evidence for this possibility, either. On the other hand, the fact that the disc pores of Microparlatoria itabicola are trilocular suggests the other possibility, the origin of the quinquelocular type from the trilocular one. Then it may be expected that M. itabicola is a primitive form of the Aspidiotinae. But it cannot be primitive in other respects. It is unique and derivative in the marginal ducts, which are similar to the 'megapores' of the Lepidosaphedini (but there is no other character in support of the view that this species is somehow related to the Lepidosaphedini). In this case the occurrence of the trilocular type may be associated with the derivative condition of the species and, therefore, atavistic. It is noteworthy that in this species (and Parlatoria camelliae) the septal processes are sulcate as in the perivulvar disc pores. This fact may also support the view that the spiracular and perivulvar disc pores of the Diaspididae have a common origin.

Perivulvar disc pores
A change of the disc pores from the trilocular to the quinquelocular type is again postulated here. It is expected to have happened early in the evolution of the Diaspididae, because the perivulvar disc pores are, so far as known, normally quinquelocular without exception. A change in secretion, from abduction to adduction, is also required. In Stock I (Table 1) the simple tri- or quadrilocular type of abdominal disc pore (of Ulucoccus danumensis) is followed by the capitate type of perivulvar disc pore with no intermediate forms between them. Expected intermediates are found in Stock II, in which Thysanaspis perkinsi shows a simple type of quinquelocular disc pore and Lopholeucaspis japonica a plain type of petal. Already in T. perkinsi the secretion is produced not as threads but as lunulae (Fig. 22). The disc pores of these species may approximately represent the transition from the Ulucoccus type to the capitate type. However, in routine taxonomic characters, the Leucaspidini and the Parlatoriini are supposed to be closely related with each other, and, therefore, the spatulate type of disc pore (represented by Lopholeucaspis japonica) may have evolved to the sulcate type (of the parlatoriines). The disc pores of the 3 species of the Aspidiotini are commonly characterized by the enlarged central pit, which is apparently a secondary modification.

Thus the present material presents perivulvar disc pores which are graded though very incompletely from the simple trilocular type to the capitate type and the sulcate type. It is hoped that further forms will fill up blank spaces in the gradation in either stock.

Differentiation between spiracular and perivulvar disc pores
An evolutionary trend from a simple to a complicated type cannot simply be applied to the spiracular disc pores. It is noteworthy that Lopholeucaspis japonica (a comparatively primitive form of the subfamily Aspidiotinae) has well-developed septal processes in the spiracular disc pores. The parlatoriine species examined are
also provided with septal processes. On the other hand, in *Odonaspis greeni* and *Pseudaonidia paeoniae* (more derivative forms of the Aspidiotinae) the spiracular disc pores are simple, having no septal processes. In the species examined of the subfamily Diaspidinae *Lepidosaphes ulmi* and *Andaspis crawii* (both belonging to the tribe Lepidosaphedini) are provided with septal processes, while the other species (belonging to the Diaspidini) have simple trilocular spiracular disc pores. (The tribes Diaspidini and Lepidosaphedini are referred to the same subfamily, but their phylogenetic relation is unknown.)

The matter may be reconsidered from another viewpoint — differentiation between the spiracular and perivulvar disc pores. As previously stated, spiracular disc pores with septal processes may be regarded as copies or incomplete copies of the perivulvar disc pores of the same species (but are they still abducent in secretion?). Thus they are less differentiated from the latter. On the other hand, the occurrence of simple spiracular disc pores in combination with complicated perivulvar disc pores implies a differentiation and, therefore, an advanced state.

The observed variety of spiracular disc pores in the limited number of the species examined has somewhat exceeded my expectation. Further observations should, therefore, be accumulated before arriving at any tenable conclusion.

**APPENDIX: ODD FORMS**

The species discussed above have been selected to represent some organizational levels of the pygidal fringe in the 2 main phylogenetic stocks of the Diaspididae. Some types of disc pores have been recognized in the species. Their taxonomic significance has been interpreted on the basis of their correspondence with the stocks and levels, and preliminary considerations have been given to their evolution.

There are various diaspidids of which taxonomic positions are uncertain. Scanning electron microscopy of disc pores may sometimes be useful for finding their positions. A few cases are given below.

*Protancepaspis torreyae*

A pupillarial form with no marginal appendages on the pygidium in the adult female and the 2nd instar; 2nd instar female with primitive ducts (which are geminate at the inner end); 2nd instar male with communal ducts surrounded by cluster ducts as in fiorininines.

Material collected in Japan (Tōkyō) on *Torreya nucifera* has been examined. The perivulvar disc pores are definitely of the capitate type, and, together with the trilocular spiracular disc pores (for which no SEM observation was possible owing to the condition of the material), indicate that the species belongs to the Diaspidinae. But they are useless for proceeding further, because, so far as known, the disc pores of the capitate type are uniform, being little different according to taxonomic groups.

*Protancepaspis* shows a mosaic of primitive and advanced characters. I wonder now if this is due to atavistic manifestations of some characters. Further, it might be possible that marginal appendages of the pygidium were lost during the course of evolution in both adult and larval stages. (*P. torreyae* is very close to *P. bidentata*, 89
the other form known of the genus. Dr. E.M. Danzig, pers. commun., 1988, examined *P. bidentata* and found that the supposed 2 species cannot be distinguished in the larval instars. Then they differ almost only in host plant.)

*Natalaspis formosana*

Adult female without lobes and gland spines or plates; with many ducts strewn on both dorsal and ventral surfaces. The 2nd instar male is not much different from the adult and 2nd instar females (differing from them in having a pair of curious processes on the apex of the pygidium), so that it is not helpful in determining the taxonomic position of the genus.

Material collected in Malaysia (Sandakan, Sabah) on *Bambusa vulgaris* has been examined. In scanning electron microscopy the perivulvar disc pores are definitely of the capitate type and the spiracular disc pores are trilocular and similar to those of *Chionaspis alnus* and *Pseudaulacaspis prunicola*. Thus these disc pores strongly suggest that the species belongs to the Diaspidinae and is related to the Diaspidini. *Natalaspis* has hitherto been referred to the Rugaspidiotini by authors.

*Smilacicola*, another Asian genus, has also been referred to the Rugaspidiotini. It is related to the Parlatoriini, manifesting an unmistakable parlatoriine pattern of characters in the 2nd instar, and belongs to the Aspidiotinae. It seems certain now that the genus has nothing to do with *Natalaspis*, and that the resemblance between the adult females of *Natalaspis* and *Smilacicola* is due to convergence. In this connection it should be emphasized that in *Smilacicola* the spiracular disc pores are quinquelocular (however, no material has been available for scanning electron microscopy; further, the known species of the genus are all devoid of perivulvar disc pores).

The present discovery arouses grave doubts about the current concept of the Rugaspidiotini. Most of the species which have been referred to the tribe are known to me merely through the literature. Whatever I can say on the tribe, therefore, is only speculative. I hope, however, that the following comments are not wholly useless for future study.

*Rugaspidiotus* and 2 other genera of the tribe, *Rugaspidiotinus* and *Annulaspis*, are American in distribution. I have examined slide-mounted adult females of *Rugaspidiotinus fuscitatis* (collected at Cabo San Lucas, Baja California, on an undetermined shrub) and found that the spiracular disc pores are definitely trilocular. This species, therefore, possibly belongs to the Diaspidinae. In Africa and Eurasia some forms in addition to *Natalaspis* and *Smilacicola* have been referred to the Rugaspidiotini: *Adiscodiaspis, Osiraspis, Nimbaspis*, and *Prodiaspis*. (The last genus probably includes *Adiscodiaspis tamaricicola* Melenotti, 1916, *Prodiaspis tamaricicola* Young, 1984, and *Circodiaspis sinensis* Tang, 1986; *P. tamaricicola* Young was originally referred to the Xanthophthalminae, but is apparently close to the other two.) According to the descriptions, *Nimbaspis reticulata, Prodiaspis tamaricicola* Young and *Circodiaspis sinensis* have trilocular disc pores. Therefore, it is possible that at least some of these Old World Rugaspidiotini belong to the Diaspidinae.

*Rugaspidiotus arizonicus*, the name-bearer of *Rugaspidiotus*, appears to be an isolated form. According to Howell et al. (1986), it is similar to the tribe Odonaspini, the subfamily Aspidiotinae, in some characters of the 1st instar. In my view the possibility may not be excluded that it is related to the Aspidiotini.
Rugaspidiotus communis Hu Jin-lin, 1987, was described from China, but it may have no relation with R. arizonicus.

After all, the Rugaspidiotini as currently composed are problematical. Some of the species may belong to the Diaspidinae, whereas others to the Aspidiotinae. Their features should be reexamined to reconstruct their patterns of characters. Their larvae and adult males should be examined as far as available. The microstructure of disc pores may also be useful at least for dividing them into the subfamilies.

**TERMS NEUMLY ADOPTED**

In the foregoing lines a few terms are newly adopted in describing disc pores. The term *septa* (sing.: *septum*) is applied to the walls which divide the pore into loculi. A trilocular disc pore is, therefore, *triseptate* and a quinquelocular one *quinqueseptate*. The expansions of septa are called *septal processes* or *petals*. The terms *abduction* and *adduction* (and the corresponding adjectives *abducent* and *adducent*) are adopted for the secreting manners of disc pores. In biology they are usually applied to the action of muscles. Literally, however, they mean ‘leading away’ and ‘bringing together’, respectively.

**REFERENCES**


Fig. 1. *Ulucoccus danumensis*, adult female: abdominal disc pore ($\times 15$ k).

Fig. 2. *Megacanthaspis langtangana*: perivulvar disc pore ($\times 15$ k).
Fig. 3. *Nikkoaspis shiranensis*: perivulvar disc pore ($\times 15$ k).

Fig. 4. *Chionaspis alnus*: perivulvar disc pore ($\times 15$ k).
Fig. 5. *Pinnaspis boehmeriae*: perivulvar disc pores (×15 k).

Fig. 6. *Pseudaulacaspis prunicola*: perivulvar disc pore (×15 k).
Fig. 7. *Fiorinia pinicola*: perivulvar disc pore (×15 k).

Fig. 8. *Lepidosaphes pallidula*: perivulvar disc pore (×15 k).
Fig. 9. *Lepidosaphes ulmi*: perivulvar disc pore (×15 k).

Fig. 10. *Andaspis crawii*: perivulvar disc pore (×20 k).
Fig. 11. *Thysanaspis perkinsi*: perivulvar disc pore (x 30 k).

Fig. 12. *Lopholeucaspis japonica*: perivulvar disc pore (x 30 k).
Fig. 13. *Parlatoria camelliae*: perivulvar disc pore \((\times 15 \text{k})\).

Fig. 14. *Microparlatoria itabicola*: perivulvar disc pore \((\times 15 \text{k})\).
Fig. 15. *Cryptoparlatorea leucaspis*: perivulvar disc pore (×15 k).

Fig. 16. *Odonaspis greeni*: perivulvar disc pore (×15 k).

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Fig. 17. *Pseudoonidia paoniae*: perivulvar disc pore (×15 k).

Fig. 18. *Aspidiotus cryptomeriae*: perivulvar disc pore (×15 k).
Fig. 19. *Lopholeucaspis japonica*, 2nd instar male: pygidium, showing abdominal disc pores (×500).

Fig. 20. *Lopholeucaspis japonica*, 2nd instar male: abdominal disc pores (×15 k).
Fig. 21. *Ulucoccus danumensis*, adult female: secretion of abdominal disc pores ($\times 8$ k).

Fig. 22. *Thysanaspis perkinsi*: secretion of perivulvar disc pores ($\times 15$ k).
Fig. 23. *Chionaspis alnus*: perivulvar disc pores secreting wax cylinders (×8 k).

Fig. 24. *Aulacaspis distylii*: perivulvar disc pores secreting wax rings (×4 k).
Fig. 25. *Aulacaspis distylii*: perivulvar disc pore secreting wax cylinders (×15 k).

Fig. 26. *Ulucoccus danumensis*, adult female: spiracular disc pore and its secretion (×8 k).
Fig. 27. *Megacanthaspis langtangana*, adult female: spiracular disc pores and their secretion (×15 k).

Fig. 28. *Chionaspis alnus*, adult female: spiracular disc pores (×8 k).
Fig. 29. *Pseudaulacaspis prunicola*, adult female: spiracular disc pore ($\times 15$ k).

Fig. 30. *Pseudaulacaspis prunicola*, adult female: secretion of spiracular disc pores ($\times 3$ k).

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Fig. 31. *Lepidosaphes ulmi*, adult female: spiracular disc pore (×15 k).

Fig. 32. *Lepidosaphes ulmi*, adult female: spiracular disc pores and their secretion (×15 k).
Fig. 33. *Andaspis crawii*, adult female: spiracular disc pore ($\times 20$ k).

Fig. 34. *Lepidosaphes pallidula*, adult female: secretion of spiracular disc pores ($\times 8$ k).
Fig. 35. *Lopholeucaspis japonica*, adult female: spiracular disc pore (×20 k).

Fig. 36. *Lopholeucaspis japonica*, adult female: a triseptate spiracular disc pore (×20 k).
Fig. 37. *Lopholeucaspis japonica*, 2nd instar female: spiracular disc pore (×20 k).

Fig. 38. *Parlatoria camelliae*, adult female: spiracular disc pore (×20 k).
Fig. 39. *Microparlatoria itabicola*, adult female: spiracular disc pore (×20 k).

Fig. 40. *Odonaspis greeni*, adult female: spiracular disc pore (×20 k).
Fig. 41. *Odonaspis greeni*, adult female: spiracular disc pore (×20 k).

Fig. 42. *Pseudaonidia paoniae*, adult female: spiracular disc pore (×15 k).