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THE SCALE INSECT GENUS CHIONASPIS:
A REVISED CONCEPT
(HOMOPTERA: COCCOIDEA: DIASPIDIDAE)

By Sadao Takagi


Scientific Results of the Hokkaido University Expeditions to the Himalaya.

Abstract

TAKAGI, S. 1985. The scale insect genus Chionaspis: a revised concept (Homoptera: Coccoidea: Diaspididae). *Ins. matsum. n. s.* 33, 77 pp., 7 tables, 30 figs. (3 text-figs., 27 pls.).

The genus *Chionaspis* is revised, and a modified concept of the genus is proposed. Fifty-nine species are recognized as members of the genus. All these species are limited to the Northern Hemisphere: many of them are distributed in eastern Asia and North America, and much fewer ones in western Asia and the Mediterranean Region. In Eurasia most species have been recorded from particular plants and many are associated with Fagaceae, while in North America polyphagy is rather prevailing and the hosts are scattered over much more diverse plants. In the number and arrangement of the modified macroducts in the 2nd instar males many eastern Asian species are uniform, while North American species show diverse patterns. Two eastern Asian species are supposed to be the most primitive among the extant species of *Chionaspis*. This supposition is supported by the discovery of another form, *Narayanaspis eugeniae*, n.g., n. sp., which occurs in Nepal and is similar to the two species in some characters of the adult females and more primitive than the latter. In some species of *Chionaspis* occurring on deciduous trees leaf-feeding individuals are remarkably different from conspecific bark-feeding ones in the shape of the median lobes, and the leaf-associated forms are interpreted as seasonal manifestations of ancestral phenotypes. A preliminary evolutionary scenario is proposed: the genus *Chionaspis* originated in eastern Asia and invaded North America in a comparatively recent time. Eight species are described as new from the subcontinent of India: *C. arkhola*, *C. castanopsidis*, *C. himalica*, and *C. sivapuriana*, all associated with fagaceous plants; *C. syzygi* and *C. lumbiniana*, both occurring on myrtaceous plants; *C. cornigera*, collected on a lauraceous tree; and *C. clematidis*, feeding on *Clematis*. A new name, *C. cheni*, is proposed for *C. betulae* Chen (preoccupied). A list of the species of *Chionaspis* is given, followed by a list of names which have been referred to *Chionaspis* or *Phenacaspis* (a synonym of *Chionaspis*).

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INTRODUCTION

The genus *Chionaspis* is one of the earliest proposed in the Diaspididae. When Signoret (1869) described it, he referred to it 10 nominal species, which, except a few unrecognizable ones, are now considered to represent only 2 species, *Chionaspis salicis* and *Pinnaspis aspidistrae*. He adopted for diagnostic characters mainly the structures of the protecting scale covers of both sexes. Thereafter, many species with pyriform female scales and white, parallel-sided and carinated male scales were referred to the genus, which, in consequence, became an aggregate of diverse, unrelated forms.

In 1883 Comstock referred to the genus 11 North American species, of which 6 are now recognized as real members. This relatively high score (55%) is due to his biogeographical field: North America is one of the regions where the genus is well represented. In 1899 Green, in the 2nd part of “The Coccidae of Ceylon”, gave a description of the genus on the basis not only of the scale covers but also of the adult females, a detailed one for his time, and enumerated 26 species occurring in Ceylon as members of the genus. In the view adopted in the present paper, however, none of these species really belong to the genus. This again is due to the fauna he worked on: the genus is of the Northern Hemisphere and is very poorly represented in low latitudes as will be shown. The nomenclatorial nucleus of the genus was fixed in that year, the European *C. salicis* having been designated for the nominifer by Cooley.

The breakup of the too broad contents of *Chionaspis* attained a peak in MacGillivray’s (1921) “The Coccidae”. In a sense, however, the most important segregation was that of *Phenacaspis* in 1899. Cooley (1903) designated the North American *C. nyssae* for the nominifer of *Phenacaspis* and described this genus as characterized by the “pygidium with the terminal pair of lobes more or less sunk into the body, and having their inner edges serrate or crenate and strongly divergent, leaving a distinct notch on the median line”. The genus *Chionaspis* was, then, restricted to forms with produced and parallel terminal lobes (median lobes).

The concept of *Chionaspis* was, thereafter, formed to the exclusion of *Phenacaspis*. A well-formed one on this line, for example, was offered by Ferris (1937) in the 1st series of his “Atlas of the Scale Insects of North America”. The North American species he referred to *Chionaspis* all have been recognized as real members until now. In the same work he rather tentatively recognized *Phenacaspis* as separable from *Chionaspis*, though he admitted that the division is to some degree arbitrary.

A view against *Phenacaspis* was advanced by Takahashi (1952; 1953). He maintained that some species divided into *Chionaspis* and *Phenacaspis* are in reality dimorphic forms of the same species, associated with the bark and leaves of the host plants, respectively. This view was rejected by Ferris (1955; 1956) in his revision of *Phenacaspis* by the reason that it was based entirely on Japanese species. He insisted that no genuine species of *Chionaspis* occur in the Japanese area, and that *Phenacaspis* as composed by him is, though very close to *Chionaspis*, a distinct and valid genus.

Takagi et al. (1967) showed that *Phenacaspis nyssae*, the nominifer of *Phenacaspis*, connects to *Chionaspis sylvatica* through intermediate individuals, and
claimed that the two should be site-caused forms of the same species. Moreover, having compared the larval stages, especially the 2nd instar males, they found that species referred to *Chionaspis* and *Phenacaspis* represent 2 distinct groups: one of these groups includes all the native North American and part of the Japanese species divided into *Chionaspis* and *Phenacaspis*, while the other is composed of the rest of the Japanese species all referred to *Phenacaspis* by Ferris and others. They maintained that part of *Phenacaspis* including the nominifer should belong to *Chionaspis* and the rest should be united with another distinct genus, *Pseudaulacaspis*. The only diagnostic character they adopted for separating *Pseudaulacaspis*, thus recomposed, from *Chionaspis* in the adult female stage was the presence of a pair of well-developed setae arising from the basal inner margins of the median lobes. *Pseudaulacaspis*, which had been represented by a few species, was now interpreted as a large genus containing many species occurring in Asia and the Australian Region.

The view that *Phenacaspis nyssae* and *Chionaspis sylvatica* are the leaf- and bark-associated forms of the same species was ascertained experimentally by Knipscher et al. (1976). I think that recent authors recognize the site-caused dimorphism (for example, Tippins et al., 1970) and agree in treating *Phenacaspis* as a synonym of *Chionaspis* (for example, Nakahara, 1975). I also believe that the modified concept of *Pseudaulacaspis* is now widely accepted. Chen (1983), however, still uses the name *Phenacaspis* in spite of his knowledge about the study made by Knipscher et al. (1976), and recognizes 37 species occurring in China as members of *Phenacaspis*, which he asserts to be a good genus. Based on his own observations he throws doubt about the real degree of the site-caused variation, and points out that some species, only with produced median lobes, occur not on the bark but on the leaves. Contrary to his doubt, the effect of the feeding sites is quite remarkable in some species; this fact itself, of course, means nothing more than the variable nature of those dimorphic species (though necessarily resulting in the suppression of the generic name *Phenacaspis*). The generic recomposition attempted by Takagi et al. (1967) was based on an invariable feature (the setae between the median lobes) of the adult females and on the 2nd instar males. Both *Chionaspis* and *Pseudaulacaspis* as recomposed embrace various cases concerning the shape and variation of the median lobes with relation to the feeding sites. In this respect, the site-caused dimorphism is a minor problem, and Chen's criticism is quite misdirected. But I can understand why he recognizes the group he calls by the name *Phenacaspis* as distinct. With the adult females alone can hardly be revealed the inclusion of the 2 different phylogenetic stocks within that group. What we are trying to classify is apparently the result of intricate evolutionary changes of characters involving parallelism and convergence, and sometimes even atavism. The view may at first appear quite absurd that many of the "*Phenacaspis*" species occurring in Asia and the Australian Region should belong to *Pseudaulacaspis*. Most of these species are remarkably different in body shape from the nominifer of *Pseudaulacaspis*. However, the body shape may also be variable within a genus as exemplified by *Howardia* (with *H. stricklandi*) and *Diaspis* (with *D. elaeidis*). In fact, the genus *Pseudaulacaspis* as recomposed shows a rather continuous, graded series of species concerning the body shape, any division within the series thus appearing arbitrary.

The present work was started in connection with my study on the scale insect
material I collected in Nepal and Bharat (India). During the course of the study I realized that the concept of *Chionaspis* still needs minor modifications in order to exclude certain species from the genus. In the following lines will be given a modified concept of the genus, followed by descriptions of 8 new species. On this occasion I have tried to enumerate all the species which should belong to *Chionaspis* as understood in this paper. This is, however, far from an overall revision of the genus. I am in no position to examine all the described species and to check all the published papers. I hope that the enumeration will give a close approximation to the known species of the genus. On the basis of the revised composition preliminary considerations will be given to some evolutionary aspects of the genus, and in this connection a new genus related to *Chionaspis* will be described.

**A revised concept of Chionaspis**

Genus *Chionaspis* Signoret, 1869

NF: *Coccus salicis* L. (designated by Cooley, 1899).


Adult female. Body elongate and fusiform; mesothorax (MS), metathorax (MT), and 1st to 3rd abdominal segments (Abd I-III) produced laterally but usually not strongly, prothorax (PR) little produced; pygidium composed of Abd IV and succeeding segments marginally (but in the median to the submarginal region Abd IV and V are distinctly marked off from each other and from the pygidium, which is, therefore, composed of Abd VI and succeeding segments), triangular or a little roundish along free margin. Anus situated at centre or somewhat towards base of pygidium. Perivulvar disc pores present in 5 groups: median, a pair of anterolateral, and a pair of posterolateral groups. Pygidial lobes well developed in 2 or 3 pairs. Median lobes (L1) usually much larger than lobules of lateral lobes (in a few species as large as the latter), united together by a basal zygosis, variable in shape according to species and in some species also to feeding sites: in one extreme L1 are almost wholly sunken into the apex of the pygidium, forming a notch in the latter, and divergent, while in the opposite extreme they are wholly produced at the apex of the pygidium, parallel, and in a few cases appressed or fused together (in some species sunken into the pygidium in the leaf-associated individuals and produced in the bark-associated ones); never with a pair of remarkable setae arising from their inner bases (though there may be recognized a pair of minute setae). Second lobes (L2) divided into inner lobule (L2a) and outer lobule (L2b), L2b usually smaller, in some species much reduced. Third lobes (L3) well represented and bilobulate in some species, merged into rugged pygidial margin in others. In some species each of lobules of L2 and L3 with a pair of slender scleroses (paraphyses) arising from basal corners and converging anteriorly, in others these scleroses are much reduced.
or practically obsolete. Gland spines occurring on Abd VIII (just laterally to L1) and preceding segments as anteriorly as thoracic region (lacking on thorax and Abd I in some species), situated marginally on Abd IV-VIII, withdrawn into ventral submarginal region on prepygidial segments; marginal gland spines well developed except on Abd VIII, usually single (in some species double) on Abd VI-VIII; submarginal gland spines usually numerous, becoming shorter into conical ones on anterior segments. Marginal dorsal macroducts as large as submarginal ones, 1 on Abd VII (just mesally to L2), opened in a membraneous pore prominence; 2 on VI, one of them opened in a pore prominence just mesally to L3; 2 on V and usually 2 on IV, associated with pore prominences or marginal serrations, these being sometimes obscure; 1 in posterolateral corner of III, sometimes opened in a slight marginal prominence (but may be counted as a submarginal macroduct, since it is often comprised in a continuous submarginal row of macroducts). Dorsal macroducts forming well-defined submedian and submarginal rows along posterior borders of abdominal segments, in some species partly accompanied or replaced by much smaller ducts or microducts which may be numerous and strewn; occurring on Abd V and some preceding segments, and in many species also on VI submedially (usually lacking submarginally on this segment). Smaller macroducts strewn on lateral sides of Abd I-III and usually also of thoracic segments. Antennae each represented by a short tube with a fleshy seta (2 minute setae are also discernible in many species and may be present in all species of the genus), situated within frontal margin. Eye spots usually at most weakly sclerotized. Anterior spiracles each with a compact cluster of disc pores, posterior spiracles each with much fewer disc pores or none; these pores are usually 3-locular (rarely 4-locular). Derm remaining membraneous in prepygidial segments; pygidium sclerotized dorsally within border of Abd V/VI, especially strongly around anus and in some patches; sclerotized also on ventral surface in about apical 3rd, especially strongly in a pair of narrow stripes arising from bases of L1 and in a pair of patches situated just mesally to posterior ends of posterolateral perivulvar disc pore groups. Usually there are 3 “bosses” on the dorsum of the abdomen on each side: the anteriormost is situated on Abd I submarginally, about as large as the anal opening, and membraneous; the 2nd on the posterior border of Abd III, usually just mesally to 1 or 2 outermost submarginal macroducts, much smaller than the boss of Abd I, well sclerotized; the posteriormost on the posterior border of Abd V just anteriorly to the marginal macroducts, quite small but well sclerotized (sometimes indiscernible).

Second instar female. L1 nearly as in adult female in shape. L2 also well represented, but L3 usually reduced to marginal serrations. Usually there are on each side of the abdomen 4 marginal macroducts, which belong to Abd IV-VII (when there are 5 macroducts, the anteriormost belongs to Abd III). Usually no macroducts in submedian and submarginal regions.

Second instar male. This stage is quite different from the adult and 2nd instar females in the marginal appendages and the ducts. Body elliptical, membraneous; segmentation obscure. Small, membraneous or little sclerotized processes occurring along margin on Abd IV-VIII; these processes may correspond to the marginal appendages of the adult and 2nd instar females, but bear little resemblance to the latter. Enlarged, conical gland spines occurring near anterior and posterior spiracles and also on base of abdomen submarginally. Ducts well represented on both
surfaces of body, most of them strewn in submedian and submarginal regions. In many species some macroducts occurring along the margin of the abdomen are modified in structure, appearing framed on one side (or at times on both sides) and, when viewed from above, C-shaped.

First instar larva. Antennae usually 6-segmented (in a few species 5-segmented), the terminal segment shorter than the preceding segments combined. A pair of enlarged dorsal ducts present on head, 8-shaped when viewed from above. Posterior extremity of abdomen with a pair of small, pointed processes between caudal setae; laterally to the caudal seta there is a well-developed and sclerotized process or lobe, accompanied just laterally by a smaller process; laterally to this, beyond a gland spine, there is a similar process. One dorsal duct occurring on each side of anus.

Remarks. As understood in the present paper, the genus Chionaspis comprises species which are fairly uniform except for the state of the pygidial lobes. These lobes, however, are also variable in some species according to feeding sites. The ducts and gland spines are also somewhat variable in occurrence. So far as known, the species are similar in the larval stages, too. A few species, however, deviate in having 5-segmented instead of 6-segmented antennae in the 1st instar. The determination of the number of the antennal segments is not always easy unless material is in good condition. For example, C. heterophyllae was illustrated by Ferris (1942) to have 5-segmented antennae, but in my observation this species has 6-segmented antennae. However, in at least 2 species, C. lumbiniana and C. syzygii, the antennae are definitely 5-segmented. In all other respects there seems to be no basis for excluding these species from Chionaspis.

The genus Chionaspis is closely related to Aulacaspis and should be revised especially in this connection. The latter has generally been understood to have a remarkably swollen prosoma. In my opinion a dozen of named species should be removed from Chionaspis to Aulacaspis in spite of the fact that in these species the prosoma is not swollen into a rounded or square mass (see under A list of names which have been referred to Chionaspis or Phenacaspis). They differ from the species here referred to Chionaspis in lacking lateral macroducts and gland spines on the 1st abdominal segment as well as on the thorax, and agree in this respect with the species which definitely belong to Aulacaspis. The occurrence of lateral macroducts and gland spines (or, at least, of lateral macroducts) up to the 1st abdominal segment (and often further anteriorly) is a diagnostic character for recognizing Chionaspis species in comparison with Aulacaspis. This interpretation excludes tropical species from Chionaspis, making the genus predominantly temperate in distribution. Aulacaspis is a group of species in which the lateral macroducts and gland spines abruptly disappear between the 1st and 2nd abdominal segments, and which do not always display an enormously swollen prosoma.

As stated in Introduction a lot of species described in or referred to Phenacaspis are members of Pseudaulacaspis. Many of them are very similar to Chionaspis species in the adult females. In spite of this, the genus Pseudaulacaspis is remote from Chionaspis and closely related to Fiorinia so far as based on the 2nd instar males. The adult females of Pseudaulacaspis and Fiorinia are also commonly characterized by having a pair of remarkable setae on the inner bases of the median lobes.
NOMINIFER OF CHIONASPIS

_C. salicis_, the nominifer of _Chionaspis_, is a well-known scale insect in Europe. In 1970 Danzig showed that the supposed species _C. micropori_, _C. polypora_, and _C. montana_, originally described from China and Central Asia, are in reality infraspecific variations of _C. salicis_, different forms sometimes occurring together and being connected by intermediate individuals. On this understanding _C. salicis_ largely overlaps with the North American _C. salicisnigrae_ in the variable pattern of dorsal ducts, so that the separation of the two is now very difficult. Comstock (1883) already regarded the two as conspecific. Danzig (1980) also treated _C. salicisnigrae_ as a junior synonym of _C. salicis_.

I am much inclined to believe that _C. salicis_ and _C. salicisnigrae_ are distinct species, being distinguishable in the 2nd instar females. In _C. salicis_ there are 5 pairs of marginal macroducts on the 3rd to 7th abdominal segments and no further dorsal ducts. In _C. salicisnigrae_ there are, in addition, smaller macroducts in the submedian and submarginal regions. In material examined (Hocking Co., Ohio, _Salix_ sp., May 19, 1960, col. & det. M. Kosztarab) the total of the smaller macroducts attains ca. 10–20 (submarginal ducts occurring on Abd II–IV, often also on I and V; submedian ducts on Abd IV–VI, sometimes also on III). Dr. Danzig examined 2nd instar females collected in the European part of the USSR (and, therefore, undoubtedly belonging to _C. salicis_) and those from Middle Asia and the Far East (Korea; Saghalien; Sikotan), and found no submedian and submarginal dorsal ducts in all of them (pers. comm.). In my view they all belong to _C. salicis_. _C. salicisnigrae_ recorded by Siraiwa (1939) from Saghalien, therefore, is probably _C. salicis_ in reality. His record includes _Alnus_ as a host plant, thus, according to Danzig (1980), possibly containing another species, _C. alnus_. Takagi et al. (1967) recorded _C. salicisnigrae_ from Japan (Kamikōtō, on _Chosenia bracteosa_, a salicaceous plant). This record is also erroneous and should be corrected to _C. salicis_ (Fig. 4).

Recently Chen (1983) recorded _C. salicis_ (and its form _C. micropori_) from some localities in China. I collected it in Himalaya (Kufri, alt. 2600 m, Himachal Pradesh, India, _Salix_ sp., Oct. 26, 1978); the adult females examined (Fig. 4) are generally similar to the European form. It seems, therefore, that _C. salicis_ is widely distributed in eastern Asia, occurring on salicaceous plants.

The diagnostic characters, presented above, of _C. salicisnigrae_ in comparison with _C. salicis_, however, may be open to criticism, because the material of that species I examined is limited to 1 locality. _C. himalaica_, sp. n., has submarginal dorsal macroducts in the 2nd instar female, but these macroducts are variable in number both individually and locally and at one extreme of the variation are reduced to a complete absence.

NEW TAXA FROM HIMALAYA, SIWALIK, AND TERAI

In this section 8 new species of _Chionaspis_ collected in Nepal and Bharat (India) are described. Five of them inhabit lauro-fagaceous forests in Himalaya at altitudes of ca. 2000–3000 m, and the other three occur in subtropical forests in Siwalik (Churia Hills) and/or Terai (lowland Nepal, alt. ca. 100–300 m). Another form,
**Narayanaspis eugeniae**, n. g., n. sp., is also described from Terai in connection with the section Evolutionary significance of the site-caused dimorphism.

The nominferous specimens (holotypes) designated for the new species are all adult females, and are deposited in the collections of the Zoological Survey of India (*C. syzygii*) and the Entomological Institute, Hokkaidō University (the other species).

**Chionaspis syzygii**, n. sp.


The collection sites in Nepal are situated in the forests of Terai. Females were collected on the leaves and twigs of the host plants, and males on the leaves.

**Adult females** (based on over 126 specimens from Dehra Dun, Nawal-Parasi, and Kanepokhari) (Figs. 1, 5, 14A & AA, 17). Showing no site-caused variation in the characters of the pygidial lobes, though tending to have more numerous external secretory organs when occurring on the leaves (Table 1). L1 and the lobules of L2 and L3 all well represented, subequal in size and similar in shape; oblongish, with the sides finely serrate or obscurely notched (often appearing almost smooth-margined). L1 forming a small notch at apex of pygidium, gently divergent, with basal inner margins parallel and separated from each other by a space about half as wide as one of the lobes; basal zygosis represented by a small arch. Paraphyses well developed on L2a, also present on other lobules, sometimes obscure on L3b. Marginal gland spines, 1-4 (usually 2-3) on Abd IV, 1 on each of V-VIII; submarginal gland spines, about 2-8 on I, 4-12 on II, and 6-11 on III in leaf-feeding individuals, tending to be fewer in twig-feeding ones; a few to several minute submarginal gland spines on each of MS and MT. Submedian macroducts occurring on Abd III-VI and submarginal ones on III-V; their numbers, though somewhat variable locally, may fall within the following ranges: submedian macroducts, 3-12 and 2-10 on III in leaf- and twig-feeding individuals respectively, 4-9 and 2-9 on IV, 2-7 and 2-7 on V, and 1-2 and 1-2 on VI; submarginal macroducts, 3-13 and 2-11 on III, 3-8 and 2-8 on IV, and 2-7 and 1-4 on V. These macroducts are arranged in single rows, but, when numerous, may form partly double rows. Lateral macroducts on MS, MT, and Abd I-III (Table 2); a few to several ones usually present on PR within margin, tending to be reduced in size. Perivulvar disc pores numerous, their numbers may fall within the following ranges: 8-26 and 7-25 in median group in leaf- and twig-feeding individuals respectively, 19-44 and 14-38 in the anterolateral, and 15-44 and 11-34 in the posterolateral. Anterior spiracle with a compact cluster of 3-locular disc pores as many as 11-28 in leaf-feeding individuals and tending to be fewer in twig-feeding ones; posterior spiracle with 10 or less disc pores (rarely without disc pores) (Table 1). Antennal tubercles short, truncate, often with 1 or a few short spinous processes. Submarginal dorsal bosses all discernible.

**Second instar female** (exuvial cast). L2a nearly as large as L1, elongate, serrate on sides; L2b smaller but well represented; a pair of slender basal scleroses well developed on L2a, rudimentary on L2b. L3 with lobules represented by low serrate
Table 1. Numbers of external secretory organs in *C. syzygi* adult females.

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<th>Kanepokhari</th>
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<tr>
<td></td>
<td>Leaves</td>
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<td>Leaves</td>
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<td>Dorsal macroducts, total</td>
<td>92-111</td>
<td>51-101</td>
<td>63-104</td>
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<tr>
<td>Lateral macroducts on Abd III, total</td>
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<td>52-75</td>
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<td>8-14</td>
<td>40-63</td>
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<td>Perivulvar disc pores, total</td>
<td>116-165</td>
<td>31-52</td>
<td>96-145</td>
</tr>
<tr>
<td>Posterior spiracular disc pores, per spiracle</td>
<td>11-25</td>
<td>4-10</td>
<td>11-26</td>
</tr>
<tr>
<td>Anterior spiracular disc pores, per spiracle</td>
<td>4-10</td>
<td>4-10</td>
<td>4-10</td>
</tr>
</tbody>
</table>

First row: range; 2nd: mean and 2 standard errors (not given for small samples); 3rd: sample size. Anterior spiracular disc pores were not always exactly counted.
base of abdomen, usually 2-3 at each site. Anterior spiracle each with 2-6 3-locular disc pores; posterior spiracles usually without disc pores (rarely with 1). In the specimens from Nawal-Parasi there is a cluster of 3-6 small, unusually short ducts laterally to anterior spiracle, but in those from Kanepokhari such ducts are not found. There are a pair of tubercular swellings on the dorsal side of the head just within the frontal margin; these swellings are membraneous and as large as the antennal tubercle.

First instar larva (exuvial cast). Antennae 5-segmented, the segment V nearly as long as the other segments combined and annulate.

Remarks. Local variations are found in the 2nd instar males as described above. The adult females examined also show some differences locally in the numbers of external secretory organs, but appear to form together an indivisible group (Fig. 1).

This species is very similar to *C. trochodendri*, which is associated with *Trochodendron aralioides* (Trochodendraceae) in Taiwan. Their agreement in the characters of the pygidial lobes is especially noteworthy (see under Evolutionary significance of site-caused dimorphism). Differences between them are mainly found in the numbers of some external secretory organs as follows:

1) The dorsal macroducts of the submedian and submarginal rows are obviously more numerous in *C. trochodendri* (Fig. 1).

2) The lateral macroducts are also more numerous in *C. trochodendri* in spite of the fact that in this species no macroducts occur on the mesothorax (some ones are always present in *C. syzygii*) and that the metathoracic macroducts are more numerous in *C. syzygii* (Table 2).

3) The gland spines are more numerous in *C. trochodendri* (5-11 on Abd I, 8-15 on II, 7-13 on III, 4-9 on IV, 1-4 on V, probably always paired on each of VI-VIII).

4) In spite of all this, the spiracular disc pores tend to be fewer in *C. trochodendri* (6-12 associated with the anterior spiracle, and 0-6 with the posterior), and in the number of the perivulvar disc pores these species cannot be distinguished (Fig. 1).

In the 2nd instar females *C. trochodendri* differs from *C. syzygii* in the inner lobule of the 3rd lobes well developed, and in the 1st instar larvae in having 6-segmented antennae.

*Chionaspis arkhola*, n. sp.

Material. Collected at Dunche and Syabru, alt. ca. 2000 m, Bagmati Zone, Nepal, on *Lithocarpus elegans* (= *L. spicata*) [local name: Arkhola] (Fagaceae), Sept. 17 and 30, 1975. NF: from Dunche.

Adult females and 2nd instar males were all collected on the upper surface of leaves.

Adult female (based on 18 specimens mostly in poor condition, having been collected after their death) (Figs. 7, 14B, 18, 19). L1 obviously larger than the lobules of L2, sunken into apex of pygidium for most of their length, divergent, serrate on inner margin; basal zygosis projected beyond bases of L1. L2 well developed, L2a oblongish, with a pair of paraphyses; L2b smaller. L3a well developed, L3b reduced to a low, serrate process. Marginal gland spines, 2-6 on Abd IV, 1-2 on V (when single, often with 2 microducts extending through), and 1 on each of VI-VIII; submarginal gland spines on Abd I-III, 2-4 on I, 2-5 on II, and 3-5 on III.
Fig. 1. Chionaspis syzygii, n. sp., and Chionaspis trochodendri, adult females. Total number of perivulvar disc pores ($x_2$) against total number of dorsal macroducts ($x_1$).

DT + DL  $x_2 = 0.96x_1 + 38.55$  $r = 0.845$  $n = 37$

NT + NL  $x_2 = 1.21x_1 + 11.90$  $r = 0.728$  $n = 36$

KT + KL  $x_2 = 1.10x_1 + 42.61$  $r = 0.711$  $n = 53$

The bar diagram for $x_2$ in KT is based on the individuals plotted in the scatter diagram and another one ($x_2 = 137$). The other bar diagrams are based on the specimens plotted in the scatter diagram.
Table 2. Lateral macroducts in *C. syzygii* and *C. trochodendri* adult females, number on one side.

<table>
<thead>
<tr>
<th>C. syzygii</th>
<th>C. trochodendri</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dehra Dun</td>
<td>Nawal-Parasi</td>
</tr>
<tr>
<td>Leaves</td>
<td>Twigs</td>
</tr>
<tr>
<td>MS</td>
<td>5-12</td>
</tr>
<tr>
<td></td>
<td>5.4</td>
</tr>
<tr>
<td></td>
<td>51</td>
</tr>
<tr>
<td>MT</td>
<td>5-12</td>
</tr>
<tr>
<td></td>
<td>9.2</td>
</tr>
<tr>
<td></td>
<td>50</td>
</tr>
<tr>
<td>Abd I</td>
<td>8-11</td>
</tr>
<tr>
<td></td>
<td>8.7</td>
</tr>
<tr>
<td></td>
<td>50</td>
</tr>
<tr>
<td>Abd II</td>
<td>5-12</td>
</tr>
<tr>
<td></td>
<td>8.4</td>
</tr>
<tr>
<td></td>
<td>52</td>
</tr>
<tr>
<td>Abd III</td>
<td>4-6</td>
</tr>
<tr>
<td></td>
<td>4.5</td>
</tr>
<tr>
<td></td>
<td>52</td>
</tr>
</tbody>
</table>

First row: range; 2nd: mean (not given for small samples); 3rd: sample size. A few to several lateral macroducts, more or less reduced in size, are often present on the prothorax in *C. syzygii*.

Submedian and submarginal macroducts on Abd III-V, often with much smaller ducts (somewhat variable in size) strewn submedially (at times also medially and submarginally) on III and IV (in a few specimens occurring anteriorly up to MT and also on Abd V); submedian macroducts few, usually about 2-4 in each row; submarginal macroducts, 4-8 on III, 3-7 on IV, and 2-4 on V. Lateral macroducts occurring on MT and Abd I-III, 4-8 on MT, 5-10 on Abd I, 4-10 on II, and 2-6 on III. Perivulvar disc pores, 9-19 in the median group, 16-34 in the anterolateral, 10-34 in the posterolateral. Spiracular disc pores 4-locular, about 4-16 associated with anterior spiracle, and 1-7 with the posterior. Submarginal dorsal bosses much reduced on Abd III and V, at times indiscernible.

*Second instar female* (exuvial cast). L1 and L2 similar to those in adult female; L3 reduced to marginal serrations. Marginal macroducts, 4 on each side. Anterior spiracle with 4 or so 4-locular disc pores.

*Second instar male* (based on 10 specimens). Marginal processes of abdomen mostly rudimentary. Modified ducts, 4 on each side, interpreted to belong to Abd II, III, IV and VII, those supposed to occur on III and IV being set close together. Anterior spiracle with 2-5 4-locular disc pores. Two or 3 gland spines occurring posteriorly to anterior spiracle, 2 laterally to posterior spiracle, and 3-4 on base of abdomen submarginally, anterior spiraculars usually much smaller than the others. About 4-8 unusually short microducts strewn in a group anterolaterally to anterior spiracular gland spines.

*First instar larva* (exuvial cast). Antennae 6-segmented.

*Remarks.* It is noteworthy that the spiracular disc pores are 4-locular in this
species, because, so far as I am aware, this type of spiracular disc pores has been known to occur only in a few peculiar genera (*Halaispis*; *Collubia*) (occasional 4-locular disc pores are known in other species: see under *C. himalaica*).

This species is variable in the dorsal ducts, which are all macroducts in some specimens but are composed of macroducts and smaller ducts (these again are variable in size and number) in the others. In this respect and some other characters this species appears to be related to *C. saitamaensis*, which is associated with *Quercus* in Japan and the Far East USSR (and also with *Tilia* in the Far East USSR). Besides having 3-locular spiracular disc pores as usual for a *Chionaspis* species, *C. saitamaensis* is distinguished from *C. arkhola* mainly by the following characters.

**Adult female:** 1) the median lobes are more developed in size in comparison with the 2nd; 2) the perivulvar disc pores are fewer (4-10, mean 7.7, in the median group, 13-23, 17.3, in the anterolateral, 9-20, 14.8, in the posterolateral, based on 30 specimens collected on the leaves of *Quercus mongolica*, Sapporo, Japan); 3) the dorsal macroducts are fewer (often lacking on Abd V submarginally and usually replaced by small ducts on III submedially).

**Second instar female:** 4) a small marginal macroduct is often present on the 3rd abdominal segment (in addition to 4 macroducts occurring on IV-VII).

**Second instar male:** 5) the submarginal gland spines occurring on the base of the abdomen are as many as 7 or 8; 6) there is no group of unusually short microducts laterally to the anterior spiracle.

*C. arkhola* is also similar to *C. himalaica*, another species associated with *Quercus* (see under *C. himalaica*).

**Chionaspis castanopsidis**, n. sp.

**Material.** Collected at Sankranti, alt. ca. 2000 m, Kosi Zone, Nepal, on *Castanopsis tribuloides* (Fagaceae), Nov. 14, 1983.

Females were collected on the undersurface of the leaves; no male scales were identified.

**Adult female** (based on 30 specimens) (Figs. 6, 14C, 20). L1 very large in comparison with L2, sunken into apex of pygidium for their most length, divergent, a little expanded apically, serrate except on a short apical margin, which is flatly rounded; basal zygosis produced anteriorly beyond bases of L1, bluntly pointed at anterior end. L2 with both lobules well represented and oblongish, L2b obviously smaller than L2a; paraphyses obscure. L3 reduced to low serrate processes. Marginal gland spines, 1-4 (usually 2-3) on Abd IV, 1 on each of V-VIII; submarginal gland spines occurring on Abd I-III, 1-4 (usually 2-3) on I, and 2-5 (3-4) on II and also on III. Submedian and submarginal macroducts occurring on Abd III-V; submedian macroducts few, 0-2 (usually 1-2) on III and also on IV, and 0-1 (1) on V; submarginal macroducts, 1-5 (2-3) on III, 1-4 (2-3) on IV, and 1-3 (1-2) on V. Lateral macroducts 2-5 (usually 2-3) on MT, 2-6 (3-4) on Abd I, 3-5 (3-4) on II, and 1-4 (2-3) on III; 1-2 lateral macroducts often present on MS, but more or less reduced in size. Perivulvar disc pores, 11-22 in the median group, 17-30 in the anterolateral, 16-27 in the posterolateral. Anterior spiracle with about 15-29 3-locular disc pores, and the posterior with 3-8.

**Second instar female** (exuvial cast). L1 as in adult female. L2 much smaller, the lobules represented by pointed processes. Four marginal macroducts on each side of abdomen.
**First instar larva** (female exuvial cast). Antennae 6-segmented.

**Remarks.** This species is somewhat similar to *C. arkhola*, but differs from the latter in the median lobes very large in comparison with the 2nd, in the 3rd lobes much reduced and in other details. In all the examined specimens of *C. castanopsidis* there have been found no small dorsal ducts in addition to the macroducts, while in *C. arkhola* some of the examined specimens have many small dorsal ducts. *C. castanopsidis* may also be similar to *C. dryina (= Phenacaspis dryina)*, which was described from Yunnan, China, as occurring on the leaves of *Quercus schottkyana*, but is distinct so far as compared with the original description of the latter.

**Chionaspis clematidis**, n. sp.

**Material.** Collected near Ilam, alt. 540 m, Mechi Zone, Nepal, on *Clematis grata* (Ranunculaceae), Nov. 5, 1983.

Females occur on young stems, and males on stems and also on the underside of leaves.

Adult female (based on 30 specimens, not all of them being in good condition) (Figs. 8, 14D, 21). L1 very large in comparison with L2, forming a deep notch at apex of pygidium, divergent, finely serrate; somewhat variable in shape, usually rather slender, gently curved, and rounded or bluntly pointed apically; basal zygosis usually little produced anteriorly beyond bases of L1, flatly rounded at the anterior end. Lateral lobes well developed; L3b with a long, slanting and serrate margin laterally to apex; paraphyses rudimentary. Marginal gland spines, 2–8 (usually 3–6) on Abd IV, 1 on each of V–VIII (rarely 2 on V). Submarginal gland spines, 1–5 on Abd I, 2–8 on II, and 4–8 on III; in addition, quite minute gland spines (about 1–6) often seen on MT and also on MS. Submedian macroducts few, 0–2 (usually 0) on Abd III, and 1–3 on each of IV–VI (in many cases 2 on IV and also on V, and 1 on VI). Submarginal macroducts, 0–1 (usually 0) on Abd II, 2–6 on III, 1–5 on IV, and 2–4 on V. Lateral macroducts, 0–5 on PR, 0–6 on MS, 5–17 on MT, 6–16 on Abd I, 2–10 on II, and 1–4 on III. Perivulvar disc pores, 8–17 in the median group, 15–29 in the anterolateral, 14–28 in the posterolateral. Anterior spiracle with about 13–30 3-locular disc pores, and the posterior with 7–16.

**Second instar female** (exuvial cast). L1 similar to those of adult female, somewhat variable in shape as well. L2b much smaller than L2a, both lobules pointed apically. Four marginal macroducts on each side of abdomen.

**Second instar male** (based on 7 specimens). Modified ducts 4 on each side, interpreted to belong to Abd II, III, IV, and VII, those supposed to belong to III and IV being set close together. Robust gland spines 2–4 (usually 3) posteriorly to anterior spiracle, 1–2 (2) laterally to posterior spiracle, and 2–4 (2–3) on base of abdomen. Anterior spiracle with 4–7 3-locular disc pores; posterior spiracle without disc pores.

**First instar larva** (exuvial cast). Antennae 6-segmented.

**Remarks.** So far as I am aware, no other species of the genus has been known to occur on *Clematis* or other genera of the family Ranunculaceae. In the shape of the median lobes, the number and arrangement of the dorsal macroducts and other features this species is similar to the leaf-form of *C. linderae*, which occurs in Japan on deciduous Lauraceae. It differs from the latter in having definitely more numerous perivulvar disc pores (total 85–121 in *C. clematidis*; 37–65 in the leaf-form of *C.
linderæ, n = 38), and also more numerous spiracular disc pores (in the leaf-form of C. linderæ the anterior spiracle with 3–15 disc pores, n = 42, and the posterior spiracle with 1–5, n = 72). Further, in the leaf-form of C. linderæ the inner lobe of the 2nd lobe extends posteriorly beyond the apices of the median lobes, and the outer lobe of the 3rd lobe is reduced to marginal serrations.

**Chionaspis cornigera**, n. sp.

**Material.** Siwapuri (Sheopuri), alt. ca. 2600 m, near Kathmandu, Bagmati Zone, Nepal, on an evergreen lauraceous tree (probably belonging to *Litsea*), Aug. 28, 1975.

Females were collected on the branches of the host plant, and males on the underside of leaves. The adult female specimens mounted are either very immature or aged and shrunk.

**Adult female** (based on 8 specimens, not all of them being in good condition) (Figs. 9, 15A, 22). Eye spot produced into a conical, strongly sclerotized process at anterior end and into a much smaller one at posterior end. L1 very large in comparison with L2, sunken into apex of pygidium for their basal half and divergent; robust, serrate, with apical margin flatly rounded; basal zygosis only a little produced anteriorly beyond bases of L1. L2 and L3 well represented, the outer lobules obviously smaller than the inner, L3b sometimes reduced to a low serrate process; paraphyses much reduced. Marginal gland spines, 5–8 on Abd IV, 2–3 on V, and 1 on each of VI–VIII; submarginal gland spines, 2–6 on I, 5–15 on II, and 8–13 on III; minute gland spines occurring in a broad submarginal region on MS (5–11) and MT (4–8). Submedian and submarginal macroducts occurring on Abd III–V; submedian macroducts, 1–5 (rarely 0) on III, 2–4 on IV, and 1–2 on V; submarginal macroducts, 5–9 on III, 3–6 on IV, and 1–3 (usually 2) on V. Lateral macroducts, 0–2 on Abd I, 4–9 on II, and 5–7 on III. Perivulvar disc pores numerous, 19–33 in the median group, 37–54 in the anterolateral, and 31–47 in the posterolateral. Anterior spiracle with a large, compact cluster of 3-locular disc pores (over 30 to ca. 60); posterior spiracle with a cluster of 12–24 disc pores.

**Second instar female** (exuvial cast). L2b much smaller than L2a, pointed apically. L3 represented by serrate processes. Marginal macroducts, 4 on each side of abdomen.

**Second instar male** (based on 5 specimens). Modified ducts, 4 on each side, interpreted to belong to Abd II, III, IV, and VII, those supposed to belong to III and IV being set close together. Two to 4 (usually 3) gland spines laterally to anterior spiracle; 2 laterally to posterior spiracle; 4–5 robust ones, accompanied laterally by a much smaller one, on base of abdomen. Five to 9 microducts strewn between anterior spiracle and body margin. Anterior spiracle with 3–6 3-locular disc pores; posterior spiracle without disc pores.

**First instar larva** (exuvial cast). Antennae 6-segmented.

**Remarks.** Among the known species of *Chionaspis* this species is unique in the development of eyes which form a 2-pointed tubercle. It bears little resemblance to any of the other species of the genus associated with lauraceous plants.

**Chionaspis himalaica**, n. sp.

**Material.** Collected at Kufri, alt. ca. 2500 m, Himachal Pradesh, Bharat (India), on *Quercus semecarpifolia* (Fagaceae), Oct. 26, 1978; at Ghora Tobela, alt. ca. 3000
m, Langtang Valley, Bagmati Zone, Nepal, on a sapling of *Q. semecarpifolia*, Sept. 23, 1975; at Ghora Tobela, on *Q. semecarpifolia*, Sept. 29, 1975. NF: from Ghora Tobela, Sept. 23.

Females were collected on the branches of the host plant (also on the leaves at Kufri). No male scales were found together.

**Adult female** (based on a total of 45 specimens: 15 from each of the 3 collection lots, all mounted from branches) (Figs. 10, 15B, 23). L1 much larger than L2, a little sunken into apex of pygidium, divergent, robust, roughly serrate on mesal margin, flat apically; basal zygosis produced beyond bases of L1. L2a oblongish, with quite rudimentary paraphyses; L2b much smaller, narrowing apically. L3 reduced to low serrate processes. Marginal gland spines, 3–8 on Abd IV, 1–4 on V, 1–2 (usually 1) on each of VI and VII, and 1 on VIII; submarginal gland spines, 1–7 on I, 2–6 on II, and 2–7 on III; a few minute submarginal gland spines often found on MT. Submedian macroducts, 0–4 (usually 1–2) on Abd III, 2–6 on IV, 1–4 on V, and 0–1 (often 0) on VI, sometimes remarkably reduced in size on III; usually a few submedian dorsal microducts occurring on MT and Abd I–III (on III, anteriorly to submedian row of macroducts), and sometimes also on IV and V (anteriorly to submedian row of macroducts on each). Submarginal macroducts, 4–10 on Abd III, 3–10 on IV, and 2–8 on V. Lateral macroducts, 1–5 on MS, 4–12 on MT, 4–13 on Abd I, 3–10 on II, and 1–6 on III; those on MS often much reduced in size and sometimes hardly distinguishable from neighbouring microducts. Perivulvar disc pores numerous, 17–32 in the median group, 28–58 in the anterolateral, and 16–44 in the posterolateral. Spiracular disc pores normally 3-locular, occasionally 4- or 5-locular, ca. 15 to over 40 associated with anterior spiracle, and 7–17 with the posterior.

**Second instar female** (exuvial cast) (Fig. 23). L1 and L2 similar to those in adult female. Marginal macroducts, 3 (on Abd V–VII), 4 (on IV–VII), or 5 (on III–VII) on one side of abdomen. Usually submarginal macroducts occurring on abdomen, as large as marginal macroducts, variable in number, 4 at maximum on one side (on Abd III–VI) (Table 3).

**First instar larva** (female exuvial cast). Antennae 6-segmented.

**Remarks.** Two adult female specimens were mounted from leaves. They differ from the branch-associated specimens in the median lobes a little more sunken into the pygidium, in the 2nd and 3rd lobes a little more developed, and in the paraphyses well represented on the inner lobule of the 2nd lobe or on both lobules of the 2nd lobe and the inner lobule of the 3rd lobe. The numbers of external secretory organs could not be fully counted owing to the poor condition of the specimens. So far as represented by the material at hand, the leaf-form is unusual in occurrence and not remarkably different from the bark-form in the shape of the median lobes.

The localities Kufri and Ghora Tobela are about 800 km distant from each other. The adult females examined, however, show no remarkable difference between these localities. The 2nd instar females are variable in the number of the macroducts, and in this feature an apparent difference was found between the localities. This stage appears also variable at the same locality (Ghora Tobela) in the number of the submarginal macroducts (Table 3). This might show that the local difference observed does not deserve regarding as specific.

It is noteworthy that in this species the spiracular disc pores are, while normally 3-locular, occasionally 4- or 5-locular. In *Gynandraspis gabonensis* these disc pores
Table 3. Occurrence of dorsal macroducts in *C. himalaica* 2nd instar females: frequency distributions in local forms.

<table>
<thead>
<tr>
<th>Locality</th>
<th>Kufri</th>
<th>Ghora Tobela</th>
</tr>
</thead>
<tbody>
<tr>
<td>Host plant</td>
<td>Aged</td>
<td>Aged</td>
</tr>
<tr>
<td>Sample size</td>
<td>15</td>
<td>46</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Marginal macroducts, total</th>
</tr>
</thead>
<tbody>
<tr>
<td>7</td>
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<tr>
<td>8</td>
</tr>
<tr>
<td>9</td>
</tr>
<tr>
<td>10</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Submarginal macroducts, total</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
</tr>
<tr>
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</tr>
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<td>3</td>
</tr>
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<td>4</td>
</tr>
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<td>5</td>
</tr>
<tr>
<td>6</td>
</tr>
<tr>
<td>7</td>
</tr>
<tr>
<td>8</td>
</tr>
</tbody>
</table>

are also normally 3-locular and occasionally 4-locular (Balachowsky et al., 1980). In *Chionaspis arkhola*, n. sp., these disc pores are always 4-locular.

*C. himalaica* is similar to *C. arkhola*. It is distinguished from the latter by the spiracular disc pores normally 3-locular and more numerous, by the perivulvar disc pores also tending to be more numerous, by the submedian dorsal microducts always few, and by other features which show rather slight differences from *C. arkhola*. In the 2nd instar females these species are quite distinct owing to the occurrence (though not constant) of submarginal macroducts in *C. himalaica*.

The comparisons above, however, are made between the branch-feeding form of *C. himalaica* and the leaf-feeding one of *C. arkhola*, so that the differences mentioned as specific are mostly tentative. *C. himalaica* may also be related to *C. saitamaensis*, of which some characters are given under *C. arkhola*.

*Chionaspis sivapuriana*, n. sp.

*Material*. Collected at Siwapuri (Sheopuri), alt. ca. 1900 m., near Kathmandu, Bagmati Zone, Nepal, on *Quercus glauca* (Fagaceae), Oct. 19, 1983.

Females and males were collected on the bark of shoots arising from near the root of the host.

*Adult female* (based on 30 teneral specimens) (Figs. 10, 15C, 24). L1 produced, parallel or a little divergent, squat, broadly rounded apically, faintly notched once subapically on either side or entire; basal zygosis narrow, much produced anteriorly. L2b obviously smaller than L2a, but well represented, both lobules with paraphyses much reduced or practically absent. L3 represented by serrate processes. Marginal gland spines, 1–3 (usually 2–3) on Abd IV, and 1 on each of V–VIII; submarginal gland spines, 1–4 on I, 2–3 on II, and 1–4 (usually 2–3) on III; sometimes 1–4 quite minute gland spines occurring on MT submarginally. Submedian dorsal macroducts, 0–3 (often 0) on Abd III, 1–5 on IV, 2–5 (usually 2–3) on V, and 0–2
(usually 0-1) on VI; submedian dorsal microducts usually occurring on I-III and sometimes also on MT, 1-2 on each segment. Submarginal macroducts, 3-6 on Abd III and also on IV, and 1-5 on V. Lateral macroducts, 1-5 on MS, 3-10 on MT, 3-13 on Abd I, 2-6 on II, and 1-4 on III. Perivulvar disc pores, 7-12 in median group, 12-26 in the anterolateral, and 9-25 in the posterolateral. Anterior spiracle with 9-25 disc pores, the posterior with 2-12; these disc pores are normally 3-locular, but some of them often appear 2- or 1-locular.

*Second instar female* (exuvial cast). L1 produced, robust, distinctly notched once or twice on each side. L2b narrowing apically. Marginal macroducts, 4 on each side.

*Second instar male* (based on 3 specimens, which are all poor in condition). Modified macroducts, 4 on each side, interpreted to belong to Abd II, III, IV, and VII, those supposed to belong to III and IV being set close together. Enlarged gland spines, 2-3 posterolaterally to anterior spiracle, 2 laterally to posterior spiracle, and 3-4 on base of abdomen. Anterior spiracle with 4-6 3-locular disc pores, the posterior without disc pores.

*First instar larva* (exuvial cast). Antennae 6-segmented.

**Remarks.** In having produced, squat, and broadly rounded median lobes this species is similar to *C. agranalata*, which was described by Chen (1983) as occurring at Kunming, Yunnan, China, on the leaves of an undetermined fagaceous plant. So far as based on his description and figures *C. agranalata* (represented by the leaf-associated form) differs from *C. sivapuriana* (branch-associated form) in the basal zygosis of the median lobes not much produced anteriorly, in having many small submedian dorsal ducts on the 2nd to 5th abdominal segments, in the disc pores associated with the anterior spiracle much fewer (4-10), in lacking disc pores at the posterior spiracles, etc.

*Chionaspis lumbiniana*, n. sp.

**Material.** Collected in the jungle of Terai, Nawal-Parasi District, Lumbini Zone, Nepal, on *Syzygium cumini* (Myrtaceae), Dec. 15, 1983.

Collected on the branches. Females deeply mining under the bark. Male scales are often crowded together especially at parts of branches where females are mining. In such cases male scales are kept perpendicular to the surface of the bark, standing on their anterior end and supporting each other.

*Adult female* (based on 30 specimens) (Figs. 11, 15D & DD, 25). When full-grown, lateral parts of MT and Abd I-III strongly produced. L1 entirely produced, appressed together, robust, broadly rounded on apical margin, serrate on lateral side, notched once or more just subapically on mesal side; basal zygosis strongly produced anteriorly, clavate, accompanied at its base by a pair of much smaller scleroses. L2a well developed, strongly oblique, serrate except on mesal to apical margin, L2b represented by a small, pointed process; L3 similar to L2; paraphyses obsolete. Marginal gland spines, 5-10 on Abd IV, 1-4 (usually 1-2) on V, 1 on each of VI-VIII; submarginal gland spines, 3-9 on I, 7-16 on II, 10-16 on III; about 1-5 minute gland spines occurring submarginally on MS and also on MT. Submedian macroducts, 2-7 (usually 3-5) on Abd III, 2-5 (3-4) on IV, and 1-4 (2-3) on V, tending to be divided into inner and outer series on III and IV. Submarginal macroducts, 6-12 on Abd III, 4-10 on IV, and 2-6 on V. Lateral macroducts, 0-4 on PR, 3-9 on MS,
5-15 on MT, 7-14 on Abd I, 6-12 on II, and 2-8 on III. Perivulvar disc pores numerous, 26-50 in median group, 32-65 in the anterolateral, and 22-52 in the posterolateral. Anterior spiracle with ca. 32 to over 50 3-locular disc pores; posterior spiracle with 7-24.

Second instar female (exuvial cast). Lobes similar to those in adult female, but L1 narrowly rounded apically and L3 obviously less developed than L2. Marginal macroducts, 4 on each side of abdomen.

Second instar male (based on 10 specimens) (Fig. 29). Modified macroducts, 6 on each side, interpreted to belong to Abd II-VII. Enlarged gland spines, 3-4 posteriorly to anterior spiracle, often accompanied by 1-3 minute ones laterally (these minute gland spines are sometimes replaced by microducts), 2 laterally to posterior spiracle, and 3 on base of abdomen submarginally, accompanied by a much smaller one laterally. Anterior spiracle with 7-10 3-locular disc pores, the posterior without disc pores.

First instar larva (exuvial cast). Antennae 5-segmented.

Remarks. This species may be close to C. ramakrishnai, which was described by Rao (1953) from Coonoor, alt. ca. 1800 m, Nilgiri, South India, as occurring on Eugenia calophylli/olia (Myrtaceae). It does not agree with Rao’s description and figures of the latter species in having serrate lobes (in C. ramakrishnai entire so far as based on Rao’s figures), in having single gland spines on the 6th and 7th abdominal segments (double gland spines), in having more numerous spiracular disc pores (15 disc pores are shown for the anterior spiracle in Rao’s figure; “about four” for the posterior spiracle), and in other details. There seems to be no serious difference between the 2 species in the arrangement of the dorsal macroducts (apparently Rao erroneously stated that “Dorsal submarginal and submedian ducts present in fourth, fifth and sixth segments”). Rao expressed some doubt as to the generic position of his species (see under his description of C. pusa in the same paper). In my opinion C. lumbiniana definitely belongs to Chionaspis and probably so does C. ramakrishnai.

C. lumbiniana is the only species of Chionaspis I know that mines under the bark of the host plant. Some other species of the genus also have entirely produced, appressed (or even fused), robust median lobes, but, so far as known, they occur on the outer surface of the bark (habit is unknown for C. ramakrishnai).

Narayanaspis, n. g.

NF: Narayanaspis eugeniae, n. sp.

Adopt female. Many characters as in Chionaspis, but L1 definitely non-zygotic, parallel, with a pair of well-developed paraphyses. L2 and L3 well developed, their lobules similar to L1 in size and shape. Ventral sclerotization of pygidium divided medially by a slender space, which is edged with a pair of slender scleroses. Submedian macroducts divided into 2 series on Abd III and IV, one series occurring infrasegmentally in front of the other; submarginal macroducts forming an irregularly multiple row on III.

Narayanaspis eugeniae, n. sp.

Material. Collected in the jungle of Terai, near the crossing of the highway and the Pasaha River, Narayani Zone, Nepal, on Eugenia sp. (Myrtaceae), Dec. 20, 1983. Females and males were collected on the undersurface of leaves; a few adult
females also on the petioles.

**Adult female** (based on 8 specimens) (Figs. 12, 16, 26, 27). When full-grown, MS, MT, and Abd I-III well produced laterally. L1 and lobules of L2 and L3 oblongish, rounded apically, obscurely notched subapically. Paraphyses well developed on L1 and L2a, less on other lobules. Marginal gland spines of Abd IV and V slender, 7-10 on IV, and 2-3 on V; those of VI-VIII much shorter, 1 on each segment. Prepygidial gland spines short and conical (those around posterolateral corner of Abd III at times more or less elongate); 3-10 on MT, 7-12 on Abd I, 9-14 on II, and 11-15 on III. Each submedian series of macroducts irregularly double on Abd III, infrasegmental series with 13-18 and the segmental with 13-29 macroducts; each series single (at time with 1 or a few macroducts out of line) on IV, infrasegmental series with 8-11 and the segmental with 8-13 macroducts; 7-13 macroducts on V forming a single row; 1-3 on VI. Submarginal macroducts, 21-30 on Abd III; 10-17 on IV, usually 1 or a few of them being out of line; 5-8 on V. Lateral macroducts, 4-12 on MS, 15-23 on MT, 18-28 on Abd I, 17-23 on II, and 9-14 on III; PR, MS, and MT with numerous ventral microducts laterally, these ducts appearing 8-shaped when viewed above. Perivulvar disc pores, 28-41 in median group, 37-56 in the anterolateral, and 33-47 in the posterolateral. Anterior spiracle with 12-26 3-locular disc pores, the posterior with 12-21. Eye spots sclerotized. Dorsal bosses of Abd III and V quite small.

**Second instar female** (exuvial cast) (Fig. 30). L1 and L2 well developed, approximately as in adult female, but L1 more separated from each other. L3 represented by low serrate processes. Marginal macroducts 4 on each side, belonging to Abd IV-VII.

**Second instar male** (based on some specimens all in poor condition) (Fig. 30). Similar to the corresponding stage of *Chionaspis* in the membraneous, poorly segmented body, the arrangement of dorsal and ventral ducts, the occurrence of well-developed gland spines near the spiracles and on the base of the abdomen, and other features, but with no trace of marginal processes on the abdomen. There are 6 large macroducts along the margin on each side of the abdomen; these macroducts are very short, so that the sclerotized inner end almost overlaps with the orifice. Other ducts all small. Three (at times 4) gland spines posteriorly to anterior spiracle; 2 laterally to posterior spiracle; and 2 on base of abdomen, accompanied by a smaller one posterolaterally. Anterior spiracle with 1 3-locular disc pore. There are a pair of tubercular swellings on the dorsal side of the head just within the margin (at times not seen) as in *C. syzygii*.

**First instar larva** (exuvial cast). Antennae 6-segmented, segment VI a little shorter than I-V combined, little annulate. Structures around posterior end of body as in *Chionaspis*.

**A new name**

*Chionaspis cheni*, new name

*Chionaspis betulae* Chen, 1983. The Chionaspidini (Diaspididae, Coccoidea, Homoptera) from China, p. 8, 90. Preoccupied by *C. lintneri betulae* Cooley, 1898 (= *C. lintneri*) and *C. betulae* Tippins & Beshear, 1970 (= *C. triformis*).

According to Chen (1983), this species is similar to *C. micropori*, which was
included within the variation of C. salicis by Danzig (1970). It is renamed here with Prof. Chen’s agreement, since it appears to be distinct from C. salicis.

COMPOSITION, DISTRIBUTION, AND HOST PLANTS

A number of species once referred to Chionaspis and Phenacaspis were removed to other genera. There still remain many others which should be excluded from Chionaspis. A dozen of them are referable to Aulacaspis as discussed under the generic description, and nearly 30 species to Pseudaulacaspis. About 20 species are indeterminate as to their generic positions. Among them the European C. austriaca differs from Chionaspis in having non-zygotic median lobes, and the North African C. kabyliensis is quite peculiar in the shape of the pygidial lobes (according to the descriptions given by Balachowsky, 1954). Three Australian species, C. angusta (= C. eucalypti), C. candida, and C. ethelae, may also be excluded from Chionaspis. Ferris (1955, 1956) redescribed them as members of Phenacaspis, yet suggested that “they [Phenacaspis candida and P. ethelae] might be included in another genus to include species from Australia”. I have grave doubt as to the occurrence of genuine members of Chionaspis in the Australian Region as well as in other parts of the Southern Hemisphere.

The genus Chionaspis as here understood is represented by 59 known species including the 8 new ones (see A list of the species of Chionaspis; I have examined 37 of them represented by at least the adult female stage).

The nominiferous species of the genus, C. salicis, is widely distributed in the Palearctic Region, while 34 species are probably native to eastern Asia and 18 others to North America. Six species in addition to C. salicis occur in western Eurasia (west of and including Punjab and Central Asia) and North Africa (Table 4). All these species are, thus, restricted to the Northern Hemisphere and largely to the temperate zone. In eastern Asia C. ramakrishnai is isolated in South India, whereas the other species known to occur in the subcontinent of India are restricted to Himalaya and Terai. C. ramakrishnai was described from Coonoor, alt. ca. 1800 m, Nilgiri. It may be very close to C. lumbiniana, which inhabits the Terai jungle. It’s occurrence in the depth of South India may not be surprising, because, according to papers in “Ecology and Biogeography in India” (Mani, ed., 1974), the mountain biota of South India is characterized by the presence of elements which have northern connections.

Undoubtedly the known eastern Asian species are only a part of the Chionaspis fauna there. About half of them are of quite recent knowledge (10 species were described by Chen, 1983, and 8 others are named in this paper). Many further species are expected to occur in southern China and eastern Himalaya.

C. salicis has been recorded from a long list of plants. Many other species of Chionaspis, however, are associated with particular plants (Table 4*). This is especially true of the eastern Asian and the western Asian-Mediterranean species. In North America polyphagy is rather prevailing. The apparent host range restric-
tion in the eastern Asian species may simply be due to very insufficient surveys in this region. Nevertheless, it is noteworthy that in eastern Asia the host association is centred on the Fagaceae (11 species of Chionaspis) and, in a smaller degree, on the Lauraceae (5 species). The species occurring in western Asia and the Mediterranean Region are also found on the Fagaceae and the Tamaricaceae. Contrarily, in North America the host association is scattered over much more numerous plant families and no species of Chionaspis are associated with the Fagaceae and the Lauraceae except for occasional records of polyphagous species. This fact, coupled with the abundance of oaks in North America, is worthy of attention.

It seems that some of the polyphagous species have main and occasional host plants. Recent detailed studies on North American species (Willoughby et al., 1974, on C. americana and C. kosztarabi; Knipscher et al., 1976, on C. nyssae) suggest that species usually associated with 1 or a few plant species may sometimes occur on other plants which are not always closely related to their main hosts. Such cases will probably increase with further surveys not only in North America but also in eastern Asia. In fact, C. alnus (usually occurring on Alnus, the family Betulaceae) and C. sailamaensis (on fagaceous plants) were recently recorded from Ribes (Grossulariaceae) and Tilia (Tiliaceae), respectively, in northeastern Asia (Danzig, 1980). In spite of these facts there must be some significance in the aforesaid difference in host association between the eastern Asian and the North American species of Chionaspis.

The host association of C. salicis may be relevant here. This species is widely distributed over temperate Eurasia and North Africa. In Europe north of the Mediterranean Region it is almost the only species of the genus and must be a postglacial invader (apart from its possible invasions in interglacial periods). It is quite polyphagous there, having been recorded from 17 plant families, while it is restricted to salicaceous plants in eastern Asia (Danzig, 1980, p. 73; also pers. comm.). Unaspis euonymi is another example of a host range expansion associated with invasion. This species was introduced into North America before 1880. Gill et al. (1982) recorded more than 20 plant genera belonging to diverse families as its hosts in North America. On the other hand, it is almost restricted to Euonymus and Pachysandra in Japan, where it is probably native*. I am not sure whether it is possible to continue such documentation for other cases of scale insect invasion, but I do not think that the cases of C. salicis and U. euonymi are accidental or exceptional. To cite a few further cases from other insect groups, Wise (1953) recorded a broad host range of the leaf-mining microlepidopteron Lithocolletis messanella in New Zealand in contrast with a restricted one in Europe, where it is probably native, and a remarkable host range expansion of the Japanese beetle, Popillia japonica, in North America is quite notorious. The host range expansion associated with invasion should be considered in terms of competition, natural enemies and plant resistance as well as climatic and other factors, and, therefore, should have a general biological significance.

After all, it seems theoretically sound to suppose that a relatively recent

* Euonymus and Pachysandra are not closely related. In 1974, at Sapporo, I tried in success to transfer Unaspis euonymi occurring on Pachysandra terminalis to isolated pots of Euonymus fortunei, on which it continued for several generations.
Table 4. Distribution of the *Chionaspis* species and plant families they are associated with.

<table>
<thead>
<tr>
<th>Host plant family</th>
<th>Western Asia &amp; Mediterranean R.</th>
<th>Eastern Asia</th>
<th>North America</th>
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</thead>
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<tr>
<td>Taxaceae</td>
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<td><em>pinifolias</em></td>
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<td>Magnoliaceae</td>
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<td>Trochodendraceae</td>
<td><em>trochodendri</em></td>
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<td></td>
<td><em>linderae</em></td>
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<td><em>furfura</em></td>
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<td><em>gedlotsiae</em></td>
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<td><em>corni</em></td>
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<tr>
<td>Styraceae</td>
<td></td>
<td><em>lintneri</em></td>
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<td>Symplocaceae</td>
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<td><em>nyssae</em></td>
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<td>Cornaceae</td>
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<td><em>corni</em></td>
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<td><em>lintneri</em></td>
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<td><em>salicisnigrae</em></td>
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<tr>
<td>Nyssaceae</td>
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<td><em>nyssae</em></td>
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<td>Caprifoliaceae</td>
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<td><em>lintneri</em></td>
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<td>Platanaceae</td>
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<tr>
<td></td>
<td><em>cheni</em></td>
<td><em>lintneri</em></td>
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<td></td>
<td><em>ortholobis</em></td>
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<td><em>triformis</em></td>
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<td>Fagaceae</td>
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<td><em>himalaica</em></td>
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### Table 4. (Continued.)

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<tr>
<th>Plant Family</th>
<th>Species</th>
<th>Number of species</th>
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<td><strong>Juglandaceae</strong></td>
<td>caryae, furfura*, lintneri*</td>
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<td><strong>Ulmaceae</strong></td>
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<td><strong>Sterculiaceae</strong></td>
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<td><strong>Ericaceae</strong></td>
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<td><strong>Myrtaceae</strong></td>
<td>lumbiniana, ramakrishnai, syzygii</td>
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<td><strong>Rhamnaceae</strong></td>
<td>acuta, ortholobis*, sasseeri*</td>
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<td><strong>Rutaceae</strong></td>
<td>sasseeri*</td>
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<td><strong>Oleaceae</strong></td>
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<td><strong>Ranunculaceae</strong></td>
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<tr>
<td>Number of species</td>
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<td>34</td>
</tr>
<tr>
<td>No. of plant fam.</td>
<td>2</td>
<td>16</td>
</tr>
</tbody>
</table>

*C. salicis*, widely distributed in Eurasia and North Africa and associated with diverse plants especially in Europe, is excluded. * Species recorded from more than one plant family.

Invasion, followed by host range expansion and rapid speciation, is responsible for the scattered host association and the prevailing polyphagy in the North American species of *Chionaspis*. By contrast, the concentrated host association in eastern Asia probably suggests an older origin of the fauna. This may also be applicable to the western Asian-Mediterranean fauna.
EVOLUTIONARY SIGNIFICANCE OF THE SITE-CAUSED DIMORPHISM

In *Chionaspis* the site-caused dimorphism of the adult females has so far been known to occur only in a limited number of species. There may be recognized some groups of species concerning the state of the median lobes with relation to feeding sites as shown in Table 5. This table is rather rough and simplified, not representing details of all cases. It is also provisional, because the site-caused dimorphism would be revealed in further species.

Some species are known only by so-called "Phenacaspis"-forms with the median lobes sunken into the apex of the pygidium and divergent. They are mostly associated with the leaves of evergreen trees. *C. syzygii* occurs on both leaves and twigs, but no site effect is discernible so far as the pygidial lobes are concerned.

A few species were collected on the stems or branches of the host plants, which are evergreen or deciduous, and yet are represented by "Phenacaspis"-forms. Remarkable site-caused dimorphism is known to occur in some eastern Asian and North American species. These species are associated with deciduous trees with the exception of *C. sozanica*, which occurs on both evergreen and deciduous maples. Usually the "Phenacaspis"-forms occur on the leaves and the other forms on the bark. In *C. nyssae* and other species intermediate individuals were recorded from leaves, petioles, leaf-buds, or fruits.

More than 30 species may be placed in a group, being represented by forms with produced median lobes (which may not wholly be produced, with the inner bases cutting into the apex of the pygidium). Many of them occur on the bark of deciduous trees, but others on the branches of evergreen plants. Three species with produced median lobes were recorded to occur on the leaves of the host plants (fagaceous trees and *Osmanthus*).

In summary, some species are represented only by "Phenacaspis"-forms associated mostly with the leaves of evergreen trees, while many others are known by forms with produced median lobes, and generally occur on the bark of deciduous or, less frequently, evergreen trees. The dimorphic species have both forms and are mostly associated with deciduous trees.

Further discussion needs some premises. The postulations adopted are as follows: 1) the lobes should be disposed at the supposed caudal angles of the segments composing the pygidium; 2) they should be uniform in size and shape in their primitive state; 3) any deviation from this state—reduction in number and differentiation in size and shape—should be derivative. On the basis of these postulations the median lobes, placed on the opposite sides of the 8th abdominal segment, are supposed to be originally separated from each other and similar in size and shape to the other pairs of lobes. In a contrasting and, therefore, derivative state the median lobes are much enlarged in comparison with the lateral lobes, connected basally by a strong zygosis, and appressed or fused together. Both these antipodal combinations of characters are found in various taxa of the Diaspididae, and there is no doubt that parallel transformations took place in many different evolutionary lines concerning the state of the lobes.

The postulations given above may be applied to the species of *Chionaspis*. These species are all derivative in having zygotic median lobes, but various in the
Table 5. State of the median lobes in relation to the feeding site in the adult females of the *Chionaspis* species.

<table>
<thead>
<tr>
<th>Western Eurasia &amp; North Africa</th>
<th>Eastern Asia</th>
<th>North America</th>
</tr>
</thead>
<tbody>
<tr>
<td>L1 deeply sunken and divergent; occurring on leaves (* also on twigs or branches)</td>
<td>arkhola, castanopsidis, dryina, keteleeriae, neolinderae, sichuanensis*, subrotunda, syzygii*, trochodendri</td>
<td>heterophyllae, pinifolias</td>
</tr>
<tr>
<td>L1 deeply sunken and divergent; occurring on stems or branches (* also on petioles)</td>
<td>camphora*, clematidis</td>
<td></td>
</tr>
<tr>
<td>Dimorphism remarkable: L1 sunken and divergent in leaf-form, produced or tending to be so in bark-form (<strong>Phenacaspis</strong>-form also occurring on bark)</td>
<td>acer, enkianthi, linderae, saitamaensis*, sosanica, wistariae</td>
<td>gleditsiae, nyssae, platani, triformis</td>
</tr>
<tr>
<td>L1 wholly or largely produced; occurring on bark (* sometimes also on leaves)</td>
<td>engeddensis, etrusca, lepineyi, parastigma, salicis*, singularis, variabilis</td>
<td>acuta, alnus*, cheni, cornigera, discadenata, gengmaensis, himalatica*, lumbiniana, megasygosis*, pseudopolypora, salicis, svavurianita, yanagicolia*</td>
</tr>
<tr>
<td>L1 produced; occurring on leaves</td>
<td>agranulata, obclavata, osmanthi</td>
<td>ramakrishnai*, rotunda**</td>
</tr>
<tr>
<td>Feeding site not recorded (* L1 wholly produced; ** L1 sunken)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of species</td>
<td>7</td>
<td>35</td>
</tr>
</tbody>
</table>

development of the zygosis and other characters of the pygidial lobes. Among them, *C. syzygii* and *C. trochodendri* appear to represent the most primitive state in the fact that the zygosis is least developed and that the median lobes and the lobules of the lateral lobes are least differentiated in size and shape. These species, therefore, may be regarded as approximating the ancestor of the extant species of
Chionaspis at least concerning the state of the pygidial lobes. These species manifest only "Phenacaspis"-forms. C. rotunda (not examined) may be closely related to C. syzygii and C. trochodendri and is represented only by a "Phenacaspis"-form likewise.

Remarkable differentiations among the pygidial lobes are seen in many species of Chionaspis: the median lobes, sunken or produced, are much enlarged and modified in shape, and the outer lobules of the lateral lobes or both lobules of the 3rd lobes are much reduced in size (Figs. 14 and 15 may give an idea about the variation). Among these species, C. americana, C. ramakrishnai, C. lumbiniana, and the bark-associated form of C. nyssae are the most derivative in that the median lobes, entirely produced at the apex of the pygidium, are appressed or fused together. The most primitive state of the pygidial lobes is, therefore, found among the species with sunken median lobes, and the most derivative among the species with produced median lobes. In this sense it may be said that in the dimorphic species the leaf-associated forms are primitive in comparison with the bark-associated ones.

The numbers of external secretory organs may also be affected by feeding sites. In C. syzygii, which shows no site effect in the characters of the lobes and is
represented only by a "Phenacaspis"-form, the macroducts, gland spines, and disc pores tend to be more numerous in individuals occurring on the leaves than in those feeding on the twigs (Tables 1 & 2). All these individuals, however, when plotted on a bivariate scatter diagram for the total numbers of these secretory organs, appear to form a continuous group. This is shown, for example, by the total number of the perivulvar disc pores plotted against that of the dorsal macroducts (Fig. 1). In the dimorphic species C. wistariae (Figs. 2 & 13) the macroducts alone are greatly variable in number on different feeding sites (Table 6). Therefore, when plotted on a scatter diagram for the perivulvar disc pores against the dorsal macroducts, individuals occurring on the bark and those on the leaflets are separated into discrete groups. Individuals occurring on the petioles and petiolules are scattered over these dimorphic groups, thus uniting them into a large, indistinguishable group, while not differing from the leaflet-associated form ("Phenacaspis fujicola") in the pygidial lobes (Fig. 2). In another Japanese species, C. linderae, the dimorphic forms are separated likewise, without individuals uniting them (Fig. 3). In this species the perivulvar disc pores are disproportionately numerous in the form with produced median lobes. No further adequate or sufficient material has been available to increase examples, but I do not think that the patterns shown by C. wistariae and C. linderae are exceptional among the dimorphic species.

What C. syzygii shows is an ordinary variation to occur within the same species.

Table 6. Numbers of external secretory organs in C. wistariae adult females.

<table>
<thead>
<tr>
<th></th>
<th>Stem</th>
<th>Petioles &amp; Petiolules</th>
<th>Leaflets</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dorsal macroducts, total</td>
<td>31-77</td>
<td>35-107</td>
<td>70-118</td>
</tr>
<tr>
<td></td>
<td>55.3±4.4</td>
<td>76.9±5.4</td>
<td>89.7±5.2</td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>30</td>
<td>21</td>
</tr>
<tr>
<td>Lateral macroducts on MT-Abd III, total</td>
<td>48-96</td>
<td>63-88</td>
<td>57-99</td>
</tr>
<tr>
<td></td>
<td>68.0±4.1</td>
<td>77.2±2.5</td>
<td>78.3±4.4</td>
</tr>
<tr>
<td></td>
<td>29</td>
<td>29</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>31.1</td>
<td>32.8</td>
<td>32.2</td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>29</td>
<td>20</td>
</tr>
<tr>
<td>Perivulvar disc pores, total</td>
<td>57-115</td>
<td>69-113</td>
<td>59-105</td>
</tr>
<tr>
<td></td>
<td>88.7</td>
<td>90.4</td>
<td>89.5</td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>30</td>
<td>21</td>
</tr>
<tr>
<td>Anterior spiracular disc pores, per spiracle</td>
<td>11-24</td>
<td>10-23</td>
<td>10-20</td>
</tr>
<tr>
<td></td>
<td>15.4</td>
<td>14.8</td>
<td>13.6</td>
</tr>
<tr>
<td></td>
<td>57</td>
<td>43</td>
<td>33</td>
</tr>
<tr>
<td>Posterior spiracular disc pores, per spiracle</td>
<td>2-7</td>
<td>3-8</td>
<td>2-8</td>
</tr>
<tr>
<td></td>
<td>4.7</td>
<td>5.5</td>
<td>5.1</td>
</tr>
<tr>
<td></td>
<td>58</td>
<td>57</td>
<td>40</td>
</tr>
</tbody>
</table>

First row: range; 2nd: mean, or, when necessary, mean and 2 standard errors; 3rd: sample size. A few (1-4) lateral macroducts often present on MS and also on PR; 1 gland spine at times on Abd I. Anterior spiracular disc pores were at times difficult to count exactly. Material from one sapling of Wisteria, Kii Peninsula, Japan.
Fig. 3. *Chionaspis linderae*, adult females. Scatter diagram: total number of periovular
disc pores ($x_2$) against total number of dorsal macroducts ($x_1$). Profiles: pygidal
lobes. Specimens from scattered localities in Japan. Some of the preparations
examined bear no data as to the feeding site, but probably the individuals with
produced median lobes were collected all or principally on the bark and those with
sunken median lobes on the leaves. The median lobes are also variable locally, being
more widely separated from each other in western Japan (B, D); these local forms are
regarded as belonging to the same species.

Black circles \[ x_2 = 0.93x_1 + 36.00 \quad r = 0.624 \quad n = 64 \]
Empty circles \[ x_2 = 0.66x_1 + 18.94 \quad r = 0.644 \quad n = 38 \]

Contrasted with this, the dimorphic patterns in *C. wistariae* and *C. linderae* are such
ones as expected for different species. This line of reasoning, coupled with the
preceding one, suggests the possibility that the leaf-form of such a dimorphic species
represents the ancestral species from which the dimorphic species derived. If this
is the case, the ancestral phenotype is reproduced on the leaves of the host in every
season, while the end product of evolution is manifested on the bark.
This supposition may not be too fantastic now. Smith (1975) in his study on Pliocene fishes of Lake Idaho maintained that reversal of evolution is not unusual. Hampé (1959) and Kollar et al. (1980) experimentally induced reptilian structures in developing chickens. Hierarchical organization of the eukaryotic genome into batteries of genes (Britten et al., 1969, 1971, 1973) makes the genome hold a broad spectrum of phenotypic potentialities including ancestral and untested (Hunkapiller et al., 1982).

A test

A crucial point in the foregoing discussion is that *C. syzygii* and *C. trochodendri* approximate the ancestor of the extant *Chionaspis* species. If this supposition is correct, there must have once existed, prior to the appearance of the first species of *Chionaspis*, a form with non-zygotic median lobes and with the other features not much different from those of *C. syzygii* and *C. trochodendri*. It should have not been derivative in comparison with these species (unless reversal of evolution is involved in their characters). Needless to say, no paleontological evidence is available. A possible test may be to see if there is any extant form which meets the qualifications given above. Apparently such a test is not always possible despite the current strong tendency (Schopf, 1977; Eldredge et al., 1984; Akimoto, 1985; etc.) to the view that a long-term steady state has prevailed even at the species level in diverse groups of animals.

Actually, I have found in the material at hand from Nepal an insect which largely fulfills the qualifications given above. It is described under the name *Narayanaspis Eugeniae* (n.g., n.sp.) in the section for new taxa. *N. Eugeniae* was collected in the jungle of Terai, where *C. syzygii* also occurs, and on *Eugenia* sp., which is close to the hosts of *C. syzygii*. This agreement may be a mere coincidence, for *C. Lumbiniana*, a very derivative species, also occurs in Terai and on *Syzygium*. The agreement may be significant of their common habitat conditions in a subtropical climate.

The state of the pygidal lobes in *N. Eugeniae* exactly agrees with what is expected. In the arrangement of the dorsal macroducts *N. Eugeniae* is notably different from most species of *Chionaspis*, but appears not so much peculiar when compared with *C. trochodendri*. In this species the submedian rows of macroducts are divided into 2 series on the 3rd abdominal segment and often also on the 4th, and the submarginal rows are often irregularly double or, on the 3rd segment, even triple (Fig. 27). It seems, therefore, that these species has a common basic pattern in the arrangement of macroducts. Another peculiarity in *N. Eugeniae* is the occurrence of numerous lateral microducts on the thoracic segments. In other adult female characters, however, there is no noticeable difference between *Chionaspis* and *Narayanaspis*. In the 1st instar larvae there is no serious difference between these genera, either.

The 2nd instar male of *N. Eugeniae* agrees in some characters with the corresponding stage of *Chionaspis*, but curiously it lacks marginal processes. It is also unique in the structure of the marginal macroducts, which show no resemblance to the modified macroducts of *Chionaspis*. I have no grounds for maintaining that this type is ancestral to the 2nd instar males of *Chionaspis*. This stage, therefore, presents a serious difficulty. Nevertheless, I do not think that this difficulty is
crucial. In some other genera of the Diaspididae the 2nd instar males manifest quite
different phenotypes between closely related species (Takagi, 1983). We simply
cannot explain at present the peculiar 2nd instar male of *Narayanaspis* on the
supposition that this genus might be closely related to and more primitive than
*Chionaspis*.

What is important here is the fact that there exists one form which, provided *C.
syzygii* and *C. trochodendri* are the most primitive among the extant species of
*Chionaspis*, largely fulfills the qualifications for representing the form ancestral to
*Chionaspis*. This fact encourages further surveys in tropical and subtropical eastern
Asia.

**SECOND INSTAR MALES**

I have examined the 2nd instar males of 13 eastern Asian and 10 North
American species of *Chionaspis*. Tippins et al. (1970) described the 2nd instar male
of another North American species (*C. betulae* Tippins & Beshear, nec Cooley = *C.
triformis*). Thus, the 2nd instar males are now known in 24 species of the genus.
They are variable in the development of the marginal processes on the abdomen and
in the numbers of the external secretory organs. Here I restrict my discussion to
the number and arrangement of the modified macroducts, because there is in the
occurrence of these ducts a remarkable difference between the eastern Asian and the
North American species (Table 7). So far as observed, the modified macroducts are
6 in number at maximum on each side of the abdomen, belonging to the 2nd to 7th
abdominal segments. In other patterns part or all of them are replaced by ducts of
usual type.

The 24 species show, as a whole, a wide range of variation concerning the
occurrence of the modified macroducts. However, the eastern Asian species are
strongly centred in one pattern (Pattern IV). Curiously enough, this pattern has not
been found in the North American species in spite of the fact that they represent all
other observed patterns.

All these species still form a small part (a little over 1/3) of the genus.
However, in North America, the species examined for the 2nd instar males exceed
half the number of the native species. In eastern Asia the species examined come
from distant areas (Japan and Nepal), and yet most of them agree in having Pattern
IV. This pattern, therefore, must also prevail in other eastern Asian species.
Under these circumstances, the observed difference between the eastern Asian and
the North American species must reflect the reality to a considerable degree.

Seemingly the 2nd instar males themselves supply no clue to determine which
pattern is the most primitive. The adult females are not of much help, either. Not
all of the the eastern Asian species manifesting Pattern IV appear to be closely
related so far as based on the adult female characters. On the other hand, the North
American *C. gleditsiae* and *C. kosztarabi* are very closely similar to each other in the
adult females, but are quite different in the 2nd instar males (the latter species
lacking modified macroducts). The Nepalese *C. lumbiniana* and the North Amer­
ican *C. nyssae* agree in having modified macroducts in all of the 2nd to 7th abdominal
segments; the adult female of *C. lumbiniana* and that of the bark-form *C. nyssae*
also agree in having closely appressed median lobes (fused together in *C. nyssae*).
Table 7. Modified macroducts in the 2nd instar males of some species of *Chionaspis*.

<table>
<thead>
<tr>
<th>Pattern</th>
<th>Abdominal segment</th>
<th>Total on one side</th>
<th>Species</th>
<th>Locality</th>
</tr>
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<tr>
<td></td>
<td>II III IV V VI VII</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>0 0 0 0 0 0</td>
<td>0</td>
<td>heterophyllae</td>
<td>N. America 1)</td>
</tr>
<tr>
<td>0</td>
<td>0 0 0 0 0 0</td>
<td>0</td>
<td>kosstarabi</td>
<td>N. America 2)</td>
</tr>
<tr>
<td>0</td>
<td>0 0 0 0 0 0</td>
<td>0</td>
<td>pinifoliate</td>
<td>N. America</td>
</tr>
<tr>
<td>I</td>
<td>0 1 0 0 0 0</td>
<td>1</td>
<td>salicisnigrae</td>
<td>N. America</td>
</tr>
<tr>
<td>II</td>
<td>0 1 1 0 0 0</td>
<td>2</td>
<td>corni</td>
<td>N. America</td>
</tr>
<tr>
<td>II</td>
<td>0 1 1 0 0 0</td>
<td>2</td>
<td>orthotoba</td>
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</tr>
<tr>
<td>II</td>
<td>0 1 1 0 0 0</td>
<td>2</td>
<td>salicis</td>
<td>Japan 3)</td>
</tr>
<tr>
<td>III</td>
<td>0 1 1 0 0 0</td>
<td>1</td>
<td>gleditsiae</td>
<td>N. America</td>
</tr>
<tr>
<td>III</td>
<td>0 1 1 0 0 0</td>
<td>1</td>
<td>triformis</td>
<td>N. America 4)</td>
</tr>
<tr>
<td>IV</td>
<td>1 1 1 0 0 0</td>
<td>4</td>
<td>alnus</td>
<td>Japan</td>
</tr>
<tr>
<td>IV</td>
<td>1 1 1 0 0 0</td>
<td>4</td>
<td>arkhola</td>
<td>Nepal</td>
</tr>
<tr>
<td>IV</td>
<td>1 1 1 0 0 0</td>
<td>4</td>
<td>clematidie</td>
<td>Nepal</td>
</tr>
<tr>
<td>IV</td>
<td>1 1 1 0 0 0</td>
<td>4</td>
<td>coringera</td>
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</tr>
<tr>
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<td>1 1 1 0 0 0</td>
<td>4</td>
<td>linderae</td>
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<tr>
<td>IV</td>
<td>1 1 1 0 0 0</td>
<td>4</td>
<td>salamaensis</td>
<td>Japan</td>
</tr>
<tr>
<td>IV</td>
<td>1 1 1 0 0 0</td>
<td>4</td>
<td>sinapuriana</td>
<td>Nepal</td>
</tr>
<tr>
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<td>1 1 1 0 0 0</td>
<td>4</td>
<td>syzygi</td>
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</tr>
<tr>
<td>IV</td>
<td>1 1 1 0 0 0</td>
<td>4</td>
<td>wistariae</td>
<td>Japan 5)</td>
</tr>
<tr>
<td>V</td>
<td>0 1 1 1 1 1</td>
<td>5</td>
<td>americana</td>
<td>N. America 6)</td>
</tr>
<tr>
<td>V</td>
<td>0 1 1 1 1 1</td>
<td>5</td>
<td>platani</td>
<td>N. America</td>
</tr>
<tr>
<td>VI</td>
<td>1 1 1 1 1 1</td>
<td>6</td>
<td>lumbiniana</td>
<td>Nepal</td>
</tr>
<tr>
<td>VI</td>
<td>1 1 1 1 1 1</td>
<td>6</td>
<td>nyssae</td>
<td>N. America 7)</td>
</tr>
</tbody>
</table>

1) Material from Spalding Co., GA, Scotch pine, Aug. 24, 1966, col. & det. H. H. Tippins. 2) Also reported by Willoughby et al. (1974). 3) Reported by Takagi et al. (1967) under the name salicisnigrae; also reported by Boratynsky (1953) from England. 4) Reported by Tippins et al. (1970) under the name betulae ("cuplike ducts on what appear to be segments 4, 5, and 7"). 5) Also reported by Takagi et al. (1967) from N. America, where the species was introduced from Japan. 6) Also reported by Willoughby et al. (1974). 7) Also reported by Knipscher et al. (1976).

These agreements in both stages may be due to phylogenetic vicariism, otherwise to convergence. In short, apparent morphological similarities do not always correspond between the 2nd instar males and the adult females. However, it should gain attention that the species which manifest Pattern IV include *C. syzygii*. This species (together with *C. trochodendri*) is supposed to represent the most primitive state in the genus concerning the characters of the pygidal lobes in the adult females (see under Evolutionary significance of the site-caused dimorphism). Pattern IV, therefore, may tentatively be taken for the most primitive. The other patterns may have arisen, primarily or secondarily, from that pattern by decrease or increase in the number of modified macroducts.

I cannot explain why many eastern Asian species, while diversified in adult female characters, have been at a stasis, and why the North American species are so diverse, in the arrangement of modified macroducts. There might have been some threshold effect. Once the primitive pattern was changed to another one, the arrangement may have become very mutable. Apart from the absence of a plausible explanation, the diversity itself indicates that the North American fauna is
composed of many derivative forms of the 2nd instar males.

AN EVOLUTIONARY SCENARIO

The genus *Chionaspis* as understood in this paper is mainly temperate in distribution and represented by abundant species in eastern Asia, with much fewer ones in western Eurasia and North Africa. It is also well represented in North America, where "it is especially well developed east of the Rocky Mountains" (Ferris, 1937). Thus, the distributional pattern of the genus is reminiscent of the well-known bicontinental distribution of the remnants from the Arcto-Tertiary flora, and, therefore, the origins of the extant species of *Chionaspis* may be attributed to a fauna which was ubiquitous in the high latitude Northern Hemisphere during a greater part of the Tertiary.

It does not seem, however, that this simple analogy can fully explain the current state of the genus. Further, phylogenetic relationships among the species have not yet been worked out, and, therefore, it is not certain whether vicarious relationships can generally be established between the species of the 2 continents. By the same reason any evolutionary scenario proposed for the genus will present only a rough outline of events which may have happened. In the following lines I propose one which can be in accord with 1) the presence of primitive forms (*C. syzygii*; *C. trochodendri*) of the genus in eastern Asia, 2) the occurrence of a related more primitive form (*Narayanaspis eugeniae*) in eastern Asia, 3) a relatively concentrated host-association in eastern Asia in contrast to a scattered one in North America, and 4) a concentration of the 2nd instar males in Pattern IV in eastern Asia in contrast to a remarkable diversity in North America. Interpretations are given for the phenomena 3) and 4) under Composition, distribution, and host plants and Second instar males.

The occurrence of primitive species of a genus in a particular region may simply be due to their extinction in other regions, so that it does not necessarily mean that the genus originated or first evolved in that region. However, if another genus which is related to and more primitive than the genus under consideration is found in the same region, the possibility will be stronger that the latter originated in that region. It may accordingly be concluded that *Chionaspis* originated somewhere in eastern Asia from a form which *Narayanaspis* represents or approximates. In this connection it is worthy of attention that *N. eugeniae* and the 2 primitive species of *Chionaspis* occur in lower latitudes (*N. eugeniae* and *C. syzygii* in lowland Nepal and *C. trochodendri* in Taiwan at altitudes of ca. 1000–2000 m) under a subtropical or warm temperate climate. The origin and early speciation of *Chionaspis* may have taken place in these climates.

The localities and hosts of the living species show that further speciation has been copious in temperate lauro-fagaceous forests, which at present extend from Himalaya through China to southern Japan. The genus expanded into cooler climates probably much later. Diversified in the adult female characters, many species have continued to manifest the primitive arrangement of modified macroducts in the 2nd instar males. It may be noteworthy that other patterns of these macroducts are found in *C. salicis* (inhabiting cool climates) and *C. lumbiniana* (specialized in habit), both species being very derivative in the pygidial lobes of the
adult females.

If the supposition that the North American fauna of *Chionaspis* originated with invasion in a relatively recent time is correct, the invasion must have been from eastern Asia through the landed Bering Strait. I have no idea as to when it occurred and how many species invaded. Above all, phylogenetic relationships should be established between the eastern Asian and the North American species before any trial is made.

I am puzzled about the species occurring in western Asia and the Mediterranean Region. These species (except the widely distributed *C. salicis*) belong to 2 groups each composed of closely related species. They are all considerably derivative in the state of the pygidial lobes in the adult females. They may have their origins in the eastern Asian fauna, but the arid climates they live in are apparently foreign to the eastern species. They may be fragments of a fauna once developed in the western regions, but no evidence is available for this possibility, too.

The site-caused dimorphism must have some ecological significance. It is mainly associated with deciduous trees and cool climates. It is not a transitional phase from the leaf-feeding to the bark-feeding mode of life, because the dimorphic forms are quite differentiated morphologically in some species. The seasonal emergence of the leaf-associated forms must have first appeared after the expansion of the genus into cooler climates, when the species concerned had evolved into well-established bark-feeders. On deciduous trees no species of armoured scale insects may be perpetual on the leaves alone; once settled on the leaves in the first instar, all females will be lost together with fallen leaves. If crawlers produced by the leaf-occurring population can move back to the bark before the fall of leaves, that population may not be wholly futile. The life history chart presented by Knipscher et al. (1976) for *C. nyssae* seems to support this possibility. The ecological significance here suggested is a possible utilization of resources which can be vacant in the absence of permanent leaf-feeders.

The scenario presented is very incomplete, but it is based on general theoretical postulations concerning the host range expansion associated with invasion and the manifestation of ancestral phenotypes. When these phenomena turn out theoretically improbable, the scenario should be rejected. The phylogenetic relationships among the species are little known, and this is one reason why the evolutionary history is only roughly outlined. In order to approach the phylogenetic relationships, however, we need a "historical reconstruction" (Ghiselin, 1972). These approaches are interwound. Knipscher et al. (1976) states: "In comparing the various stages of *C. nyssae* with the same stages of other species of *Chionaspis*, apparent morphological relationships may vary greatly from one instar to the next". Tippins et al. (1970) pointed out that the bark-associated form of *C. triforinis* ("C. betulae") resembles *C. acericola* (represented by the bark-form alone so far) and the leaf-form of that species is similar to the leaf-form of *C. gleditsiae*. In such cases purely formal comparisons alone are apparently insufficient and impotent. If the leaf-associated forms of the dimorphic species are manifestations of ancestral phenotypes, resemblance between these forms may reflect phylogenetic relationship, while resemblance between the bark-forms may indicate convergence (when combined with less similar leaf-forms). If the arrangement of the modified macroducts has long been locked to Pattern IV in eastern Asian species, the possession of this
pattern does not necessarily mean that the species concerned are particularly closely related. I suggested that the arrangement became mutable after the primitive pattern was changed into another. If this was the case, different patterns do not always mean a remote phylogenetic relationship.

Finally, *Aulacaspis* is undoubtedly closely related to *Chionaspis*, but it is apparently derivative in comparison with the latter (see under A revised concept of *Chionaspis*). Inquiry into the relationship between these genera should be put off to the accomplishment of my study on abundant material of *Aulacaspis* at hand.

**ACKNOWLEDGEMENT**

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A LIST OF THE SPECIES OF CHIONASPIS

Chionaspis acer
   Takagi & Kawai, 1966 [Phenacaspis].

Chionaspis acericola
   Hollinger, 1923; Ferris, 1937; Kosztarab, 1964.

Chionaspis acuta
   Far East USSR (Maritime Province). On Rhamnus (Rhamnaceae).

Chionaspis agranulata
   Chen, 1983.
   Continental China (Yunnan). On a fagaceous plant.

Chionaspis alnus
   Japan; Korea; Mongolia; Far East USSR (Maritime Province to the Sayan Mountains; Sakhalien; South Kuriles). On Alnus (Betulaceae); Alnus, Betula (Betulaceae), and Ribes (Grossulariaceae) were recorded as hosts in Far East USSR.

Chionaspis americana
   Johnson, 1896; Cockerell, 1897 [C. furfurus var. ulmi]; MacGillivray, 1921 [Fundaspis americana]; Lindinger, 1932 [Jaapia americana]; Ferris, 1937; Willoughby & Kosztarab, 1974.
   U.S.A. (throughout central, eastern, and southern states, and California). On Ulmus (Ulmaceae); also recorded from Celtis (Ulmaceae), Ligustrum (Oleaceae), Tilia (Tiliaceae), Crataegus (Rosaceae), and Prunus (Rosaceae) by Willoughby et al. (1974); records from other plants may need reexamination.

Chionaspis arkhola
   Takagi, 1985.
   Nepal. On Lithocarpus (Fagaceae).

Chionaspis camphora
   Chen, 1983 [Phenacaspis].
   Continental China (Sichuan; Guizhou). On Cinnamomum (Lauraceae).

Chionaspis caryae
   Cooley, 1898; Ferris, 1942; Kosztarab, 1964.
   U.S.A. (central, eastern, and southern states). On Carya and Juglans (both genera belonging to the Juglandaceae).

Chionaspis castanopsidis
   Takagi, 1985.
   Nepal. On Castanopsis (Fagaceae).

Chionaspis cheni
Chionaspis clematidis
Takagi, 1985.
Nepal. On *Clematis* (Ranunculaceae).

Chionaspis corni
Cooley, 1899; Ferris, 1937; Kosztarab, 1964.
U.S.A. (central, eastern, and southern states, and also Utah and California). On *Cornus* (Cornaceae); also recorded on *Ribes* (Grossulariaceae) in California.

Chionaspis cornigera
Takagi, 1985.
Nepal. On a lauraceous tree.

Chionaspis discadenata

Chionaspis dryina
Ferris, 1953 [*Phenacaspis*].
Continental China (Yunnan). On *Quercus* (Fagaceae).

Chionaspis engeddensis
India (Punjab); Central Asia (Tadzhik; Uzbek; Turkmen; Kazakh); Azerbaidzhan; Armenia; Iraq; Palestine. On *Tamarix* (Tamaricaceae).

Chionaspis enkianthi
Takahashi, 1953; Ferris, 1956 [*Phenacaspis*].

Chionaspis etrusca
Leonardi, 1908; Ferris, 1937; Balachowsky, 1954.
Western Mediterranean Region (Italy; France; Spain; North Africa); introduced into U.S.A. and Mexico. On *Tamarix* (Tamaricaceae).

Chionaspis floridensis

Chionaspis furfur
Canada and U.S.A. (central, eastern, and southern states, and also California nurseries). On rosaceous plants (*Chaenomeles, Crataegus, Cydonia, Malus, Prunus, Pyracantha, Pyrus,* and *Sorbus*); also recorded from *Juglans* (Juglandaceae), *Staphylea* (Staphyleaceae), and *Ulmus* (Ulmaceae).

Chionaspis gengmaensis
Chen, 1983 [*Phenacaspis*].
Continental China (Yunnan). On *Populus* (Salicaceae).

Chionaspis gleditsiae
Sanders, 1903; Dietz & Morrison, 1916 [*Phenacaspis spinicola*]; Ferris, 1937 [*Chionaspis gleditsiae and Phenacaspis spinicola*].
U.S.A. (central, eastern, and southern states; also recorded from California). On *Gleditsia* (Leguminosae). *P. spinicola* is the leaf-form of *C. gleditsiae*.

**Chionaspis heterophyllae**
Cooley, 1897 [*Chionaspis pinifoliae heterophyllae*]; Ferris, 1942 [*Phenacaspis*].
U.S.A. (eastern to southern states); Caribbean Region. On *Pinus* (Pinaceae).

**Chionaspis himalaica**
Takagi, 1985.
Nepal and India (Himalach Pradesh). On *Quercus* (Fagaceae).

**Chionaspis ketelaeriana**
Ferris, 1953 [*Phenacaspis*].
Continental China (Yunnan). On *Keleleeria* (Pinaceae).

**Chionaspis kosztarabii**
U.S.A. (eastern states). On *Fraxinus* (Oleaceae) and *Ostrya* (Betulaceae).

**Chionaspis lepineyi**
Europe (Gruziya; Armenia; Hungary; Switzerland; Spain) and North Africa (Morocco). On *Quercus* and *Castanea* (both genera belonging to the Fagaceae).

**Chionaspis linderae**
Takahashi, 1952; Takahashi, 1953; Ferris, 1955 [*Phenacaspis*].

**Chionaspis lintneri**
Comstock, 1883; Cooley, 1898 [*Chionaspis lintneri betulae*]; Ferris, 1937; Kosztarab, 1964.
Eastern Canada; eastern U.S.A. On *Alnus* (Betulaceae), *Betula* (Betulaceae), *Juglans* (Juglandaceae), *Styrax* (Styracaceae), and *Viburnum* (Caprifoliaceae).

**Chionaspis longiloba**
Cooley, 1899; Ferris, 1937; Kosztarab, 1964.
U.S.A. (eastern and southern states). On *Salix* and *Populus* (both genera belonging to the Salicaceae).

**Chionaspis lumbiniana**
Takagi, 1985.
Nepal. On *Syzygium* (Myrtaceae).

**Chionaspis megazygosis**
Chen, 1983.
Continental China (Yunnan). On *Eurya* (Theaceae).

**Chionaspis neolinderae**
Chen, 1983 [*Phenacaspis*].
Continental China (Jiangxi). On *Lindera* (Lauraceae). Another form occurring on a fagaceous plant in Fujian was also referred to *C. neolinderae* by Chen.

**Chionaspis nyssae**
Comstock, 1881; Cockerell, 1899 [*Phenacaspis*]; Sanders, 1904, [*Chionaspis sylvatica*]; Ferris, 1937 [*Chionaspis sylvatica and Phenacaspis nyssae*]; Takagi & Kawai, 1967 [*Phenacaspis nyssae is the leaf-form of Chionaspis sylvatica*]; Knipscher, Miller, & Davidson, 1976.
U.S.A. (eastern and southern states). On *Nyssa* (Nyssaceae); also recorded from *Celtis* (U-
maceae), *Lindera* (Lauraceae), *Quercus* (Fagaceae), *Symlocos* (Symlocaceae), and *Crataegus* (Rosaceae).

**Chionaspis obclavata**
Chen, 1983 *Chionaspis obclavata*, p. 10; *C. obclavata*, p. 7, 91; *C. obclavatas*, p. 105.
Continental China (Fujian). On *Quercus* (Fagaceae).

**Chionaspis ortholobis**
Comstock, 1881; Ferris, 1937.
Canada (British Columbia) ; U.S.A. (western states). On *Ceanothus* (Rhamnaceae), *Rhamnus* (Rhamnaceae), *Alnus* (Betulaceae), *Salix* (Salicaceae), *Populus* (Salicaceae), *Platanus* (Platanaceae), *Fremontia* (Sterculiaceae), and *Arctostaphylos* (Ericaceae).

**Chionaspis osmanthi**
Ferris, 1953 *Penacaspis*.
Continental China (Yunnan). On *Osmanthus* (Oleaceae).

**Chionaspis parasigma**
Balachowsky, 1954.
Iran. On *Quercus* (Fagaceae).

**Chionaspis pinifoliae**
Fitch, 1856 *Aspidiotus*; Comstock, 1881; Cockerell, 1895 *Chionaspis pinifoliae var. semianuera*; Ferris, 1937 *Phenacaspis*; Balachowsky, 1954 *Phenacaspis*.
Canada; U.S.A.; Mexico; Cuba; El Salvador; Honduras. On *Pinus*, *Abies*, *Cedrus*, *Picea*, *Tsuga*, and *Pseudotsuga* (all belonging to the Pinaceae), and also on *Taxus* and *Torreya* (both belonging to the Taxaceae).

**Chionaspis platani**
Cooley, 1899; Hollinger, 1923 *Chionaspis parkii*; Ferris, 1937 *Chionaspis parkii* and *Phenacaspis platani*; Kosztarab, 1964 *Chionaspis parkii*, *Phenacaspis occidentalis*, and *Phenacaspis platani*; Nakahara, 1975 *Phenacaspis occidentalis = Phenacaspis platani*.
U.S.A. (eastern and southern states). On *Platanus*.
P. *platani* and *P. occidentalis* are the leaf-associated form of *C. parkii* (*P. platani* was also recorded from the bark).

**Chionaspis pseudopolyphora**
Chen, 1983.
Continental China (Yunnan). On *Quercus* (Fagaceae).

**Chionaspis ramakrishnai**
Ramakrishna Ayyar, 1930 *Pinnaspis ramakrishnae Green (MS)*; Rao, 1953.
India (Nilgiri). On *Eugenia* (Myrtaceae).

**Chionaspis rotunda**
Takahashi, 1935 *Phenacaspis*.
China (Taiwan). On *Quercus* (Fagaceae).

**Chionaspis saitamaensis**
Kuwana, 1928; Takagi, 1961 *Phenacaspis*; Danzig, 1980.
Japan; Far East USSR (Maritime Province). On *Quercus* (Fagaceae); recorded from *Quercus* and *Tilia* (Tiliaceae) in the Far East USSR.
The species described by Ferris (1955) under the name *Phenacaspis saitamensis* [sic] (Kuwana) seems to be identical with *Pseudaulacaspis kuwanai* Takahashi (= *Phenacaspis quercus* Kuwana).
*Phenacaspis saitamensis* [sic] recorded by Chen (1983) from China also belongs to *Pseudaulacaspis*.

**Chionaspis salicis**
Linnaeus, 1758 [Coccus]; Balachowsky, 1954; Ferris, 1955; Danzig, 1980. Names proposed for forms occurring on different plants in Europe were synonymized with *C. salicis*: *Aspidiotus* Vaccini *Bouche*, 1851; *Aspidiotus Populi* Baerensprung, 1849; *Chionaspis aceris* Signoret, 1869; *Chionaspis alni* Signoret, 1869; *Chionaspis fraxini* Signoret, 1869; *Chionaspis sorbi* Douglas, 1893; etc. Other names proposed for Asian forms were also united with *C. salicis*: *Chionaspis micropori* Marlatt, 1908; *Chionaspis montana* Borchsenius, 1949; and *Chionaspis polypora* Borchsenius, 1949. According to Danzig (1970), *Chionaspis caucasioni* Hadzibeili, 1963, is also a synonym of *Chionaspis salicis*.

Temperate Eurasia (Japan; Korea; China; Mongolia; Indian Himalaya; USSR, Far East to Europe; Turkey; Iran; Continental Europe; England) and North Africa (Algeria; Morocco). On *Salix* and other salicaceous plants; also recorded from many species of plants belonging to diverse families especially in Europe.

*Chionaspis salicis nigrae*

Walsh, 1868 [*Aspidiotus*]; Cockerell, 1898 [*Chionaspis ortholobis Bruneri*]; Ferris, 1937. Widely distributed in Canada and U.S.A., but “records from western United States are...erroneous” (Ferris, 1937). On *Salix* and *Populus* (both genera belonging to the Salicaceae); also recorded from *Fraxinus* (Oleaceae), *Cornus* (Cornaceae), *Liriodendron* (Magnoliaceae), and *Amelanchier* (Rosaceae). Records of *C. salicis nigrae* from Saghaliien and Japan should be corrected to *S. salicis*.

*Chionaspis sasscareri*

Cockerell & Robbins, 1909; Ferris, 1942. U.S.A. (California). On orange (Rutaceae) and *Ceanothus* (Rhamnaceae).

*Chionaspis sichuanensis*

Chen, 1983 [*Phenacaspis*]. Continental China (Sichuan). On a lauraceous plant.

*Chionaspis singularis*


*Chionaspis sivapuriana*


*Chionaspis sozanica*

Takahashi, 1933; Ferris, 1956 [*Phenacaspis*]; Takagi, 1970. China (Taiwan); Japan (Ryōkyō). On *Acer* (Aceraceae).

*Chionaspis subrotunda*

Chen, 1983 [*Phenacaspis*]. Continental China (Sichuan). On a fagaceous plant.

*Chionaspis syzygii*

Takagi, 1985. Nepal (Terai) and India (Uttar Pradesh). On *Syzygium* and *Cleistocalyx* (both genera belonging to the Myrtaceae).

*Chionaspis triformis*


*Chionaspis trochodendri*

Chionaspis variabilis
Central Asia (Tadzhik). On *Tamarix* and *Myricaria* (both genera belonging to the Tamaricaceae).

Chionaspis wistan'ae
Cooley, 1897; Kuwana, 1931 [Phenacaspis fujicola]; Ferris, 1942; Takahashi, 1953 [Phenacaspis fujicola is the leaf-form of *Chionaspis wistan'ae*].
Japan; also introduced to U.S.A. (California; Pennsylvania). On *Wisteria* (Leguminosae). Chen (1983) recorded "Phenacaspis fujicola Kuwana" from China (Yunnan) as occurring on an undetermined shrub.

Chionaspis yanagicola
Kuwana in Kuwana & Muramatsu, 1932 [Phenacaspis]; Takahashi, 1953 [Phenacaspis].
Japan. On *Salix* (Salicaceae).

A LIST OF NAMES WHICH HAVE BEEN REFERRED TO *CHIONASPIS* OR *PHENACASPIS*

Name/reference to *Chionaspis* or *Phenacaspis*/original reference/author(s) and date/and disposition are given in the mentioned order. Abbreviations: C., *Chionaspis*; P., *Phenacaspis*; NF, nominifer (type-species).

*abbrideliae*/P./P./Chen, 1983/referable to *Pseudaulacaspis*.
*acer*/P., C./P./Takagi & Kawai, 1966/a sp. of C.
*acericola*/C./C./Hollinger, 1923/a sp. of C.
*aceris*/C./C./Signoret, 1869/ = *C. salicis*.
*acuminata*/C./C./Green, 1896/NF of *Unaspis*.
*acuta*/C./C. acutus/Danzig, 1976/a sp. of C.
*aegyptiaca*/C./C. graminis* aegyptiaca/Hall, 1923/ = Duplachionaspis natalensis.
*africana*/C./C./Newstead, 1912/NF of *Gramenaspis*.
*agonidis*/C./C./Lindinger, 1907/an invalid emendation for *agonis*.
*agonis*/C., P./C./Fuller, 1897/doubtfully referable to *Pseudaulacaspis*.
*agranulata*/C./C./Chen, 1983/a sp. of C.
*akebiae*/C., P./C./Takahashi, 1952/regarded as a form of *Pseudaulacaspis cockerelli*.
*alnigerrimenata*/C./C./Green, 1896/ = *Inehoaspis dentiloba*.
*alanica*/C./C./Kuwan, 1928/a sp. of C.
*amausis*/C./C./Lindinger, 1910/NF of *Inchoaspis*; = Inchoaspis dentiloba.
*ambigua*/C./C. ambigua/Brain, 1920/referred to *Andaspis*.
*americanana*/C./C./Johnson, 1896/NF of *Fundaspis*; retained in C.
*angustica*/P., C./C./Green, 1904/generic position indeterminate.
*angustior*/C./C./Riley & Howard, 1893/a nomen nudum.
*annandalei*/C./C./Green, 1919/unretainable in C.
*arkhola*/C./C./Takagi, 1973/sp. of C.
*arthrocromenri*/C., P./C./Lindinger, 1911/referred to *Duplachionaspis*.
*arrundinariae*/C., P./C./Green, 1899/NF of *Canaspis*; referred to *Greenaspis*.
*asiatica*/C./C./Archangelskaya, 1930/referred to *Tecaspis*.
*asperati*/C./C./Laing & Cockerell, 1929/referred to *Duplachionaspis*.
*aspidistrae*/C./C./Signoret, 1869/referred to *Pinnaspis*.
*assimilis*/C./C./Maskell, 1889/referred to *Unaspis*.
*asteliae*/C./C./Lepidosaphes/Green, 1929/referred to *Andaspis*.

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a labian/C., P./C./Takahashi, 1933/supposed to belong to Ledaspis.
atticola/C./C. acuminata var./Green, 1922/referred to Unaspis.
excuca/C./P./C./Cooley, 1897/= Pseudaulacaspis cockerelli.
auallis/C./C./Newstead, 1920/referred to Dentachionaspis.
ausralis/P./P./Laing, 1925/possibly a sp. of Pseudaulacaspis.
aussatina/C./P./C./Lindinger, 1912/unretainable in C.

bambusae/C./C./Cockerell, 1896/referred to Unachionaspis.
bambusfoliae/C./C./Takahashi, 1930/referred to Greenaspis.
barbyi/C./C./Balachowsky, 1930/="C." austriaca.
hinilina/P./P./Hall, 1946/referred to Voraspis.
berlesii/C./P./C./Lindinger, 1907/an emendation for berlesii.
berlesii/C./P./C./Leonardi, 1898/referred to Duplachionaspis.
berliniae/C./C. (Pinnaspis) communis var./Hall, 1928/referred to Africaspis.
beute/C./C./Green, 1898/= C. lintneri.
beute/C./C./C./Cooley, 1898/altered to cheni.
biclavis/C./C./Comstock, 1883/NF of Howardia and also of Megalodiaspis.
bilobis/C./C./Newstead, 1895/referred to Contigaspis.

braini/C./C./Lindinger, 1931/= Rolaspis lounsburyi.
brasilios/C./C./Signoret, 1869/= Pinnaspis aspidistrae.
bridelae/C./P./C./Takahashi, 1933/referable to Pseudaulacaspis.
brmneri/C./C. ortholobis subsP./Cockerell, 1898/= C. salicisignae.
bupleri/P./C./Marchal, 1904/NF of Getulaspis.
bussii/C./P./C./Newstead, 1911/NF of Daraspis.
cacti/C./C./Kuwana, 1931/unretainable in C.
caffra/C./C./Brain, 1920/referred to Africaspis.
calcarata/C./Lepidosaphes/Ferris, 1921/referred to Dactylaspis.
candida/C./C./Green, 1905/generic position indeterminate.
candida/C./C./Banks, 1906/altered to inday.
capensis/C./C./Newstead, 1917/NF of Dentachionaspis ; = Dentachionaspis lounsburyi.
capperidis/C./C./Lindinger, 1932/an emendation for capperisi.
capperisi/C./C./Brain, 1919/referred to Dentachionaspis.
carissae/C./P/Poliaspis/Cockerell, 1902/referred to Rolaspis.
caroli/C./C./Green, 1919/referred to Lineaspis.
carpenteri/C./C./Laing, 1929/NF of Voraspis.
caryae/C./C./Cooley, 1898/a sp. of C.
cassine/C./C./Newstead, 1911/= Africaspis chionaspiformis.
castanosapis/C./C./Kuwana, 1931/a sp. of C.
ceanoki/C./Lepidosaphes/Ferris, 1919/referred to Aonidomytilus.
ceassiae/C./P./Kuwana, 1928/referred to Pseudaulacaspis.
centres/C./P./C./Ferris, 1933/referable to Pseudaulacaspis.
centripetalis/C./C./Green in Misra, 1923/a nomen nudum ; = Dentachionaspis centripetalis Rao, 1953.
ceratoniae/C./C./P./P./Marchal, 1904/referred to Voraspis.
cealwico/C./C. these var./Green, 1905/= Pinnaspis exerchata.
chaetachmae/C./C./Brain, 1919/referred to Rolaspis.
chaetachme/C./C./Lindinger, 1932/an emendation for chaetachmae.
cheni/C./C./Kuwana, 1931/a new name for betulae Chen; a sp. of C.
chinensis /C. , P. /C./Cockerell, 1896/referable to Pseudaulacaspis.
chionaspiformis /C. /"? Diaspis" /Newstead, 1910/NF of Africaspis.
chionaspisformis /C. /Hemicionaspis/Lindinger, 1910/an invalid emendation for Hemichionaspis
    chionaspiformis (= Diaspis chionaspiformis).

terifina /C. /Green, 1919/referable to Dentachionaspis.
chitinosa /C./Lepidosaphes (Coccomytilus)/Lindinger, 1910/generic position indeterminate.
cinnamonis /C. /Green, 1905/NF of Proceraspis.
cintri /C. /Comstock, 1883/referred to Unaspis.
clematidis /C. /C./Cockerell, 1897/referred to Pseudaulacaspis.
chionaspiformis /C./"? Diaspis" /Newstead, 1910/NF of Alricaspis.
chionaspisformis /C./Hemicionaspis/Lindinger, 1910/an invalid emendation for Hemicionaspis
    chionaspiformis (= Diaspis chionaspiformis).

terifina /C. /Green, 1919/referred to Dentachionaspis.
chitinosa /C./Lepidosaphes (Coccomytilus)/Lindinger, 1910/generic position indeterminate.
cinnamonis /C. /Green, 1905/NF of Proceraspis.
cintri /C. /Comstock, 1883/referred to Unaspis.
clematidis /C. /C./Cockerell, 1897/referred to Pseudaulacaspis.
chionaspisformis /C./"? Diaspis" /Newstead, 1910/NF of Alricaspis.
chionaspisformis /C./Hemicionaspis/Lindinger, 1910/an invalid emendation for Hemicionaspis
    chionaspiformis (= Diaspis chionaspiformis).

terifina /C. /Green, 1919/referable to Dentachionaspis.
chitinosa /C./Lepidosaphes (Coccomytilus)/Lindinger, 1910/generic position indeterminate.
cinnamonis /C. /Green, 1905/NF of Proceraspis.
cintri /C. /Comstock, 1883/referred to Unaspis.
clematidis /C. /C./Cockerell, 1897/referred to Pseudaulacaspis.
chionaspisformis /C./"? Diaspis" /Newstead, 1910/NF of Alricaspis.
chionaspisformis /C./Hemicionaspis/Lindinger, 1910/an invalid emendation for Hemicionaspis
    chionaspiformis (= Diaspis chionaspiformis).

terifina /C. /Green, 1919/referable to Dentachionaspis.
chitinosa /C./Lepidosaphes (Coccomytilus)/Lindinger, 1910/generic position indeterminate.
cinnamonis /C. /Green, 1905/NF of Proceraspis.
cintri /C. /Comstock, 1883/referred to Unaspis.
clematidis /C. /C./Cockerell, 1897/referred to Pseudaulacaspis.
chionaspisformis /C./"? Diaspis" /Newstead, 1910/NF of Alricaspis.
chionaspisformis /C./Hemicionaspis/Lindinger, 1910/an invalid emendation for Hemicionaspis
    chionaspiformis (= Diaspis chionaspiformis).

decemvarent /C. , P. /C./Green, 1903/referable to Greenaspis.
dendrobi /P.//P./Kuwana, 1931/referable to Pseudaulacaspis.
dentilobis /C./C./Newstead, 1910/NF of Inchoaspis.
depressa /C. /C./Zehntner, 1897/referred to Aulacaspis.
defecta /C. /C. biclavis var./Maskell, 1895/ = Howardia biclavis.
difficilis /C./C./Cockerell, 1896/referred to Aulacaspis.
diffusa /P./P./Brimblecombe, 1960/a sp. of Pseudaulacaspis ?
dilata /C. , P. /C./Green, 1899/ = Pseudaulacaspis cockerelli.
dilatilobis /Lepidosaphes /Green, 1922/generic position indeterminate.
diosmoe /C. (Diaspis)/Brain, 1920/NF of Versiculaspis.
diospyrs /C. (Pinnaspis)communis var./Hall, 1929/referred to Africaspis.
diplasia /Lepidosaphes /Laing, 1925/referred to Tecaspis.
discadenata /C./C. discadenatus /Danzig, 1976/a sp. of C.
distichlii /C. /C./Ferris, 1921/referred to Haliaspis.
distincta /C./Diaspis/Leonardi, 1914/referred to Ledaspis.
distorta /C. /C./Newstead, 1917/NF of Assymetraspis.
divergens /C. /C. graninis var./Green, 1899/referred to Duplacchionaspis.
dryina /P. /P./Ferris, 1953/referable to C.
dubia /C. , P. /C./Maskell, 1882/referred to Pseudaulacaspis.
dysostyi /C. , P. /C./Maskell, 1885/referred to Pinnaspis.
ekebergiae /C. , P. /C./Cockerell, 1896/referable to Anulacaspis.
eloangi /C. , P. /C./Green, 1896/referable to Anulacaspis.
elongata /C./Molitaspis/Green, 1896/NF of Greenaspis.
engeddenisi /C. /C./Bodenheimer, 1924/a sp. of C.
entianthi /C. , P. /C./Takahashi, 1953/a sp. of C.
ericacea /P. /P./Ferris, 1953/referable to Pseudaulacaspis.
etheae /C. , P. /C./Fuller, 1897/generic position indeterminate.
etrusa /C. /C./Leonardi, 1908/a sp. of C.
eucalypti /C. , P. /C./Froggatt, 1914/ = "C." angusta.
euoelegii /C. , P. /C./Maskell, 1892/referred to Pseudaulacaspis.
euoniima /C. /C./Comstock, 1881/referred to Unaspis.
euphorbiaceae /C. /C./Brain, 1919/NF of Monaspis.
eualbida /C. /C./Cockerell, 1902/NF of Nelaspis ; referred to Duplacchionaspis.
exicata /C. /C.(Pinnaspis)/Hall, 1929/referred to Gadaspis.

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exercitata / C. / Green, 1896/referred to Pinnaspis.

fervisi / P. / P. / Mamet, 1959/ = Pseudaulacaspis cockerelli.

cici / C. / C. / Newstead, 1917/referred to Africaspis.

fiorii / C. / Lepidosaphes / Leonardi, 1913/generic position indeterminate.

flava / C. / P. / C. / Green, 1899/referred to Unaspis.

floridensis / C. / C. / Takagi, 1969/a sp. of C.

fodiens / C. / C. / Green, 1899/NF of Nudaclaspis.

formosa / C. / P. / C. / Green, 1904/generic position indeterminate.

formosana / P. / P. / Takahashi, 1934/referable to Aulacaspis.

foresyliae / P. / P. / Kanda, 1941/referable to Pseudaulacaspis.

fraxini / C. / C. / Signoret, 1869/ = C. salicis.

frenchii / C. / C. / Green, 1915/generic position indeterminate.

fujicola / P. / P. / Kuwana, 1931/ = C. wistariae.

fulva / C. / C. / Kuwana, 1931/ = C. furfurana.

fungorum / C. / C. / Newstead, 1914/NF of Mittalaspis.

furfur / C. / C. / Fitch, 1857/a sp. of C.

galliformens / C. / C. / Green, 1899/NF of Parachionaspis.

gengmaensis / P. / P. / Chen, 1983/referable to C.

gibber / C. / C. (Dinaspis) / Hall, 1929/referred to Dentaspis.

gleditsiae / C. / C. / Sanders, 1903/a sp. of C.

globosa / C. / C. / Brain, 1919/referred to Dentaspis.

gossypii / C. / (Hemicnionaspis) aspidistrae var. / Newstead, 1906/ = Pinnaspis strachani.

graminella / C. / C. / Brain, 1899/referred to Duplachionaspis.

graminicola / C. / C. / Takahashi, 1934/referred to Acanthomytilus.

graminis / C. / C. / Green, 1896/NF of Duplachionaspis.

gyphæniformis / C. / C. / Maskell, 1894/a sp. of Pseudaulacaspis?

gyphæniformis / C. / C. / Newstead, 1906/a nomen nudum.

harmotruides / C. / C. / Green, 1922/referable to Pseudaulacaspis / = Pseudaulacaspis subcorticalis?

hargreavesi / C. / C. / Laing, 1925/referred to Dentaspis.

harrisi / P. / Lepidosaphes / Laing, 1929/a sp. of Pseudaulacaspis?

hattori / C. / C. / Kanda, 1941/supposed to be a form of Pseudaulacaspis cockerelli.

hedoytidis / C. / P. / C. / Green, 1899/referred to Aulacaspis.

hempelii / C. / C. / Lepage, 1935/referred to Niveaspis.

herbae / C. / P. / Green, 1899/referred to Aulacaspis.

heterophyllae / C. / P. / C. pinifolii var. / Cooley, 1897/a sp. of C.

hikosani / C. / “C. (?)” / Kuwana, 1902/NF of Kuwanaspis.

hilli / P. / Lepidosaphes / Laing, 1929/a sp. of Pseudaulacaspis?

himalaica / C. / C. / Takagi, 1934/a sp. of C.

howardi / C. / C. / Cooley, 1898/referred to Kuwanaspis.

humei / C. / P. / Brain, 1919/referred to Duplachionaspis.

imbiricata / C. (Dinaspis) / Brain, 1920/referred to Euclaspis.

imbiricata / C. / C. / chaetachmae var. / Hall, 1929/altered to C. spiculata Hall.

india / C. / P. / Banks, 1906/referable to Pseudaulacaspis.

indigofera / C. / C. (Pinnaspis) / Hall, 1928/referred to Contigaaspis.

javanensis / C. / C. / Kuwana, 1931/referable to Pinnaspis.

kabylensis / C. / C. / Balachowsky, 1930/generic position indeterminate.

kentrie / P. / C. / P. / Kuwana, 1931/referable to Pseudaulacaspis.

kenya / P. / P. / Hall, 1946/referred to Aulacaspis.

ketolepis / P. / P. / Ferris, 1953/referable to C.

kiggelariae / C. / C. (Poliaspis) / Brain, 1919/referred to Tecaspis.
kindinent/C./, P./C./Kuwana, 1909/a lapsus of kiushiuensis.
kiushiuensis/C./, P./C./Kuwana, 1928/an emendation for kinshinensis ; referred to Pseudaulacaspis.
kosstarabi/C./, C./Takahashi, 1967/a sp. of C.
kuwano/C./C./Takahashi, 1953/a new name for C. quercus Kuwana (originally P. quercus); a
sp. of Pseudaulacaspis.
kuzunoi/C./Aulacaspis/Kuwana in Kuwana & Muramatsu, 1932/NF of Miscanthaspis, which was
synonymized with Aulacaspis.
lactea/P./Mytilaspis/Maskell, 1895/generic position indeterminate.
lanigera/C./C./laniger/Newstead, 1920/NF of Sclopetaspis.
lata/C./C./Cockerell, 1886/= Pinnaspis aspidistrae.
latiflora/P./P./Takagi & Kawai, 1966/referred to Pseudaulacaspis.
lepineyi/C./C./Balachowsky, 1928/NF of Marchaliella; a sp. of C.
leucadendri/C./C./Brain, 1920/referred to Rolaspis.
linderae/C./P./Takahashi, 1952/a sp. of C.
linderae/C./C./Green, 1922/referred to Kuwanaspis.
lintneri/C./C./Comstock, 1883/a sp. of C.
lithocarpi/C./C./Takahashi, 1942/generic position indeterminate.
lithocarpicola/C./C./Takahashi, 1942/generic position indeterminate.
litseae/C./C./Green, 1937/an emendation for litzeae; referable to Aulacaspis.
litzeae/C./P./C./eugeniae var./Green, 1896/emended to litseae.
longiloba/C./C./Cooley, 1899/a sp. of C.
longissima/C./C./Green, 1930/a nomen nudum; ==Kuwanaspis longissima
Rao, 1953; referable to Takahashiiola or Acanthomytilus.
lounsburyi/C./, P./C./Cooley, 1898/referred to Rolaspis.
lounsburyi/C./Dinaspis/Leonardi, 1914/NF of Dentachionaspis.
lumbiniana/C./C./Takagi, 1985/a sp. of C.
lutea/C., P./C./Newstead, 1911/related to Daraspis ?
machili/C./, P./Diaspis/Takahashi, 1931/referable to Aulacaspis.
machinensis/C./C./Zehntner, 1898/referred to Aulacaspis.
majores/C./C./Cockerell, 1894/referred to Pseudaulacaspis ; a sp. of Rutherfordia ?
malloti/C./C./Rutherford, 1914/NF of Rutherfordia.
manni/C./, P./C./Green, 1907/referable to Pseudaulacaspis.
margariteae/C./C./Brain, 1919/referred to Dentachionaspis.
marginalis/P./Lepidosaphes/Leonardi, 1914/generic position indeterminate.
mashonae/C./C./Diaspis/Hall, 1928/NF of Ledaspis.
mawritensis/C./C./simplex var./de Charmoy, 1899/a nomen nudum ; ==Kuwanaspis longissima
Rao, 1953; referable to Takahashiiola or Acanthomytilus.
megadactyla/P./Pseudaulacaspis/Takagi, 1970/a sp. of Pseudaulacaspis.
megaloboa/C./P./C./Green, 1899/referable to Pseudaulacaspis.
megazygosis/C./C./Chen, 1983/a sp. of C.
micropori/C./C./Marlatt, 1908/= C. salicis.
micos/C./C./Maskell, 1885/indeterminate.
micos/C./C./(Hemichionaspis)/Newstead, 1917/= Pinnaspis strachani.
mitesu/C./C./Kuwana, 1931/referred to Pseudaulacaspis cockerelli.
momii/P./P./Kuwana, 1931/referred to Pseudaulacaspis.
mowedi/C./C./nanae subsp./Rungs, 1934/referred to Duplachionaspis.
mowotides/C./C./Pinnaspis communis var./Hall, 1928/= Africaspis chionaspiformis.
muccaeriae/C./C./aspidistriae var./Green, 1896/referred to Pinnaspis.
myrti/C./Aspidiotus/Bouché, 1851/unrecognizable.
**mytilaspiformis** C./C./Newstead, 1912/referred to *Tecaspis*.

*natalensis* C./C./*C. spartinae* var./Maskell, 1896/referred to *Duplachionaspis*.

*nemansensis* P./P./Cockerell, 1902/ = *Pseudaulacaspis* cockerelli.

*nemansensis* C./C./*C. Signoret, 1886/ = *Unaspis* euonymi.

*nectinerae* P./P./Chen, 1983/a sp. of *C.*

*nerii* C./C./Newstead, 1895/referred to *Voraspis*.

*nigerensis* C./C./*C. spartinae* var./Maskell, 1896/referred to *Duplachionaspis*.

*nileae* C./C./P./Cockerell, 1902/ = *Pseudaulacaspis* cockerelli.

*nemausensis* P./P./Chen, 1886/ = *Unaspis* euonymi.

*neolinderae* P./P./Chen, 1983/a sp. of *C. nerii* C./C./Newstead, 1895/referred to *Voraspis*.

*nigricans* C./C./*C. spartinae* var./Maskell, 1895/referred to *Pseudaulacaspis*.

*nigricans* C./C./*C. spartinae* var./Maskell, 1895/referred to *Pseudaulacaspis*.

*nileae* C./C./P./Cockerell, 1895/ = *Pseudaulacaspis* cockerelli.

*nemansensis* C./C./*C. spartinae* var./Maskell, 1896/referred to *Duplachionaspis*.

*nigerensis* C./C./*C. spartinae* var./Maskell, 1895/referred to *Pseudaulacaspis*.

*nileae* C./C./P./Cockerell, 1902/ = *Pseudaulacaspis* cockerelli.

*nemansensis* C./C./*C. spartinae* var./Maskell, 1896/referred to *Duplachionaspis*.

*nigerensis* C./C./*C. spartinae* var./Maskell, 1895/referred to *Pseudaulacaspis*.

*nileae* C./C./P./Cockerell, 1895/ = *Pseudaulacaspis* cockerelli.

*nemansensis* C./C./*C. spartinae* var./Maskell, 1896/referred to *Duplachionaspis*.

*nigerensis* C./C./*C. spartinae* var./Maskell, 1895/referred to *Pseudaulacaspis*.

*nileae* C./C./P./Cockerell, 1902/ = *Pseudaulacaspis* cockerelli.

*nemansensis* C./C./*C. spartinae* var./Maskell, 1896/referred to *Duplachionaspis*.

*nigerensis* C./C./*C. spartinae* var./Maskell, 1895/referred to *Pseudaulacaspis*.

*nileae* C./C./P./Cockerell, 1895/ = *Pseudaulacaspis* cockerelli.

*nemansensis* C./C./*C. spartinae* var./Maskell, 1896/referred to *Duplachionaspis*.

*nigerensis* C./C./*C. spartinae* var./Maskell, 1895/referred to *Pseudaulacaspis*.

*nileae* C./C./P./Cockerell, 1902/ = *Pseudaulacaspis* cockerelli.

*nemansensis* C./C./*C. spartinae* var./Maskell, 1896/referred to *Duplachionaspis*.

*nigerensis* C./C./*C. spartinae* var./Maskell, 1895/referred to *Pseudaulacaspis*.

*nileae* C./C./P./Cockerell, 1895/ = *Pseudaulacaspis* cockerelli.

*nemansensis* C./C./*C. spartinae* var./Maskell, 1896/referred to *Duplachionaspis*.

*nigerensis* C./C./*C. spartinae* var./Maskell, 1895/referred to *Pseudaulacaspis*.

*nileae* C./C./P./Cockerell, 1895/ = *Pseudaulacaspis* cockerelli.

*nemansensis* C./C./*C. spartinae* var./Maskell, 1896/referred to *Duplachionaspis*.

*nigerensis* C./C./*C. spartinae* var./Maskell, 1895/referred to *Pseudaulacaspis*.

*nileae* C./C./P./Cockerell, 1895/ = *Pseudaulacaspis* cockerelli.

*nemansensis* C./C./*C. spartinae* var./Maskell, 1896/referred to *Duplachionaspis*.

*nigerensis* C./C./*C. spartinae* var./Maskell, 1895/referred to *Pseudaulacaspis*.

*nileae* C./C./P./Cockerell, 1895/ = *Pseudaulacaspis* cockerelli.

*nemansensis* C./C./*C. spartinae* var./Maskell, 1896/referred to *Duplachionaspis*.

*nigerensis* C./C./*C. spartinae* var./Maskell, 1895/referred to *Pseudaulacaspis*.

*nileae* C./C./P./Cockerell, 1895/ = *Pseudaulacaspis* cockerelli.

*nemansensis* C./C./*C. spartinae* var./Maskell, 1896/referred to *Duplachionaspis*.

*nigerensis* C./C./*C. spartinae* var./Maskell, 1895/referred to *Pseudaulacaspis*.

*nileae* C./C./P./Cockerell, 1895/ = *Pseudaulacaspis* cockerelli.

*nemansensis* C./C./*C. spartinae* var./Maskell, 1896/referred to *Duplachionaspis*.

*nigerensis* C./C./*C. spartinae* var./Maskell, 1895/referred to *Pseudaulacaspis*.

*nileae* C./C./P./Cockerell, 1895/ = *Pseudaulacaspis* cockerelli.

*nemansensis* C./C./*C. spartinae* var./Maskell, 1896/referred to *Duplachionaspis*.

*nigerensis* C./C./*C. spartinae* var./Maskell, 1895/referred to *Pseudaulacaspis*.

*nileae* C./C./P./Cockerell, 1895/ = *Pseudaulacaspis* cockerelli.

*nemansensis* C./C./*C. spartinae* var./Maskell, 1896/referred to *Duplachionaspis*.

*nigerensis* C./C./*C. spartinae* var./Maskell, 1895/referred to *Pseudaulacaspis*.

*nileae* C./C./P./Cockerell, 1895/ = *Pseudaulacaspis* cockerelli.

*nemansensis* C./C./*C. spartinae* var./Maskell, 1896/referred to *Duplachionaspis*.

*nigerensis* C./C./*C. spartinae* var./Maskell, 1895/referred to *Pseudaulacaspis*.

*nileae* C./C./P./Cockerell, 1895/ = *Pseudaulacaspis* cockerelli.

*nemansensis* C./C./*C. spartinae* var./Maskell, 1896/referred to *Duplachionaspis*.

*nigerensis* C./C./*C. spartinae* var./Maskell, 1895/referred to *Pseudaulacaspis*.

*nileae* C./C./P./Cockerell, 1895/ = *Pseudaulacaspis* cockerelli.

*nemansensis* C./C./*C. spartinae* var./Maskell, 1896/referred to *Duplachionaspis*.

*nigerensis* C./C./*C. spartinae* var./Maskell, 1895/referred to *Pseudaulacaspis*.

*nileae* C./C./P./Cockerell, 1895/ = *Pseudaulacaspis* cockerelli.

*nemansensis* C./C./*C. spartinae* var./Maskell, 1896/referred to *Duplachionaspis*.

*nigerensis* C./C./*C. spartinae* var./Maskell, 1895/referred to *Pseudaulacaspis*.

*nileae* C./C./P./Cockerell, 1895/ = *Pseudaulacaspis* cockerelli.

*nemansensis* C./C./*C. spartinae* var./Maskell, 1896/referred to *Duplachionaspis*.

*nigerensis* C./C./*C. spartinae* var./Maskell, 1895/referred to *Pseudaulacaspis*.

*nileae* C./C./P./Cockerell, 1895/ = *Pseudaulacaspis* cockerelli.
ramakrishnai/C./C./Rao, 1953/a sp. of C.
reticulata/C./C. (Dinaspis)/Hall, 1928/= Ledaspis reticulata Malenotti, 1916.
retiger/C./C./Cockerell, 1901/referred to Tecaspis.
rhododendri/C./C./Green, 1899/referred to Pinnaspis.
richiei/C./C./Laing, 1929/referred to Dentachionaspis.
rosae/C./C./Goethe, 1884/unrecognizable.
rotunda/P./P./Takahashi, 1935/referable to C.
rotundiloba/C./C./Laing, 1929/referred to Africaspis; a sp. of another genus?
saccharifolii/C./C./Zehntner, 1897/referred to Duplachionaspis.
saltamaensis/C., P./C./Kuwana, 1928/a sp. of C.
salicis/C./Coccus/Linnaeus, 1758/NF of C.
salicisnigrae/C./Aspidiotus/Walsh, 1868/a sp. of C.
sandwicensis/P./P. eugeniae var./Fullaway, 1932/= Pseudaulacaspis cockerelli.
sasahawai/P./Pseudaulacaspis/Takagi, 1970/a sp. of Pseudaulacaspis.
sassceri/C./C./Cockerell & Robbins, 1909/a sp. of C.
chizosoma/C./C./Takagi, 1970/NF of Superturmaspis; referable to Aulacaspis.
scribiculatum/C./C./Green, 1899/referred to Pinnaspis.
squatiae/C./C./Brain, 1920/referred to Africaspis.
semiaurea/C./C./Cockerell, 1895/= C. pinifoliae.
supra/C./C./Green, 1900/= Pinnaspis theseae.
siuuenensis/P./P./C./Chen, 1983/a sp. of C.
siula/C./C./C./Lupo, 1938/referred to Duplachionaspis.
signata/C./Fiorinia/Maskell, 1897/NF of Unachionaspis.
simplices/C./C./Green, 1899/referred to Natalaspis.
singularis/C./C./Bazarov & Shmelev, 1968/a sp. of C.
sinoculis/C./C./Hall, 1928/referred to Tecaspis.
sinopurpurea/C./C./Takagi, 1908/a sp. of C.
solani/C./C./C./Green, 1917/a nomen nudum.
sozanica/C., P./C./Takahashi, 1933/a sp. of C.
spartiae/C./C./Comstock, 1883/NF of Halaspis.
spartophilae/C./C./Signoret, 1870/unrecognizable.
speculata/C./C./Green, 1919/NF of Xiphuraspis.
spiculata/C./C./Hall, 1946/a new name for C. chaetachmae var. imbricata Hall; = Rolaspis lounsburyi.
sierculae/C./C./Laing, 1932/unretainable in C.
striata/C./C./Newstead, 1897/NF of Lineaspis.
strobilanthi/C., P./C./Green, 1905/referable to Pseudaulacaspis.
subcorticatus/C., P./C./Green, 1905/referred to Pseudaulacaspis.
subnudata/C./C./Newstead, 1912/NF of Contigaspis.
subrotunda/P./P./Chen, 1983/referable to C.
substriata/C./C./Newstead, 1910/NF of Dentaspis.
subvisci/C./C./C./Pinnaspis/Hall, 1929/referred to Tecaspis.
susuki/C./P./Siraiwa, 1939/= Aulacaspis kuzunoi.
sylvatica/C./C./Sanders, 1904/= C. nyssae.
syringae/C., P./C./Borchsenius, 1938/regarded as a form of Pseudaulacaspis cockerelli.
syzygii/C./C./Takagi, 1985/a sp. of C.
takahashii/P./P./Ferris, 1955/referred to *Pseudaulacaspis* ; = *Pseudaulacaspis manni* (= C. manni) (D.J. Williams, pers. comm.).

tangana/P., C./P./Lindinger, 1910/unretainable in C.
tegalensis/C./C./Zehntner, 1898/referred to *Aulacaspis*.
tenata/C., P./C./Green, 1922/referable to *Pseudaulacaspis*.
tenuidiscus/C./C./Newstead, 1920/NF of *Salaspis*.
thoea/C./C./Maskell, 1891/referred to *Pinnaspis*.
thea/C./C. prunicola var./Maskell, 1896/a sp. of *Pseudaulacaspis*?
thoracica/P./P./Robinson, 1917/referred to *Aulacaspis*.
timida/C./C. timidus/Cockerell, 1892/a nomen nudum.
triformis/C./C./Tippins & Beshear, 1974/a new name for *C. betulae* Tippins & Beshear; a sp. of C.
trochodendri/P., C./P./Takahashi, 1936/referred to C.
tuberculata/C./C. (Pinnaspis)/Hall, 1929/referred to *Gadaspis*.
tursioides/C./C./Laing, 1929/ = *Tecaspis retigera*.
uapacae/C./C. (Diaspis)/Hall, 1928/referred to *Ledaspis*.
uenoi/C./C./Takagi, 1970/referable to *Aulacaspis*.
ulmi/C./C. furfuris var./Cockerell, 1897/ = C. americana.
untalii/C., P./C. (P.) visci var./Hall, 1929/NF of *Tecaspis*.
unilateralis/C., P./C./Newstead, 1913/NF of *Sinistraspis*.
unita/C./C./Lindinger, 1910/ = *Africaspis chionaspiiformis*.
usambavica/C./C./Lindinger, 1913/referred to *Voraspis*.
vaccinii/C./Aspidiotus/Bouché, 1851/ = C. salicis.
vandalius/C./Coccus (Diaspis)/Reimer, 1890/a nomen nudum.
variabilis/C./C./Bazarov & Shmelev, 1968/a sp. of C.
varicosa/C., P./C. eugeniae var./Green, 1896/referable to *Pseudaulacaspis*.
venia/C./C./Menon & Khan, 1961/a sp. of *Pseudaulacaspis*?
verecunda/C./C. permutans var./Green, 1899/ = *Unaspis permutans*.
vermiciformis/C./C./Takahashi, 1930/NF of *Takahashiiella*.
vicina/P./Euvoraspis vicinus/Mamet, 1954/ = *Pseudaulacaspis subcorticalis*.
visci/C., P./C. (P.)/Brain, 1919/referred to *Tecaspis*.
vitis/C., P./C./Green, 1896/referable to *Aulacaspis*.
vuilleti/C./C./Marchal, 1909/NF of *Marchalaspis*.

whitehillii/P./P./Hall, 1946/NF of *Rolaspis*.
wistariae/C., P./C./Cooley, 1897/a sp. of C.
xanthurhoeae/C., P./C./Fuller, 1897/a sp. of *Pseudaulacaspis*?
xerotidis/C., P./C./Maskell, 1895/referred to *Pseudaulacaspis*.
yanagicola/C., P./P./Kuwana in Kuwana & Muramatsu, 1932/a sp. of C.
yanonensis/C./C./Kuwana, 1923/referred to *Unaspis*.

zlocistii/C./Leptidosaphes (Coccomytilus)/Bodenheimer, 1924/ = *Nilotaspis halli*. 

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Fig. 5. *Chionaspis syzygii*, n. sp., adult female: pygidium. Upper: Dehra Dun, India, on *Syzygium*. Lower: Kanepokhari, Nepal, on *Cleistocalyx*. 
Fig. 6. *Chionaspis* spp., adult female: pygidium. Upper: *C. trochodendri*, Ali-Shan, Taiwan, on *Trochodendron*. Lower: *C. castanopsidis*, n. sp.
Fig. 7. *Chionaspis arkhola*, n. sp., adult female: pygidium. Focused on dorsal (upper) or ventral (lower) surface. Dunche.
Fig. 8. *Chionaspis clematidis*, n. sp., adult female : pygidium. Focused on dorsal (upper) or ventral (lower) surface.
Fig. 9. *Chionaspis cornigera*, n.sp., adult female: pygidium. Focused on dorsal (upper) or ventral (lower) surface.
Fig. 10. *Chimaspis* spp., adult female: pygidium. Upper: *C. himalaica*, n. sp., Ghora Tobela, Nepal. Lower: *C. sirapura*. n. sp.
Fig. 11. *Chionaspis lumbiniana*, n. sp., adult female: pygidium. Focused on dorsal (upper) or ventral (lower) surface.
Fig. 12. *Narayanaspis eugeniae*, n. g., n. sp., adult female: pygidium.
Fig. 14. *Chionaspis* spp., adult female: pygidial margin in ventral (A-D) or dorsal (AA) view.  
A, AA: *C. syzygi*, n. sp., Dehra Dun, India, on *Syzygium*.  
B: *C. arkhola*, n. sp., Dunche.  
C: *C. castanopsidis*, n. sp.  
D: *C. clematidis*, n. sp.
Fig. 16. *Narayanspis eugeniae*, n. g., n. sp., adult female. Upper: apex of pygidium in ventral view. Lower: pygidial margin in dorsal view.
Fig. 17. *Chionaspis syzygii*, n. sp., adult female: body, antennae, anterior spiracle, and dorsal bosses. Dehra Dun, India, on *Syzygium.*
Fig. 18. *Chionaspis arkhola*, n. sp., adult female: body, antenna, and anterior spiracle.
Dunche.
Fig. 19. *Chionaspis arkhola*, n. sp., adult female: dorsal ducts. Upper: Syabru; lower: Dunche.
Fig. 20. *Chionaspis castanopsidis*, n. sp., adult female: body, antenna, and dorsal boss on prothorax.
Fig. 21. *Chionaspis clematidis*, n. sp., adult female: body, antenna, and variation of median lobes.
Fig. 22. *Chionaspis cornigera*, n. sp., adult female: body, antenna, and eye.
Fig. 23. *Chionaspis himalaica*, n. sp., adult female: body and antenna. Second instar female, exuvial cast: pygidial margin in dorsal view (upper left). Ghora Tobela, Nepal.
Fig. 24. *Chionaspis sivapuranana*, n. sp., adult female: body.
Fig. 25. *Chionaspis lumbiniana*, n. sp., adult female: body and antenna.
Fig. 26. *Narayanaspis eugeniae*, n. g., n. sp., adult female: body, eye, antenna, anterior spiracular disc pores, and one of lateral microducts on thorax. Body outline of a full-grown adult female (lower right).
Fig. 27. Adult female: dorsal ducts. Upper: *Narayanaspis eugeniae*. Lower: *Chionaspis trochodendri*, Ali-Şan, Taiwan, on *Trochodendron*. 0.1 mm
Fig. 28. *Chionaspis syzygii*, n., sp., 2nd instar male: body. Nawal-Parasi District, Nepal, on *Syzygium*.
Fig. 29. *Chionaspis lumbiniana*, n. sp., 2nd instar male: body and pygidial margin.
Fig. 30. *Narayanaspis eugeniae*, n. g., n. sp., 2nd instar male: body, antenna, anterior spiracle, and marginal macroducts. Second instar female, exuvial cast: pygidal lobes in ventral view (upper left).