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Author(s)	Takagi, Sadao
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THE GENUS *MEGACANTHASPIS*,
A POSSIBLE RELIC OF AN EARLIER STOCK
OF THE DIASPIDIDAE
(HOMOPTERA : COCCOIDEA)

By SADAO TAKAGI

Abstract

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The genus *Megacanthaspis* (= *Nanmuaspis*, n. syn.) is revised. Five included species are described: *M. leucaspis*, n. sp., Japan; *M. phoebia* (= *Nanmuaspis phoebia*), n. comb., Continental China; *M. litseae*, Taiwan; *M. langtangana*, n. sp., Nepal; and *M. actinodaphnes*, Japan. So far as represented by these species the genus is 'Sino-Japanese' in distribution and associated with Lauraceae. Morphoclines are constructed for adult female and second instar characters, and relationship among the species is discussed. The adult females of these species while very close in general body structure are remarkably different in the state of the gland tubercle and gland spine system, in which they roughly represent successive evolutionary stages. A preliminary scheme for subclassifying the Diaspididae is proposed, based on the pattern of organization of the pygidial margin. It is deemed from the position in this scheme and the geographical distribution that the genus is a relic of an earlier stock of the Diaspididae.

Author's address. Entomological Institute, Faculty of Agriculture, Hokkaidô University, Sapporo, 060 Japan.

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INTRODUCTION

The genus *Megacanthaspis* is a small group of scale insects, comprising only five species so far as represented by the material at hand. It is interesting for two reasons. First, it seems to be isolated in the Diaspididae in morphological characters. Second, the five species have been collected all within the boundary of the floristic 'Sino-Japanese Region'. All this may point to the possibility that the genus is a relic of an earlier stock of the Diaspididae.

Our knowledge of the biogeography of the Coccoidea is still very poor owing to the formation of taxa remaining at different stages of trial and also to faunal investigations generally very insufficient. However, there is reason to believe that coccoid biogeography has a close correspondence with plant biogeography.

The Sino-Japanese Region is a well-established concept based on many flowering plants common and restricted to Japan, Korea, the Continental China except the south, and the Himalayas. Taiwan is linked with this region by its mountainside flora. On the south this region merges into its luxuriant neighbours in South and Southeast Asia, where some local floras at higher altitudes embrace, in common with a great part of the Sino-Japanese Region, various kinds of lucidophyllous trees.

The origin of the Sino-Japanese flora, though it may not be single, is basically attributed to escapes from the Arcto-Tertiary flora, which largely failed to survive in the Northern Hemisphere except for eastern Asia and eastern and western North America. In fact, the Sino-Japanese flora includes a lot of spermatophytes which are isolated among the extant taxa in varying degrees and deemed to be primitive in various features. On the basis of the supposed connection between flowering plants and coccoids in biogeography any coccoid taxa isolated in morphological features and restricted to this region may be worthy of study in respect to their possible primitive origin.

The material of the species studied, except for *M. phoebia*, was collected by myself, and I cannot but notice how rarely I encountered them in spite of the fact that their host plants are generally found in abundance and that they occur exposed on the leaves. This paucity of collection records may be thought of as an essential difficulty in recognizing the distribution of the genus. But, if there exist 'Sino-Japanese' elements of Coccoidea, *Megacanthaspis* would be deemed a candidate, for it is only known from main areas of this region: Japan, Taiwan, the Continental China and the Himalayas.

Before going further, I wish to thank Dr. F. Tang, Agricultural University of Shansi, Taiku, Shansi, People's Republic of China, for his kindness in giving me the material of *M. phoebia*. Dr. H. Kanai, National Science Museum, Tôkyô, Japan, identified one of the host plants.

GENERIC COMPOSITION AND DIAGNOSIS

When this genus was proposed on the basis of the type-species alone, the presence of unusually robust marginal gland spines was thought of as a remarkable character of the genus. This character was also found true of the second species *M. litseae*. However, in the composition here adopted the five species of the genus form a graded series concerning the robustness of the marginal gland spines (Table 6), and in one of these species, *M. leucaspis*, which represents

the opposite extreme of the series, the marginal gland spines are all slender, approaching the state usual with many other Diaspididae. *M. leucaspis* also differs by the female scale which looks smooth and, in contrast with the ones of the other species which appear felty, is less particular for a diaspidid. In fact, the texture of the felty scales is so unique that it makes a field identification of the genus easy (Fig. 22). However, there has been found no other differences between *M. leucaspis* and the other species worthy of consideration in connection with the generic composition, both in the adult females and in the larval instars.

Except for the marginal gland spines, the adult females of all these species are very similar in the structure and disposition of external organs. They are also very close in the numerical correlation among external secretories. When the numbers of gland tubercles and perivulvar disc pores are plotted against the number of the macroducts, the four species other than *M. leucaspis* assemble close together and fall about the straight lines obtained for *M. leucaspis* (Fig. 20).

I have no doubt that all these species belong to the same genus. In this connection, *Nanmuaspis*, erected for one of them, should be sunken as a synonym of *Megacanthaspis*.

Megacanthaspis

Megacanthaspis Takagi, 1961, *Insecta Matsumurana* 24: 97 [type-species: *Megacanthaspis actinodaphnes*, occurring in Japan].

Megacanthaspis: Takagi, 1970, *Insecta Matsumurana* 33: 128 [a second species, *M. litseae*, described from Taiwan].

Nanmuaspis Tang, "1977", *The Scale Insects of Horticulture and Forest of China* 1: 148 [type-species: *Nanmuaspis phoebia*, occurring in Chekiang, China]. New synonymy.

Adult female. Body elongate and slender, with metathorax and free abdominal segments at most only a little lobed laterally; derm membranous. Pygidium rounded along posterior margin, somewhat sclerotized medially on dorsum and towards apex on ventrum, with a marginal series of serrate processes or plates, none of which are sclerotized enough to call lobes. Gland tubercles occurring caudad of anterior spiracles, laterocaudad of posterior spiracles and submarginally on 1-3 anterior abdominal segments. Marginal gland spines occurring on the succeeding segments as posteriorly as abd. viii; slender, each with a single microduct (in *M. leucaspis*), or more or less enlarged to plump processes, each with 1 or more microducts, and occurring singly on each segment (in the other species). Macroducts short and broad, with the orifice surrounded by a sclerotized rim; are largely confined to the dorsal surface on the abdomen and to the ventral on the meso- and metathorax; dorsal macroducts tending to be arranged in segmental rows but not in well-defined series, occurring as posteriorly as abd. vii (in addition, 1 or a few present at or near apex of pygidium in 4 species), those occurring on pygidial margin not differentiated in size. Perivulvar disc pores present in an arch, which sometimes shows an indication of being divided into a broad median group and smaller lateroposterior ones. Anal opening situated cephalad of centre of pygidium. Anterior spiracles each with a small group of trilocular disc pores. Antennae each with a long seta.

Second instar female. Body oblong. Pygidium rounded on posterior margin, with a marginal series of serrate processes similar to those in the adult female. Gland tubercles few, occurring laterad of spiracles and submarginally on abd. i.

Marginal gland spines occurring singly on abd. ii-viii, tending to be robust in the species with enlarged gland spines in the adult females, but usually with a single microduct even in such species. Marginal macroducts of abdomen short and broad, 3-5 on each side, belonging to abd. iii (or iv or v)-vii. Anterior spiracles each with 1 or a few trilobular disc pores.

Second instar male. Body oval. Remarkably different from the 2nd instar female by having rather abundant macroducts both dorsally and ventrally. Marginal gland spines minute, each with a single microduct (in *M. leucaspis*), or more or less enlarged, each with more than 1 microduct (in *M. phoebia*, *M. litseae* and *M. langtangana*).

First instar female. Exuvial cast obovate. Two pairs of minute pointed processes present near posterior extremity of body, the inner pair being situated between apical setae. Antennae 5-segmented, the terminal segment as long as or little shorter than the 1st-4th combined. Enlarged dorsal ducts lacking on head.

First instar male. Practically as in first instar female (in 4 species examined).

Scales. Slender, with exuvial cast(s) terminal.

Host plants. Lauraceae. Both females and males occur on the undersurface of the leaves.

Distribution. The known species fall within the boundary of the floristic 'Sino-Japanese Region' (Fig. 21).

DESCRIPTION OF SPECIES

Megacanthaspis leucaspis, new species

Material. Collected at Wakayama Experiment Forest, Hokkaidô University, Kozagawa, Wakayama-ken, Kii Peninsula, Honsyû, Japan, on *Actinodaphne longifolia* (= *Litsea acuminata*), 7 Jan. 1962; at Nati, Wakayama-ken, on *A. longifolia*, 6 Nov. 1971; at Nametoko, Ehime-ken, Sikoku, Japan, on *A. longifolia*, 10 May 1963. Holotype (adult female), from Nati, deposited in the collection of the Entomological Institute, Hokkaidô University, Sapporo, Japan.

Adult female (Figs. 1, 2). Body with segmentation rather distinct. Pygidium broadly rounded, with serrate marginal processes on abd. v-viii (more or less rudimentary on v); apically with another pair of processes, which are much narrower than the adjacent serrate processes, shallowly incised once or twice, and a little retreated. Gland tubercles on meso- and metathorax and abd. i-iii (Table 1). Marginal gland spines slender, occurring on abd. iv-viii, each with a single microduct, 1 or 2, or at times 3, on each side of each segment (Table 1), the opposite members on abd. viii widely separated. Dorsal macroducts mostly in ill-defined segmental rows on abd. iii-vii, scattered submarginally on abd. i and ii. Ventral macroducts scattered between gland tubercles and lateral body margin on meso- and metathorax and 2 basal abdominal segments, rather abundant on thorax and abd. i. Posterior spiracles each usually with 1 or 2 trilobular disc pores (Table 1).

Second instar female (Fig. 3). Marginal gland spines slender, each with a single microduct. Marginal macroducts 4 on each side of abdomen, belonging to abd. iv-vii.

Second instar male (Fig. 4). Marginal gland spines minute, each with a single microduct. Dorsal macroducts strewn so regularly on abdomen as to form 3 pairs of longitudinal lines, of which the submedian pair are short, usually running

through abd. iv-vi. Ventral macroducts more numerous, mostly strewn in a broad submarginal zone through thorax and abdomen.

First instar female, exuvial cast (Fig. 5).

Scale. Scale of female with secretory cover smooth, white, and convex dorsally, with lateral sides subparallel. Scale of male with secretory cover white, subparallel on lateral sides, flattened posteriorly, with a slight median carina.

Remarks. The adult females examined show a wide range of variation in the numbers of the macroducts, gland spines and perivulvar disc pores (Table 1). Especially in the number of the macroducts the difference is remarkable between the specimens from Nati and those from Kozagawa. The specimens from Nametoko, though quite few, seem to connect them. In the numbers of the gland spines and perivulvar disc pores, too, all these specimens seem to form a continuous series (Fig. 6). Although I cannot offer any explanation for the difference between the forms from Nati and Kozagawa - localities only 20 km distant - they, together with the connecting form from Nametoko, are tentatively referred to the same species. Further, no difference is found between these forms in the second instar females and males.

Megacanthaspis phoebia, new combination

Nanmuaspis phoebia Tang, "1977", The Scale Insects of Horticulture and Forest of China I: 148 [Chekiang, China, on "nanmu"].

Material. Collected at Hangchow, Chekiang, China, on *Phoebe shearerii*, 30 March 1969.

Adult female (Figs. 7, 8). Body with segmentation obscure. Pygidium with serrate processes on abd. vi-viii. Gland tubercles on meso- and metathorax and 2 basal abdominal segments (Tables 2, 3). Marginal gland spines in 6 pairs on abd. iii-viii, more or less enlarged, becoming robuster anteriorly, each with 1-4 microducts (Table 3), the members of the posteriormost pair widely separated from each other. Dorsal macroducts forming more or less of segmental rows; a pair of macroducts at apex of pygidium between the posteriormost gland spines. Ventral macroducts scattered between gland tubercles and lateral body margin on meso- and metathorax and abd. i. Posterior spiracles without disc pores.

Second instar female (Fig. 7). Marginal gland spines slender, each with 1 microduct. Marginal dorsal macroducts 3 on each side of abdomen, belonging to abd. v-vii.

Second instar male (Fig. 9). Marginal gland spines inconspicuous, those on abd. iv-viii are low tubercles and almost indistinguishable from associated serrate processes, each with 2 or more microducts. Ventral macroducts forming more or less of 3 pairs of longitudinal rows on abdomen, scattered submarginally on thorax lateroposteriorly to each spiracle. Dorsal macroducts submedially forming 2 pairs of longitudinal rows on abdomen and submarginally scattered in a broad zone through thorax and abdomen.

Scale. Scale of female with secretory cover slender, highly convex dorsally, felty in texture, dark brown. Scale of male flattened, smooth, with an obscure median carina, white, stained with brown along the carina.

Megacanthaspis litseae

Megacanthaspis litseae Takagi, 1970, Insecta Matsumurana 33: 130 [Taiwan, on *Litsea aokoensis*].

Material. Collected at Fen-chi-hu, Taiwan, on *Litsea akoensis*, 11 Apr. 1965.

Adult female (Figs. 10, 11). Body with segmentation obscure. Pygidium with serrate marginal processes on abd. vii and viii. Gland tubercles on meso- and metathorax and abd. i (Table 2). Marginal gland spines enlarged to robust conical processes, in 7 pairs belonging to abd. ii–viii, each with 2 or more microducts (Table 3), the members of the posteriormost pair widely separated from each other. Dorsal macroducts forming obscure segmental rows on pygidium, rather scattered on prepygidial abdomen; 1 submarginal macroduct sometimes present medially on pygidium. Ventral macroducts in a well-defined oblique row laterad of posterior spiracle, but rather scattered between anterior and posterior spiracles and on base of abdomen. Posterior spiracles without disc pores. A minute sclerotized boss present on margin anteriorly to enlarged gland spine of abd. iv and also that of abd. vi.

Second instar female (Fig. 12). Marginal gland spines more or less robust; members of the posteriormost pair widely separated, each of them with 2 or 3 microducts; members of the penultimate pair each with 1 or 2 microducts; other marginal gland spines each with 1 microduct. Marginal dorsal macroducts 5 on each side of abdomen, belonging to abd. iii–vii.

Second instar male (Fig. 12). Robust marginal gland spines on abd. iii–viii, the anteriormost with 2 microducts, accompanied with a minute gland spine just posteriorly, the others each with 3 or more microducts, the posteriormost set close but not appressed together. Macroducts rather numerous, forming more or less of longitudinal rows on ventral surface, but appearing rather scattered on dorsal surface.

Scale. Scale of female with secretory cover felty in texture, dark brown, and highly convex dorsally. Scale of male similar to that of female in texture and colour, but flattened dorsally, with a median carina.

Megacanthaspis langtangana, new species

Material. Collected at Langtang Valley, 1820 m, Bagmati Zone, Nepal, on *Machilus duthiei* (identified by Dr. H. Kanai), 30 Sept. 1975. Holotype (adult female) deposited in the collection of the Entomological Institute, Hokkaido University.

Adult female (Fig. 13, 14). Body with segmentation indistinct. Pygidium rather narrowly rounded on posterior margin, with serrate marginal processes on abd. vi–viii. Gland tubercles caudad of both pairs of spiracles and submarginally on abd. i (Table 2). Marginal gland spines more or less enlarged to conical processes, in 7 pairs belonging to abd. ii–viii, each with 2 or more microducts (Table 3), the posteriormost pair appressed together at apex of pygidium. Dorsal macroducts mostly in sparse segmental rows on abd. iii–vii; 1 marginal dorsal macroduct at apex of pygidium. Ventral macroducts arranged in a well-defined row laterad of posterior spiracle, but rather scattered between anterior and posterior spiracles and on base of abdomen. Posterior spiracles lacking disc pores.

Second instar female (Fig. 15). Marginal gland spines rather robust, each with a single microduct, the members of the posteriormost pair widely separated from each other. Marginal dorsal macroducts 4 on each side of abdomen, belonging to abd. iv–vii.

Second instar male (Fig. 16). Marginal gland spines more or less conical and, except the posteriormost, rather small; gland spine of abd. ii with 1 or 2

microducts, usually with an additional minute gland spine just posteriorly; gland spine of abd. iii usually with 2 microducts, often with an additional minute gland spine just posteriorly; gland spines of abd. iv-vii each with 2 or 3 microducts; members of the posteriormost pair particularly enlarged, set close but not appressed together, each with 3 or 4 microducts.

Scale (Fig. 22). Scale of female with secretory cover felty in texture, dark brown, highly convex dorsally. Scale of male subparallel on lateral sides, flattened posteriorly, whitish, with a brown stripe medially.

Megacanthaspis actinodaphnes

Megacanthaspis actinodaphnes Takagi, 1961, *Insecta Matsumurana* 24: 98 [Kyûsyû, Japan, on *Actinodaphne longifolia*].

Material. Collected at Siro-yama, Kagosima, Kyûsyû, Japan, on *Actinodaphne longifolia* (= *Litsea acuminata*), 12 May 1957, 23 Apr. 1963; at Nametoko, Ehimeken, Sikoku, Japan, on *A. longifolia*, 10 May 1963.

Adult female (Figs. 17, 18). Body with segmentation indistinct. Pygidium with serrate marginal processes on abd. vi-viii (more or less reduced on vi). Gland tubercles caudad of both pairs of spiracles and submarginally on abd. i (Table 2). Marginal gland spines enlarged to robust conical processes in 6 pairs, each usually with 2 or more microducts (Table 3); the anteriormost pair of these processes is assumed to belong to abd. ii, while the succeeding one definitely belongs to abd. iv; posterior to the anteriormost process is a gland tubercle, which is, then, assumed to belong to abd. iii; members of the posteriormost pair appressed together at apex of pygidium. Dorsal macroducts mostly in ill-defined segmental rows on pygidium, rather scattered on prepygidial abdomen. Ventral macroducts in a well-defined row laterad of posterior spiracle, scattered between anterior and posterior spiracles and on base of abdomen. Posterior spiracles without disc pores. A minute sclerotized boss present on margin anteriorly to marginal gland spine of abd. iv and also that of abd. vi.

Second instar female (Fig. 19). Marginal gland spines more or less robust, each with 1 microduct, the members of the posteriormost pair widely separated from each other. Marginal dorsal macroducts 4 on each side of abdomen, belonging to abd. iv-vii.

Scale. Scale of female with secretory cover felty in texture, dark brown, and highly convex dorsally. Scale of male unknown.

KEY TO THE SPECIES

Adult female and second instar with gland spines and a series of serrate, non-glanduliferous processes (plates) along pygidial margin; with no lobes; macroducts short and broad, with the orifice surrounded by a sclerotized rim.

Adult female

- 1. Marginal gland spines slender, each with a single microduct; scale smooth and white. *M. leucaspis*
- Marginal gland spines more or less enlarged, each with 1 or more microducts; scale felty and dark brown. 2
- 2. Gland spines of posteriormost pair separated. 3
- Gland spines of posteriormost pair appressed together. 4
- 3. Plates occurring on abd. vi-viii; marginal gland spines not much enlarged to

- conical processes. *M. phoebia*
- Plates occurring on abd. vii-viii; marginal gland spines much enlarged to conical processes. *M. litseae*
- 4. Pygidium with 1 macroduct at apex of pygidium on the base of the appressed gland spines. *M. langtangana*
- Pygidium with no macroduct on the base of the appressed gland spines. *M. actinodaphnes*

Second instar female

- 1. Marginal macroducts 3 on each side of abdomen. *M. phoebia*
- Marginal macroducts 4 or 5 on each side of abdomen. 2
- 2. Marginal macroducts 5 on each side of abdomen. *M. litseae*
- Marginal macroducts 4 on each side of abdomen. 3
- 3. Pygidium apically with 2 pairs of processes (1 pair of plates and, more mesad, 1 pair of narrower, little serrate processes) between apicalmost gland spines. *M. leucaspis*
- Pygidium apically with a pair of processes (plates) between apicalmost gland spines. *M. langtangana* and *M. actinodaphnes* (Marginal gland spines tending to be robuster in *M. actinodaphnes* than in *M. langtangana*.)

Second instar male

- 1. Marginal gland spines each with a single microduct. *M. leucaspis*
- Marginal gland spines, at least of pygidium, each with 2 or more microducts. 2
- 2. Marginal gland spines inconspicuous, almost indistinguishable from associated plates. *M. phoebia*
- Marginal gland spines enlarged to conspicuous, conical processes at least at apex of pygidium. 3
- 3. Posteriormost marginal gland spines not much larger than the adjacent ones. *M. litseae*
- Posteriormost marginal gland spines noticeably larger than the others. *M. langtangana*

RELATIONSHIP AMONG THE SPECIES

In Table 6 are given some morphoclines constructed for adult female and second instar characters of the five species of *Megacanthaspis*. Polarity is determined by out-group comparisons for Morphocline I, II, X, XIa and XIb (see under Generic composition and diagnosis), and by supposed unidirectional changes for IV, Vb, VIII and XIc. For the other morphoclines, which are constructed for the numbers of some secretories, polarity is not determined, though decrease rather than increase may have more likely been the case with these numbers.

The five species show striking structural similarities as reflected in the correlation among the numbers of external secretories (Fig. 20) in spite of their remarkable differences in the gland spine and gland tubercle system. They form a well-graded series of the changing state of this system, so far as the replacement of components by enlarged gland spines and further modification in disposition are concerned (Table 4). The sequence *M. leucaspis*→*M. phoebia*→*M. litseae*→*M. langtangana*→*M. actinodaphnes* may represent successive stages of the changing system. But the occurrence of extremely robust gland spines in *M. litseae* and *M. actinodaphnes* does not coincide with this sequence. Further discrepancies among morphoclines show that the sequence cannot be an approximation to an ancestral-descendant series.

However, through all the morphoclines constructed *M. leucaspis* most often appears at one extreme which is primitive in the morphoclines with determined polarity. Therefore, it must more or less approach to the ancestral form from which all these species have evolved.

The opposite extreme is in most cases occupied by *M. litseae* or *M. actinodaphnes*. These two species are commonly characterized not only by the extremely robust marginal gland spines but also by sclerotized bosses which occur in positions exactly coinciding between them. These bosses are very minute and may easily be overlooked, but are certainly lacking in the other species. Not only are *M. litseae* and *M. actinodaphnes* both much derived forms, but they seem, by sharing these characters, to be closely related cladogenetically, the former representing a stage preceding that of the latter in the gland spine and gland tubercle system.

If this view is right, the character that the posteriormost enlarged gland spines are appressed together at the apex of the pygidium and that is shared by the Nepalese *M. langtangana* and the Japanese *M. actinodaphnes* must have evolved in parallel in the lines leading to these species. In fact, this character is a result of the reduction of the interspace between the posteriormost gland spines, so that it belongs to Group II in the character weight system proposed by Hecht and Edwards (1976) and should be weighted less than the characters shared by *M. litseae* and *M. actinodaphnes*.

No geographical regularity is found throughout the members of the genus in connection with their supposed evolutionary state. In Japan the most primitive *M. leucaspis* and the much derived *M. actinodaphnes* occur on the same host species. They were even found to coexist on the same leaves at Nametoko. It is no surprise that the closely related *M. litseae* and *M. actinodaphnes* occur in Taiwan and Japan, respectively, but the species inhabiting the opposite side of the Taiwan Strait, *M. phoebia*, is not particularly related with the Taiwanese species. All this may suggest that the genus carries a long complicated history in spite of the general resemblance among the five species and also that the known species are fragments rather than a large part of the genus.

POSITION AND SIGNIFICANCE OF THE GENUS

Subclassification of the Diaspididae

There is no comprehensive subclassification of the Diaspididae which has found a general agreement. In 1966 Borchsenius in his catalogue of this group classified all the genera known at that time in two families, five subfamilies, 12 tribes and 22 subtribes. I agree with him about some of these higher taxa so far as their conceptual cores are concerned and their categories are ignored, but not on the classificatory system as a whole. Indeed, we are still in the pioneer stage of establishing an evolutionarily significant system for this group as well as for the whole Coccoidea.

In proceeding with this complicated task I would like to restart from a simple viewpoint: the pattern of organization of the pygidial margin. For, after all, this part of body undoubtedly displays the most outstanding characters within the Diaspididae. This approach, however, is not simple work, because it is also this part that often entails drastic secondary changes. And this is the reason why the

rugaspidiotines and odonaspidines have long been erroneously classified in various systems proposed by authors.

In Table 7 are recognized four levels in the pattern of organization, beginning from the state with no marginal appendages and succeedingly going up to a more complicated state of the margin, and two major types, intersecting the levels but the lowest one, in the combination of appendages. A preliminary scheme for subclassifying the Diaspididae is presented, based on a framework produced by combining these levels and types. It comprises seven groups or "sets" of taxa formed in accord with this framework.

The majority of the Diaspididae belong to Level III and can be divided into two groups, Set S-III and P-III. It seems that the lobes are primarily bilobulate in Set S-III except the median lobes, which are not divided in the adult females and second instar larvae. In the second instar male of *Fiorinia horii*, however, the median lobes are often bilobulate (Takagi 1979). On the other hand, the lobes are all without any trace of a division into lobules in Set P-III.

The patterns characteristic of Set S-III and P-III are not always obvious. In the adult females the Rugaspidiotini and the Odonaspidini show no trace of the P-III pattern, but they clearly manifest this pattern in the larvae of the first instar and also in the males, or sometimes in both males and females, of the second instar. The distinction between the plates and the gland spines is also often obscure. In general the plates are broad, with the apex elaborately fimbriate, while the gland spines are slender and simple, with the apex pointed. But the appendages which should be plates so far as based on the combination of characters are often slender and little or not fimbriate. The gland spines are sometimes frayed apically. All this can be ascribed to secondary modifications.

The forms referred to Level II are characterized by having lobes and nonglanduliferous plates, plus gland spines in Set S-II. They are also commonly characterized by the lobes including the median pair at times irregularly divided into lobules in the adult females, though it seems that usually the lobes except the median pair are bilobulate in Set S-II and all single in P-II.

To Level I are referred a few genera, in which nonglanduliferous plates are well developed and yet no distinct lobes are found. This state is deemed to be primary for these genera. There are, in addition, gland spines in Set S-I.

Set 0 is an assemblage of forms which have no pygidial appendages. However, among the species of *Thysanococcus*, which is placed here, *T. squamulatus* is an exception, having sparse gland spines on the pygidial margin in the second instar female (Stickney 1934). *Comstockiella* is referred to this set, because the "lobe 2" (Howell and Tippins 1976) in the first instar larva appears, in my own examination, to be a mere marginal prominence. Borchsenius (1966) separated *Phoenicococcus*, together with *Colobopyga* and allies, from the Diaspididae, recognizing the family Phoenicococcidae for them, and allocated *Comstockiella* to the Aspidiotinae and *Xanthophthalma* to its own subfamily, both within the boundary of the Diaspididae. The separation of *Phoenicococcus* and others into a distinct family is not adopted here mainly on the basis of Stickney's (1934) study. Any forms primarily lacking pygidial appendages should belong to Level 0, however diverse they are in other features.

Praecocaspis, *Radionaspis* and part of *Protodiaspis* may be referable to Set 0, but the information available is not sufficient for locating them in the framework. Some genera appear to have no places in the framework. *Ancepaspis* and

Protancepaspis have apparent pygidial appendages in the first instar in spite of the absence of processes distinctly identifiable with lobes, plates or gland spines in the adult female and second instar, though it is not certain what these appendages are (Stickney 1934, Takagi and Kawai 1973). *Xiphuraspis* may not be placed in the framework either, if the pygidial appendages of the adult female are all gland spines, but practically nothing is known about its larval instars. As well known, the second instar often reveals the primary adult female state when the latter has undergone a great secondary change. I believe that most if not all diaspidid genera will eventually fall within the framework.

This scheme may appear too simple and rough. But it would be worthy of preliminary consideration in subclassifying the Diaspididae on the supposition that the levels in the framework correspond to evolutionary stages and the types to phylogenetic stocks. It is supposed that Level 0 corresponds to the earliest stage in the evolutionary history of the Diaspididae, and that the extant elements of Set 0 are relics of the earliest stock which radiated on this level of the pygidial organization. The other levels, Level I-III, are supposed to correspond to successive evolutionary changes, which took place in each of the phylogenetic stocks.

Based on the scheme as here interpreted, the subclassification of the Diaspididae should reflect both the supposed phylogenetic stocks and evolutionary stages. Primarily nonappendiculate forms may eventually be divided into different higher taxa, which are more or less isolated. It is uncertain whether there are any known forms of this stage which are ancestral or anyhow particularly closely related to the supposed phylogenetic stocks of the appendiculate forms.

The evolutionary interpretation of the scheme also postulates that the pygidial lobes originated from plates at least twice. This may be taken as showing the scheme to be unapt, yet accords with the fact that the lobes are bilobulate in one group whereas always single in the other. It is not possible to guess from the scheme whether the plates originally appeared once or more. In this respect the scheme is obviously incomplete, wanting especially in appendiculate forms preceding Level I.

Genera of Level I

The genus *Megacanthaspis* belongs to Set S-I. Some species of *Protodiaspis* are also referred to this set; though none of them have been examined by myself, their pygidial lobes described as such should all be plates on account of their shape and variability. If the other species of *Protodiaspis* represent modifications "simply due to increasing adaptation to the pupillarial type of existence" (McKenzie and Nelson-Rees 1962), they may all be placed in Set-SI (except *P. cinchonae*, which seems to belong to the *Pseudoparlatoria*-group). *Megacanthaspis* and *Protodiaspis*, however, differ in the ducts and other features. *Thysanaspis* and *Pygalataspis* also belong to Level I, but to Type P, forming together Set P-I. They much differ in features other than the pygidial margin.

Megacanthaspis, *Thysanaspis* and *Pygalataspis* are known from eastern Asia including Japan, China and the Himalayas (Fig. 21), while *Protodiaspis* is centred in southwestern North America and Central America. Thus, the genera referred to Level I show as a whole an Asio-American bicontinental pattern of distribution, a parallel to some patterns of disjunct distribution in plant biogeography. If this parallelism is not a mere chance, it may suggest a common geologic background to these diaspidid genera and the plant taxa concerned.

The available pieces of information themselves, concerning the morphology and distribution of each genus, may be fragmentary, but they afford all together combined evidence in support of the view that these isolated genera are relics of earlier forms of the Diaspididae. This in turn may support the scheme presented in Table 7.

In this connection it is interesting that *Kuwanaspis* and *Nikkoaspis*, which belong to the lower lobate level, are centred in eastern side of Asia, overlapping in distribution with *Megacanthaspis*, *Thysanaspis* and *Pygalataspis*. It seems that East Asia, including the Himalayas, is one of the regions where we can expect to find further forms relevant to the early evolutionary stage of the appendiculate Diaspididae*. On the other hand, the elements of Set 0, the supposed relics of the earliest stock of the Diaspididae, are scattered in the tropics and subtropics of the world.

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* It should be mentioned that our knowledge about the scale insect fauna of Southeast Asia, which neighbours the Sino-Japanese Region on the north, is still very meagre. Little is known about the scale insect fauna associated with the mountain flora of tropical Asia, while part of the latter is supposed to have some connection with the temperate flora of East Asia.

TABLES

Table 1. Numbers of external secretories in adult female *M. leucaspis*.

Secretary	Locality		
	Nati	Nametoko	Kozagawa
Macroducts, total number	228-289 ($\bar{x}=260.3$) [$n=10$]	210-230 [$n=3$]	130-220 ($\bar{x}=181.9$) [$n=15$]
Gland tubercles			
mesothorax, one side	5-11 (8.8) [20]	6- 8 [6]	3-11 (7.1) [30]
metathorax, "	5- 9 (6.9) [20]	5- 7 [6]	3- 9 (5.8) [30]
abd. i, "	6-10 (8.3) [20]	5- 8 [6]	3- 9 (6.7) [30]
abd. ii, "	5- 8 (6.4) [20]	4- 7 [6]	4- 7 (5.3) [29]
abd. iii, "	2- 5 (3.4) [20]	2- 3 [6]	1- 3 (2.2) [29]
meso- and metathorax and abd. i, total*	42-56 (47.8) [10]	37-44 [3]	25-54 (39.2) [15]
Gland spines on abd. iv-viii, number per segment on one side	1- 3 (2.1) [100]	1-2 (1.7) [30]	1- 2 (1.3) [148]
Gland tubercles and gland spines, total number	81-97 (87.8) [10]	70-77 [3]	48-91 (66.5) [15]
Perivulvar disc pores, total number	34-44 (39.1) [10]	35-37 [3]	27-41 (32.3) [15]
Disc pores associated with anterior spiracle	3- 5 (4.1) [20]	3- 6 [6]	2- 7 (4.4) [28]
Disc pores associated with posterior spiracle	0- 2 (1.0) [20]	1- 2 [6]	0- 2 (1.0) [30]

* Given for comparing with the other species.

Table 2. Numbers of external secretories in adult female *M. phoebia*, *M. litseae*, *M. langtangana* and *M. actinodaphnes*.

Secretary	<i>M. phoebia</i>	<i>M. litseae</i>	<i>M. langtangana</i>	<i>M. actinodaphnes</i>
Macroducts, total number	172-217 ($\bar{x}=198.5$) [$n=15$]	159-212 ($\bar{x}=183.9$) [$n=21$]	149-196 ($\bar{x}=176.4$) [$n=32$]	129-173 ($\bar{x}=147.9$) [$n=37$]
Gland tubercles				
mesothorax, one side	3- 6 (4.4) [35]	1- 5 (3.2) [40]	2- 6 (4.2) [63]	2- 5 (3.5) [74]
metathorax, "	2- 6 (4.0) [35]	3- 5 (3.7) [42]	3- 8 (5.1) [64]	2- 4 (3.2) [73]
abd. i, "	3- 9 (6.0) [36]	5-12 (8.4) [42]	5-12 (8.9) [64]	5-12 (8.2) [73]
meso- and metathorax and abd. i, total	25-32 (28.7) [16]*	23-36 (30.5) [20]	23-42 (36.5) [31]	24-37 (29.7) [35]
Perivulvar disc pores, total number	25-41 (32.1) [39]	22-37 (27.7) [47]	25-43 (35.1) [51]	19-24 (21.5) [38]
Disc pores associated with anterior spiracle	3- 8 (4.8) [65]	3- 8 (6.0) [28]	3- 6 (4.4) [59]	1- 5 (3.3) [67]

* Total number of gland tubercles occurring on meso- and metathorax and abd. i and ii: 29-38 ($\bar{x}=34.1$) [$n=16$].

Table 3. Number of microducts extending through enlarged marginal gland spines in adult female *M. phoebia*, *M. litseae*, *M. langtangana* and *M. actinodaphnes*.

	<i>M. phoebia</i>	<i>M. litseae</i>	<i>M. langtangana</i>	<i>M. actinodaphnes</i>
Number per gland spine				
Abd. ii	—*	2-5 ($\bar{x}=3.3$) [n=42]	2-5 ($\bar{x}=3.9$) [n=61]	1-3 ($\bar{x}=2.0$) [n=74]
Abd. iii	1-4 (3.4) [32]	2-4 (3.6) [41]	2-5 (3.8) [63]	—**
Abd. iv	2-4 (3.2) [32]	3-5 (3.6) [42]	2-4 (3.7) [62]	2-4 (2.8) [74]
Abd. v	1-4 (2.7) [32]	3-5 (4.0) [41]	3-4 (3.8) [62]	2-6 (3.1) [72]
Abd. vi	1-4 (3.0) [32]	3-4 (3.9) [42]	3-7 (4.0) [63]	2-4 (3.8) [73]
Abd. vii	1-4 (2.8) [32]	4-7 (5.7) [42]	3-6 (4.5) [60]	3-5 (3.9) [72]
Abd. viii	1-4 (2.9) [32]	5-8 (6.6) [42]	2-5 (3.4) [61]	2-4 (3.0) [70]
Mean	3.0	4.4	3.9	3.1
Total number	28-45 (35.9) [16]	54-66 (61.8) [19]	46-60 (54.5) [26]	33-41 (36.9) [31]

* 2-4 gland tubercles, $\bar{x}=2.8$, $n=36$; ** Replaced by 1 gland tubercle.

Table 4. Gland spines and gland tubercles in the adult females of the 5 species of *Megacanthaspis*.

	Abd. ii	Abd. iii	Abd. iv	Abd. v	Abd. vi	Abd. vii	Abd. viii
<i>M. leucaspis</i>	tt	tt	s~ss	s~ss	s~ss	s~ss	s~ss
<i>M. phoebia</i>	tt	S	S	S	S	S	S
<i>M. litseae</i>	S	S	S	S	S	S	S
<i>M. langtangana</i>	S	S	S	S	S	S	S-S
<i>M. actinodaphnes</i>	S	t	S	S	S	S	S-S

t or tt, gland tubercle(s); s or ss, gland spine(s); S, enlarged gland spine; S, enlarged gland spine, especially robust to form a conical process; S-S and S-S, elements of the posteriormost pair appressed together at the apex of the pygidium.

Meso- and metathorax and abd. i with tt in all the species.

Table 5. Numbers of some macroducts in the 5 species of *Megacanthaspis*.

	<i>M. leucaspis</i>	<i>M. phoebia</i>	<i>M. litseae</i>	<i>M. langtangana</i>	<i>M. actinodaphnes</i>
Adult female: median macroduct(s) on or near apex of pygidium	0	2*	0~1**	1	0
Second instar female: marginal macroducts on one side of abdomen	4	3	5	4	4

*3 in 1 specimen; **2 in 1 specimen.

Table 6. Morphoclines constructed for the 5 species of *Megacanthaspis*.

Feature	Character	Sequence of species
<i>Adult female</i>		
I. Gland spine and gland tubercle system	Replacement by enlarged gland spines and further modification in disposition (Table 4)	<i>leucaspis</i> → <i>phoebia</i> → <i>litseae</i> → <i>langtangana</i> → <i>actinodaphnes</i>
II. Marginal gland spines	a. Enlargement to robuster processes	<i>leucaspis</i> → <i>phoebia</i> → <i>langtangana</i> → $\left[\begin{array}{l} \textit{litseae} \\ \textit{actinodaphnes} \end{array} \right]$
	b. Number of microducts, fewer: more numerous (Table 3)	<i>leucaspis</i> → $[\textit{phoebia} : \textit{actinodaphnes} : \textit{langtangana} : \textit{litseae}]$
III. Gland tubercles on thorax and abd. i	Total number, mean, more numerous: fewer (Tables 1, 2)	<i>leucaspis</i> : <i>langtangana</i> : <i>litseae</i> ⇒ <i>actinodaphnes</i> ⇒ <i>phoebia</i>
IV. Marginal serrate processes of pygidium	Reduction in number and development	<i>leucaspis</i> → <i>phoebia</i> → <i>langtangana</i> → <i>actinodaphnes</i> → <i>litseae</i>
V. Macroducts	a. Total number, mean, more numerous: fewer (Tables 1, 2)	<i>leucaspis</i> N: <i>phoebia</i> : <i>litseae</i> : <i>langtangana</i> : <i>actinodaphnes</i>
	b. Median dorsal macroducts at apex of pygidium, reduction in number to disappearance (Table 5)	<i>phoebia</i> → <i>langtangana</i> → <i>litseae</i> → $\left[\begin{array}{l} \textit{leucaspis} \\ \textit{actinodaphnes} \end{array} \right]$
VI. Perivulvar disc pores	Total number, mean, more numerous: fewer (Tables 1, 2)	<i>leucaspis</i> N: <i>langtangana</i> : <i>phoebia</i> : <i>litseae</i> : <i>actinodaphnes</i>
VII. Anterior spiracular disc pores	Mean number, more numerous: fewer (Tables 1, 2)	<i>litseae</i> : <i>phoebia</i> : <i>langtangana</i> ⇒ <i>leucaspis</i> : <i>actinodaphnes</i>
VIII. Posterior spiracular disc pores	Reduction to disappearance (Table 1)	<i>leucaspis</i> → $\left[\begin{array}{l} \textit{phoebia} \\ \textit{litseae} \\ \textit{langtangana} \\ \textit{actinodaphnes} \end{array} \right]$
<i>Second instar female</i>		
IX. Abdominal marginal macroducts	Total number, more numerous: fewer (Table 5)	<i>litseae</i> : $\left[\begin{array}{l} \textit{leucaspis} \\ \textit{langtangana} \\ \textit{actinodaphnes} \end{array} \right] : \textit{phoebia}$
X. Marginal gland spines	a. Enlargement to robuster processes	<i>leucaspis</i> → <i>phoebia</i> ⇒ <i>langtangana</i> → <i>actinodaphnes</i> → <i>litseae</i>
	b. Number of microducts, increase	$\left[\begin{array}{l} \textit{leucaspis} \\ \textit{phoebia} \\ \textit{langtangana} \\ \textit{actinodaphnes} \end{array} \right] \rightarrow \textit{litseae}$

Second instar male
 (*M. actinodaphnes* excluded)
 XI. Marginal gland spines

- a. Enlargement to robuster or more conspicuous processes *leucaspis*→*phoebia*→*langtangana*→*litseae*
 b. Number of microducts, increase *leucaspis*→ $\left[\begin{array}{c} \textit{langtangana} \\ \textit{phoebia} \end{array} \right]$ →*litseae*
 c. Space between posteriormost gland spines, decrease $\left[\begin{array}{c} \textit{leucaspis} \\ \textit{phoebia} \end{array} \right]$ → $\left[\begin{array}{c} \textit{langtangana} \\ \textit{litseae} \end{array} \right]$

→, polarity; :, polarity undetermined (or both directions may be involved); *leucaspis* N, sample from Nati. The sequence constructed for the numbers of secretories are partly based on statistically insignificant differences between adjacent species.

Table 7. A preliminary scheme for subclassifying the Diaspididae based on the marginal organization of the pygidium.

		Gland spine type TYPE S		Plate type TYPE P
19	Appendiculate level	Lobate level	LEVEL III SET S-III L + D + S <i>Diaspidini</i> <i>Lepidosaphedini</i>	SET P-III L + P' <i>Aspidiotini</i> <i>Parlatoriini</i> <i>Odonaspidini</i> <i>Rugaspidiotini</i>
			LEVEL II SET S-II L + P + S <i>Kuwanaspis</i> <i>Nikkoaspis</i>	SET P-II L + P <i>Leucaspidini</i>
		Nonlobate level	LEVEL I SET S-I P + S <i>Megacanthaspis</i> <i>Protodiaspis</i> [part]	SET P-I P <i>Thysanaspis</i> <i>Pygalataspis</i>
Nonappendiculate level	LEVEL 0	SET 0 No pygidial appendages <i>Comstockiella</i> <i>Colobopyga</i> ; <i>Halimococcus</i> ; <i>Madhalimococcus</i> ; <i>Platycoccus</i> ; <i>Thysanococcus</i> <i>Phoenicococcus</i> <i>Xanthophthalma</i>		

L: lobes; D: pore prominences (latadentes); S: gland spines; P: plates; P': glanduliferous plates.

The tribes are substantially the same in composition as the corresponding tribes or subtribes defined by Balachowsky in his works.

PLATES

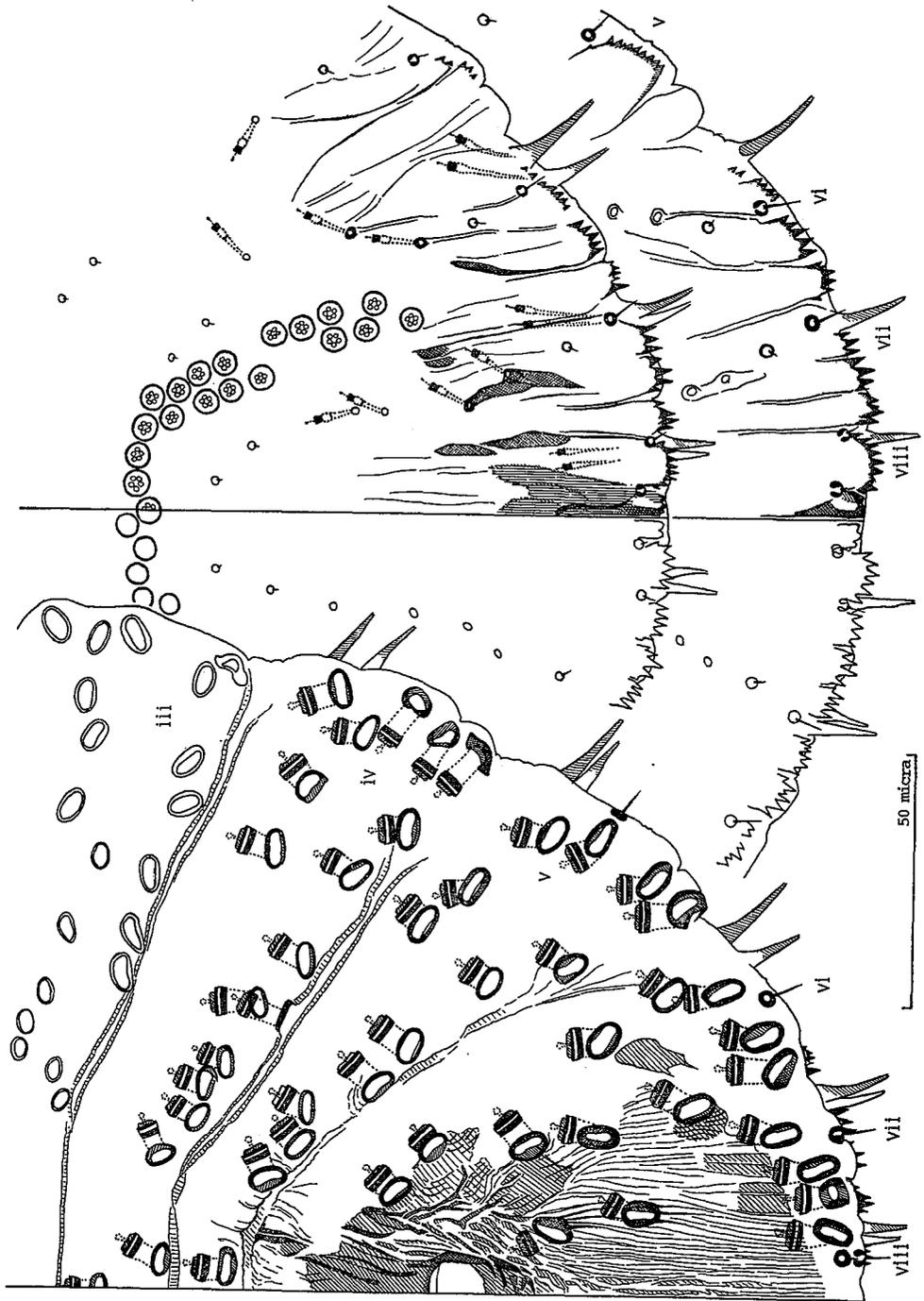


Fig. 1. *Megacanthaspis leucaspis*, new species: adult female, pygidium. Nati (left and right above) and Kozagawa (right below), Kii Peninsula, Japan, on *Actinodaphne longifolia*.

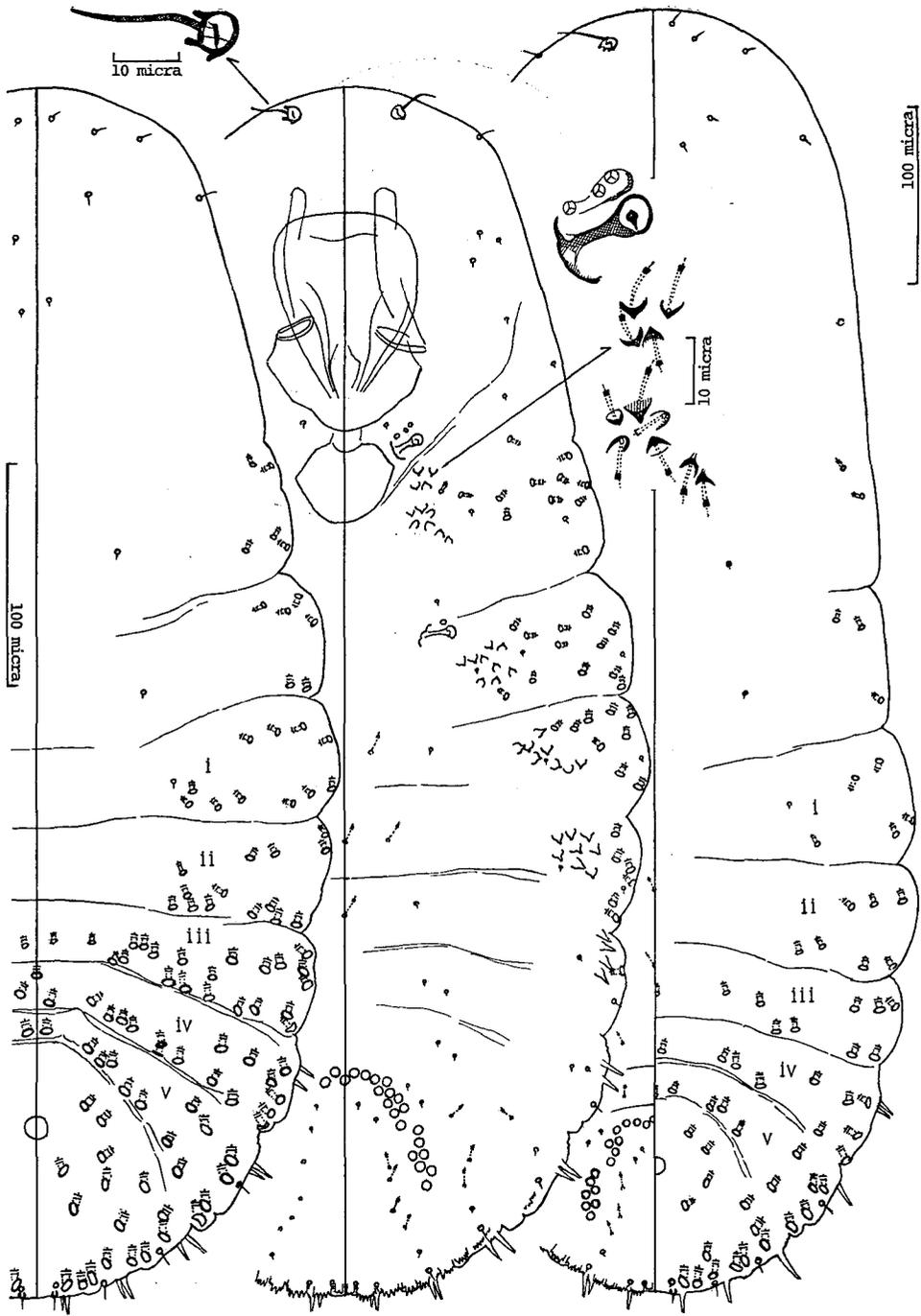


Fig. 2. *Megacanthaspis leucaspis*, new species: adult female. Nati (left and middle) and Kozagawa (right), Kii Peninsula, Japan, on *Actinodaphne longifolia*.

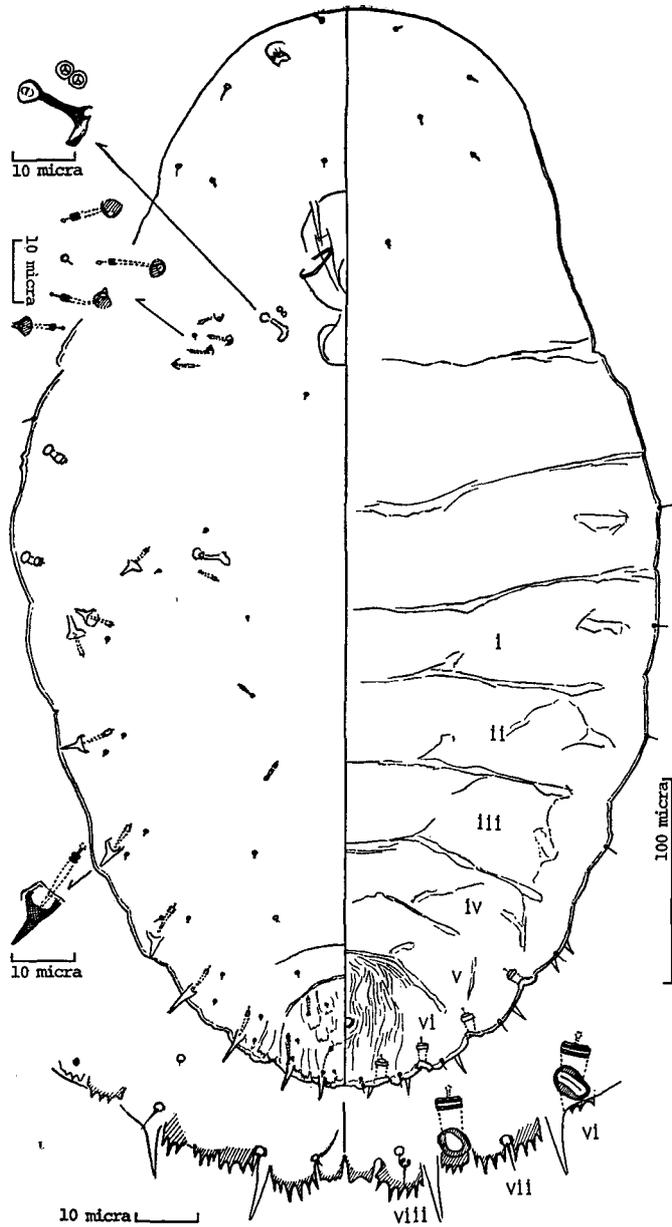


Fig. 3. *Megacanthaspis leucaspis*, new species: second instar female, body of a matured individual (above) and pygidial margin of a young individual (below). Nati (above) and Kozagawa (below), Kii Peninsula, Japan, on *Actinodaphne longifolia*.

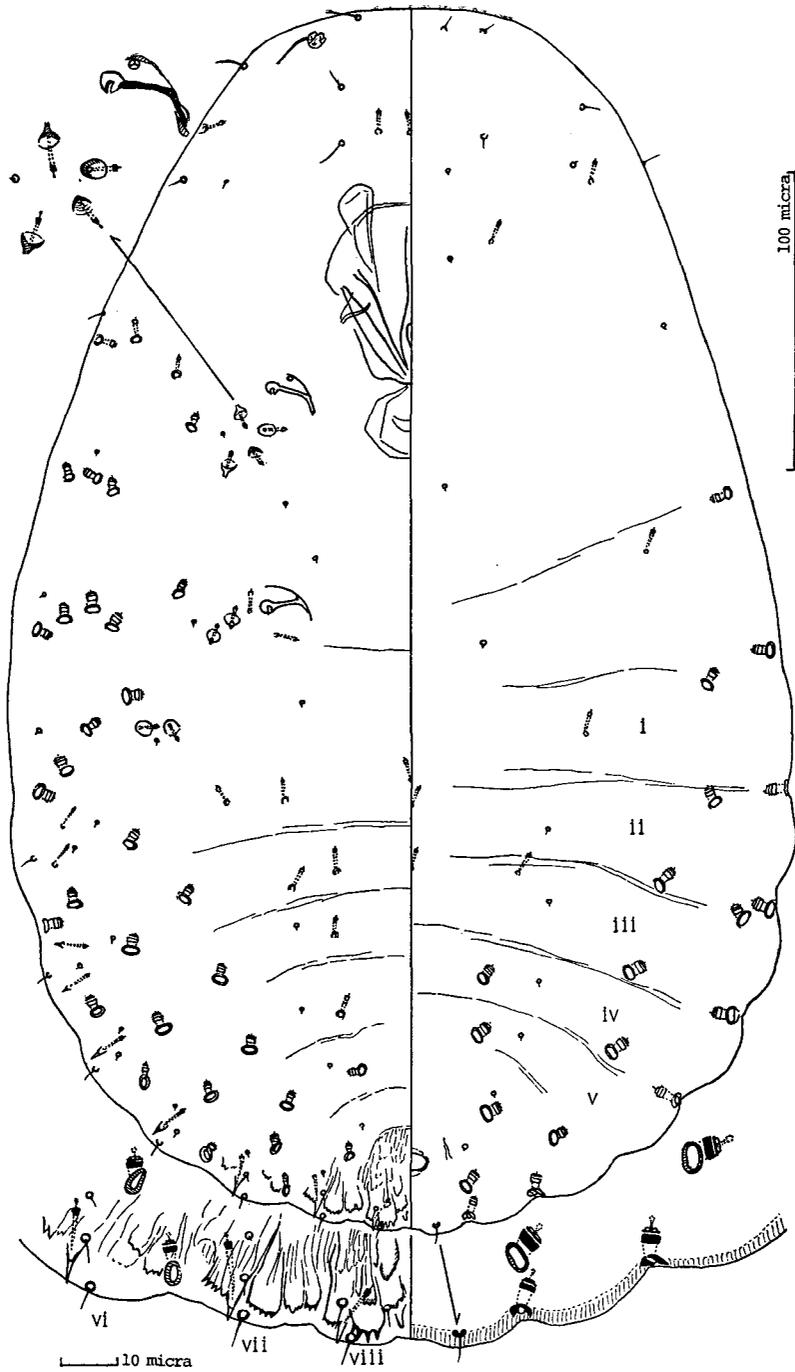


Fig. 4. *Megacanthaspis leucaspis*, new species: second instar male. Nati, Kii Peninsula, Japan, on *Actinodaphne longifolia*.

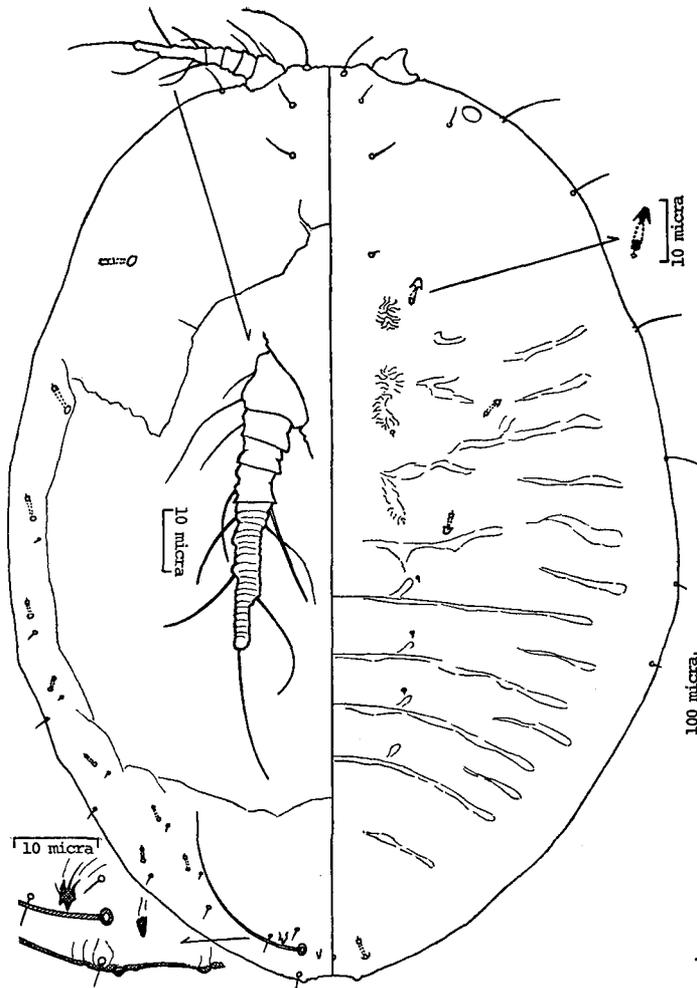
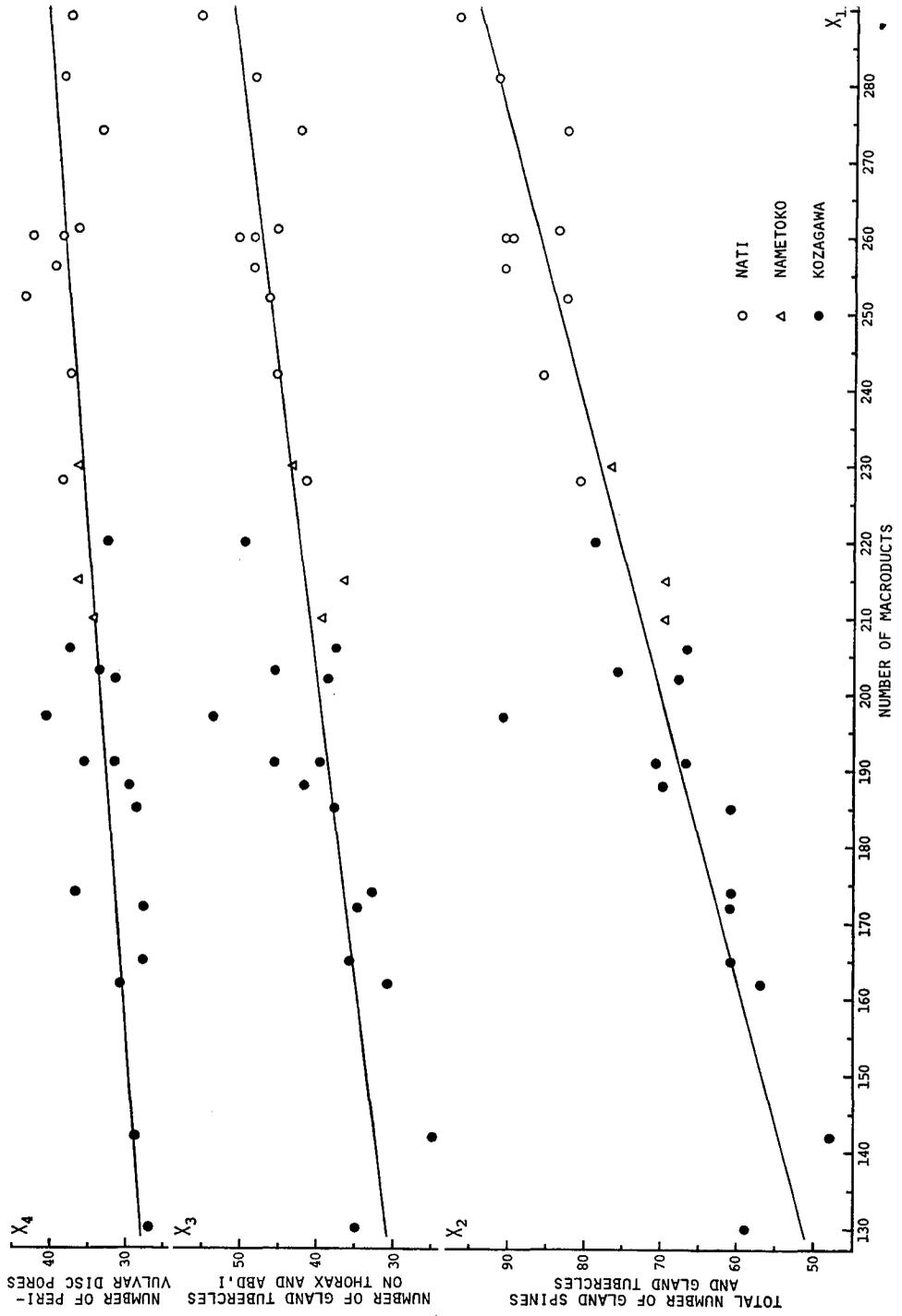


Fig. 5. *Megacanthaspis leucaspis*, new species: first instar female, exuvial cast (mouthparts and legs, pushed back to the posterior end of the body, are omitted). Nati, Kii Peninsula, Japan, on *Actinodaphne longifolia*.

Fig. 6. *Megacanthaspis leucaspis*, new species: adult female. Scatter diagrams for the numbers of some external secretories.

$$\begin{aligned}
 X_2 &= 0.27X_1 + 16.20 & r &= 0.90 \\
 X_3 &= 0.13X_1 + 14.18 & r &= 0.77 \\
 X_4 &= 0.08X_1 + 17.90 & r &= 0.73
 \end{aligned}$$





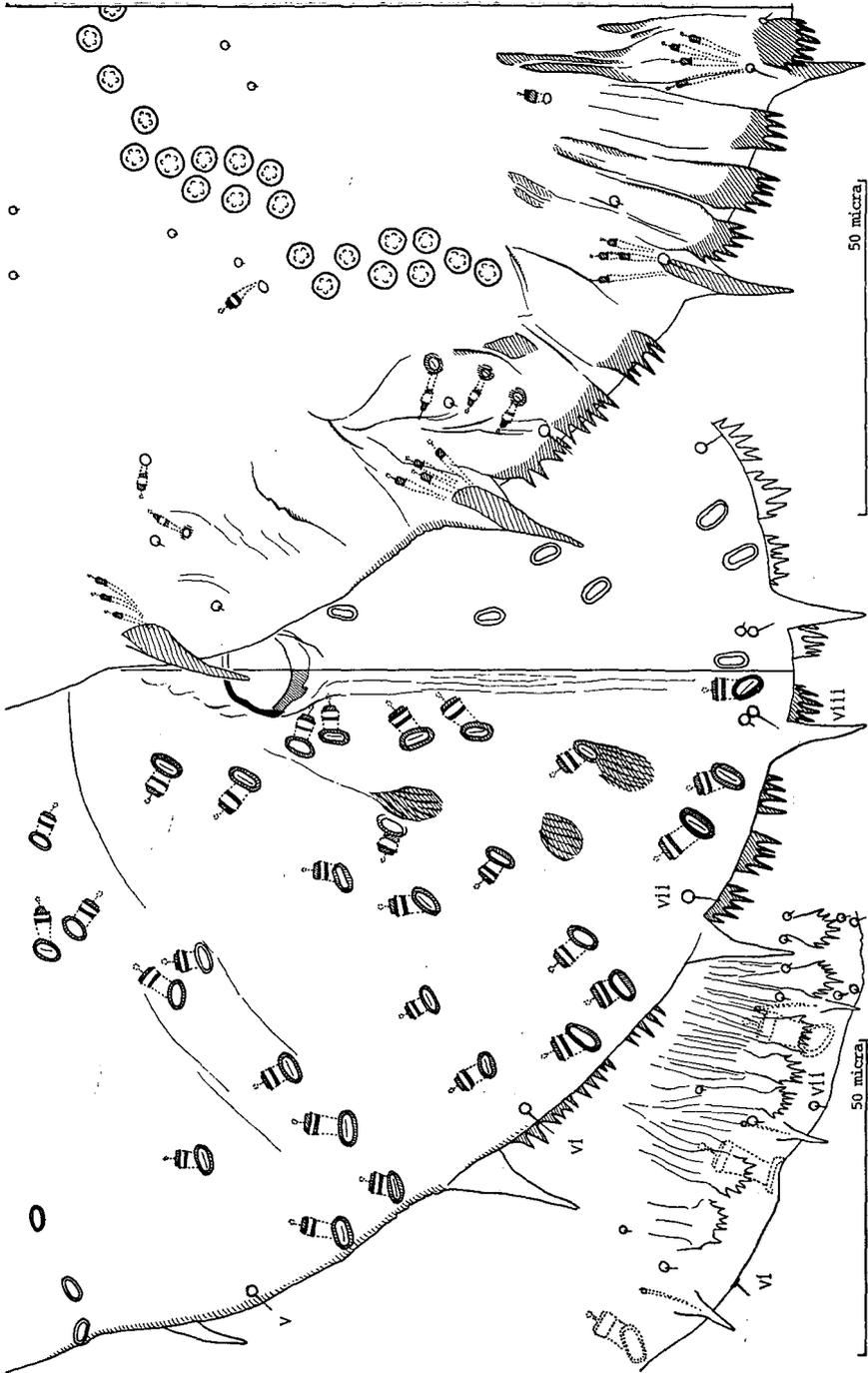


Fig. 7. *Megacanthaspis phoebia* (= *Nanmuaspis phoebia*), new combination: adult female, pygidium; and second instar female, pygidial margin (left corner). Hangchow, China, on *Phoebe sheaverii*.

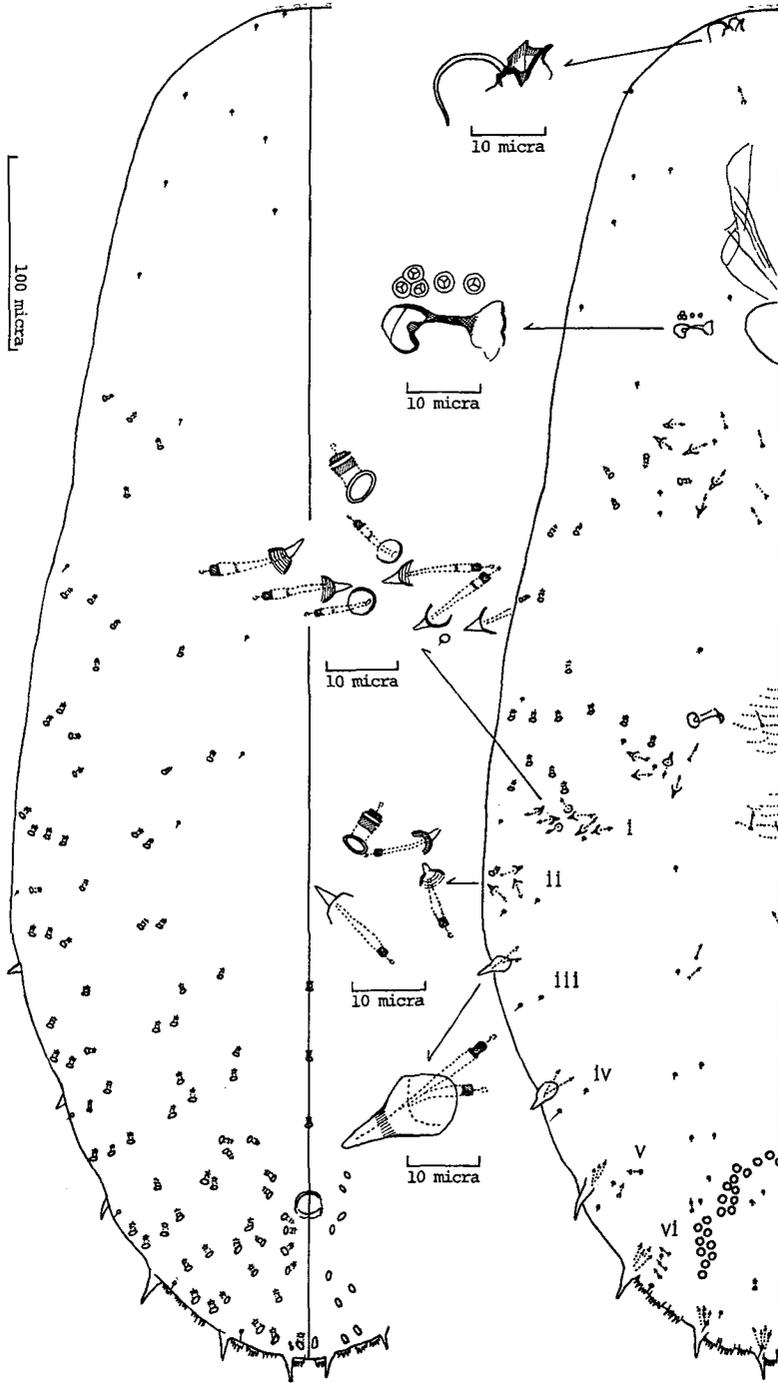


Fig. 8. *Megacanthaspis phoebia* (= *Nannuaspsis phoebia*), new combination: adult female. Hangchow, China, on *Phoebe shearerii*.

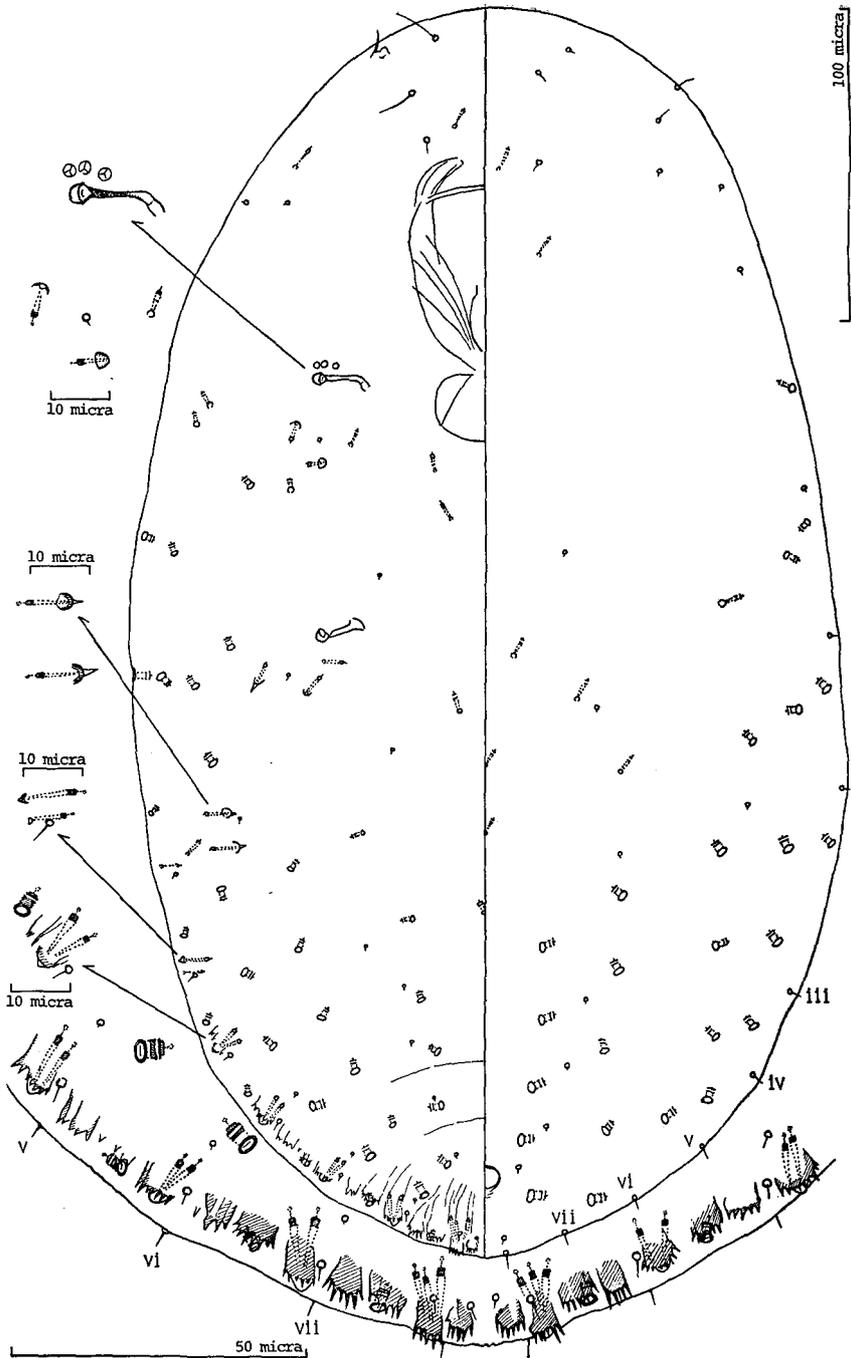


Fig. 9. *Megacanthaspis phoebia* (= *Nanmuaspis phoebia*), new combination: second instar male. Hangchow, China, on *Phoebe shearerii*.

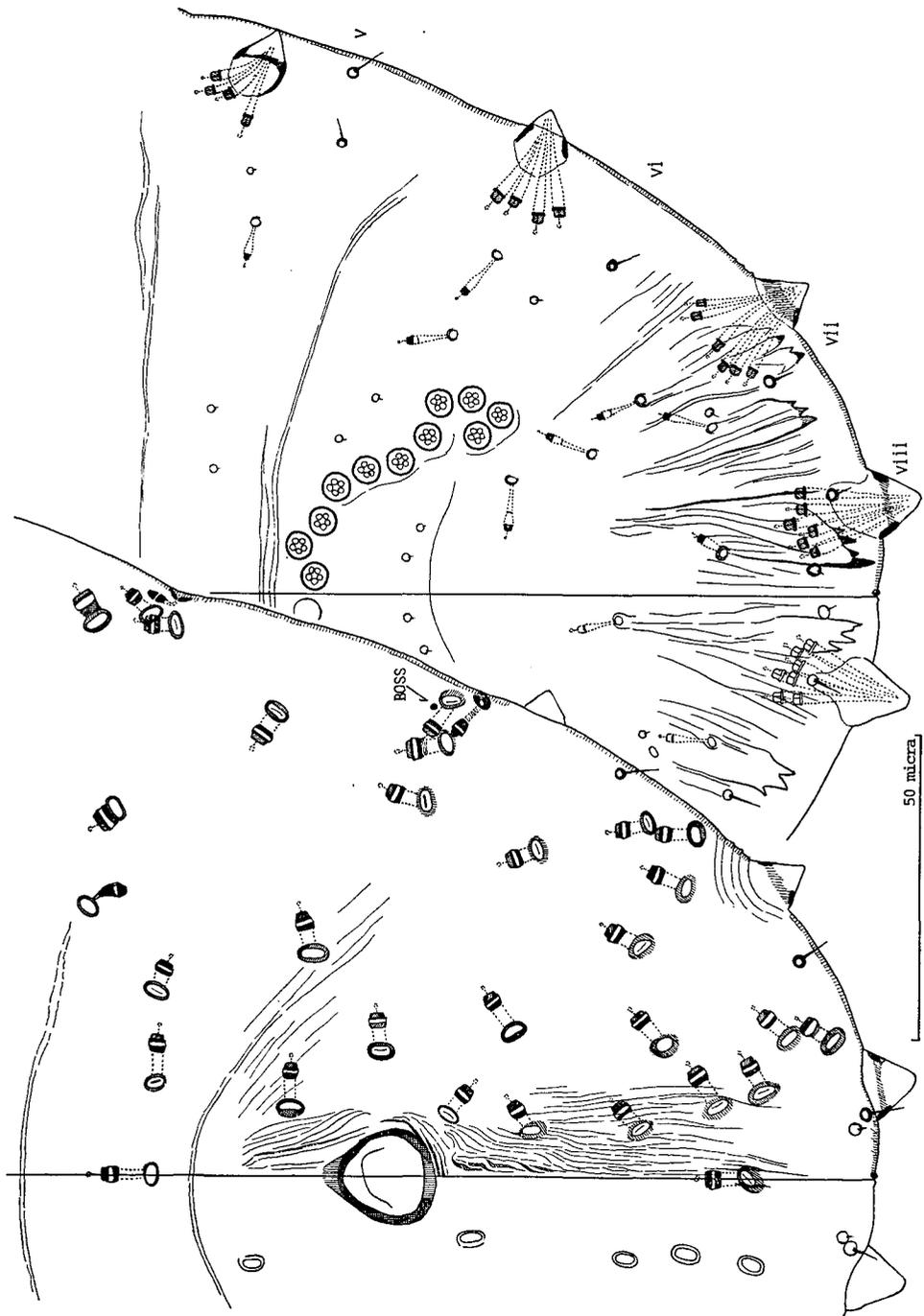


Fig. 10. *Megacanthaspis litseae*: adult female, pygidium. Fen-chi-hu, Taiwan, on *Litsea akoensis*.

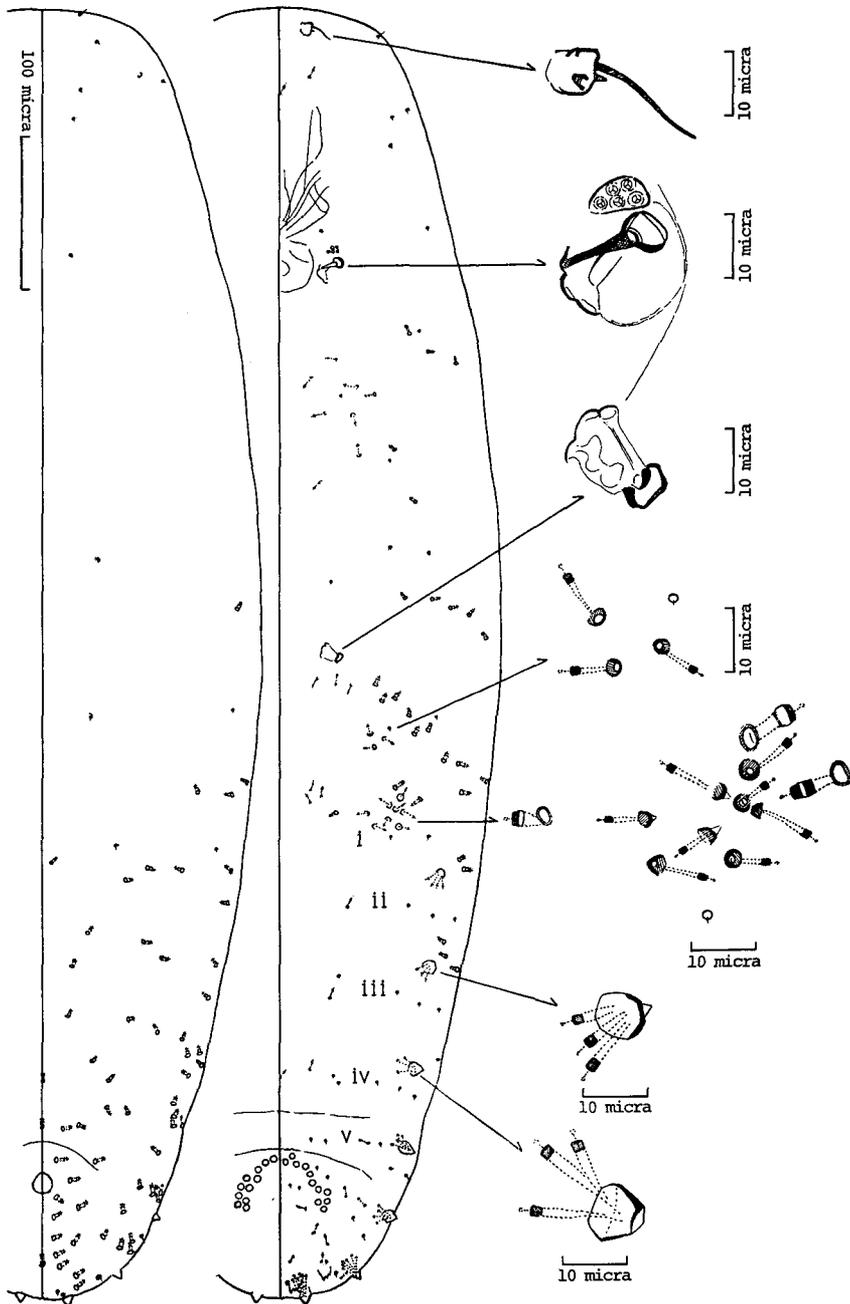


Fig. 11. *Megacanthaspis litseae*: adult female. Fen-chi-hu, Taiwan, on *Litsea akoensis*.

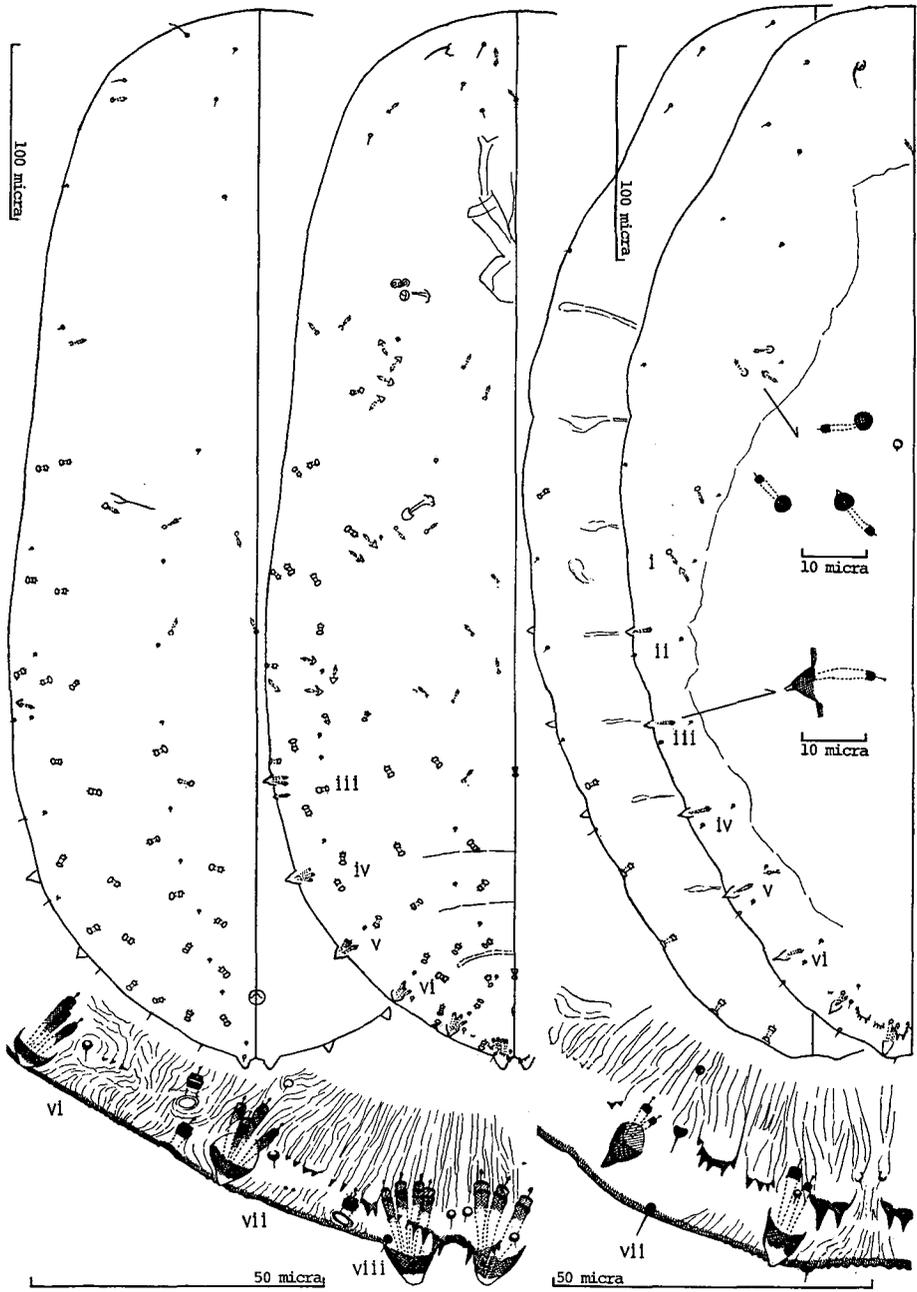


Fig. 12. *Megacanthaspis litseae*: second instar male (left two and left below); and second instar female, exuvial cast (right two and right below; mouth-parts, pushed back to the posterior extremity of the body, are omitted from the drawing at right extreme). Fen-chi-hu, Taiwan, on *Litsea akoensis*.

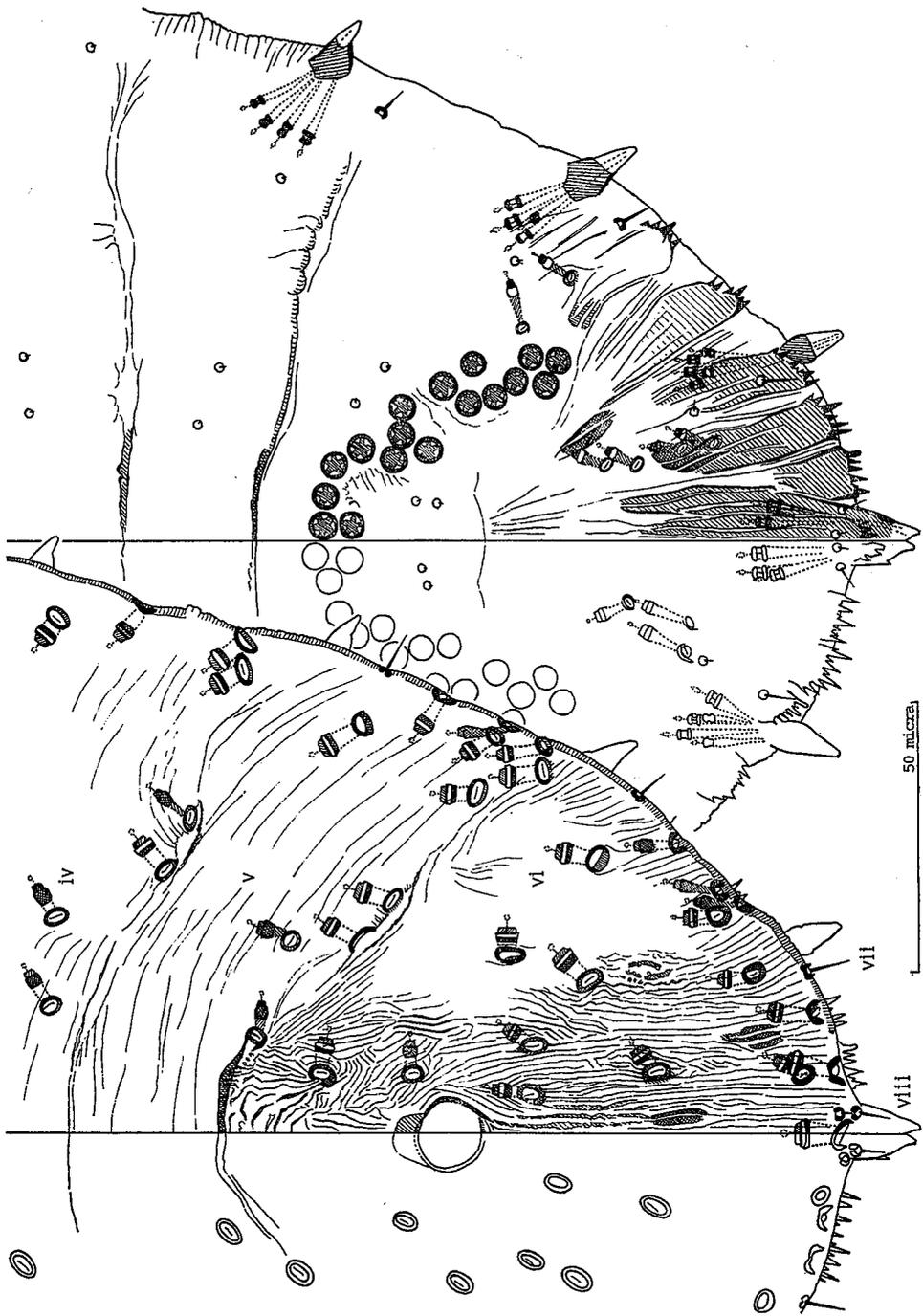


Fig. 13. *Megacanthaspis langtangana*, new species: adult female, pygidium. Langtang Valley, Nepal, on *Machilus duthiei*.

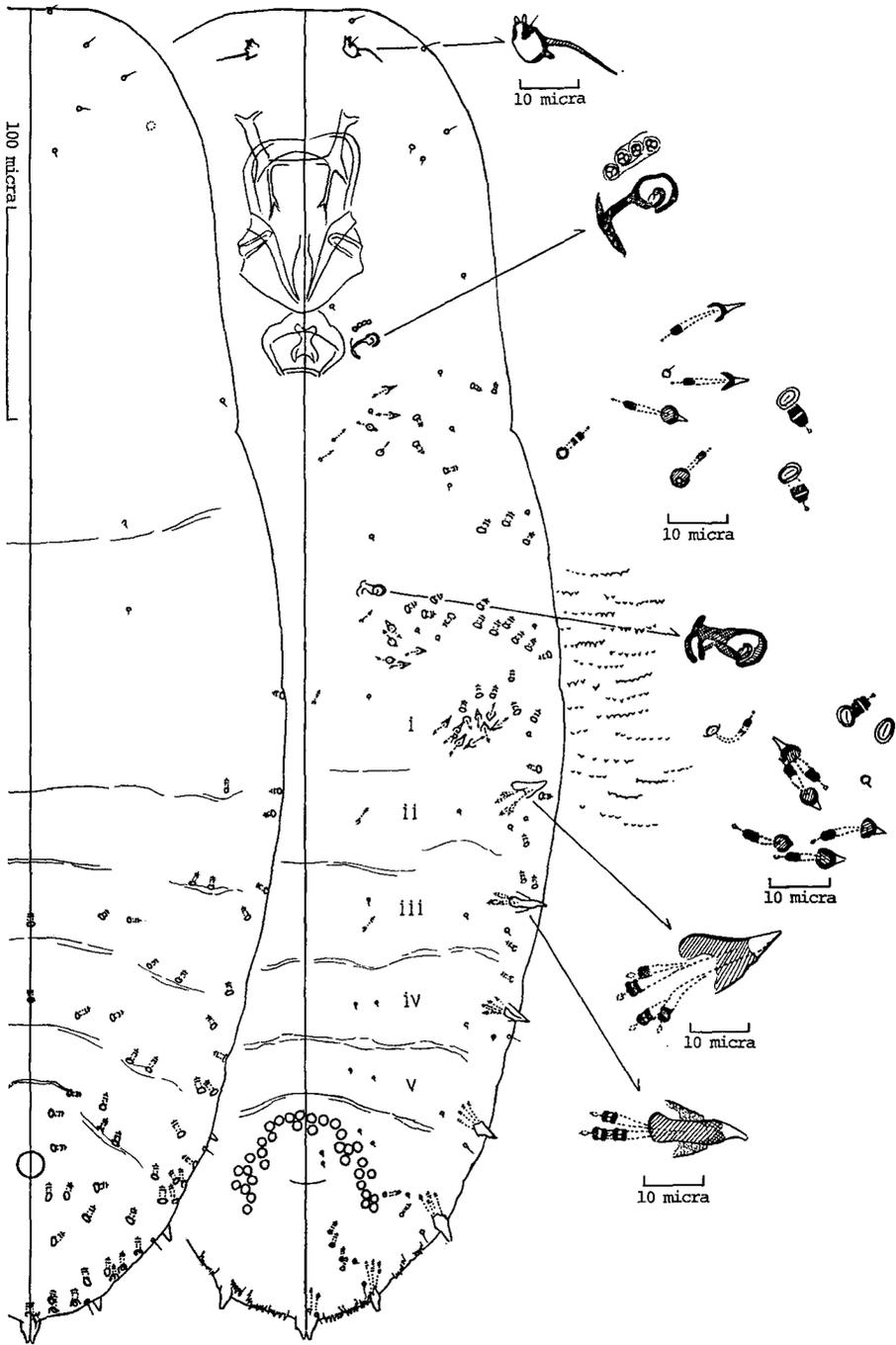


Fig. 14. *Megacanthaspis langtangana*, new species: adult female. Langtang Valley, on *Machilus duthiei*.

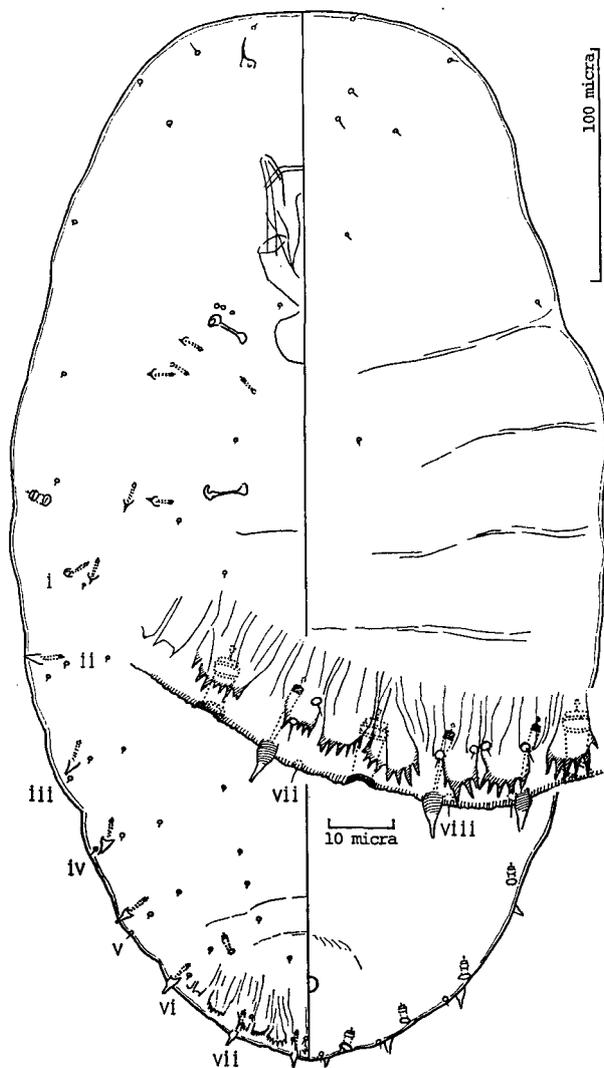
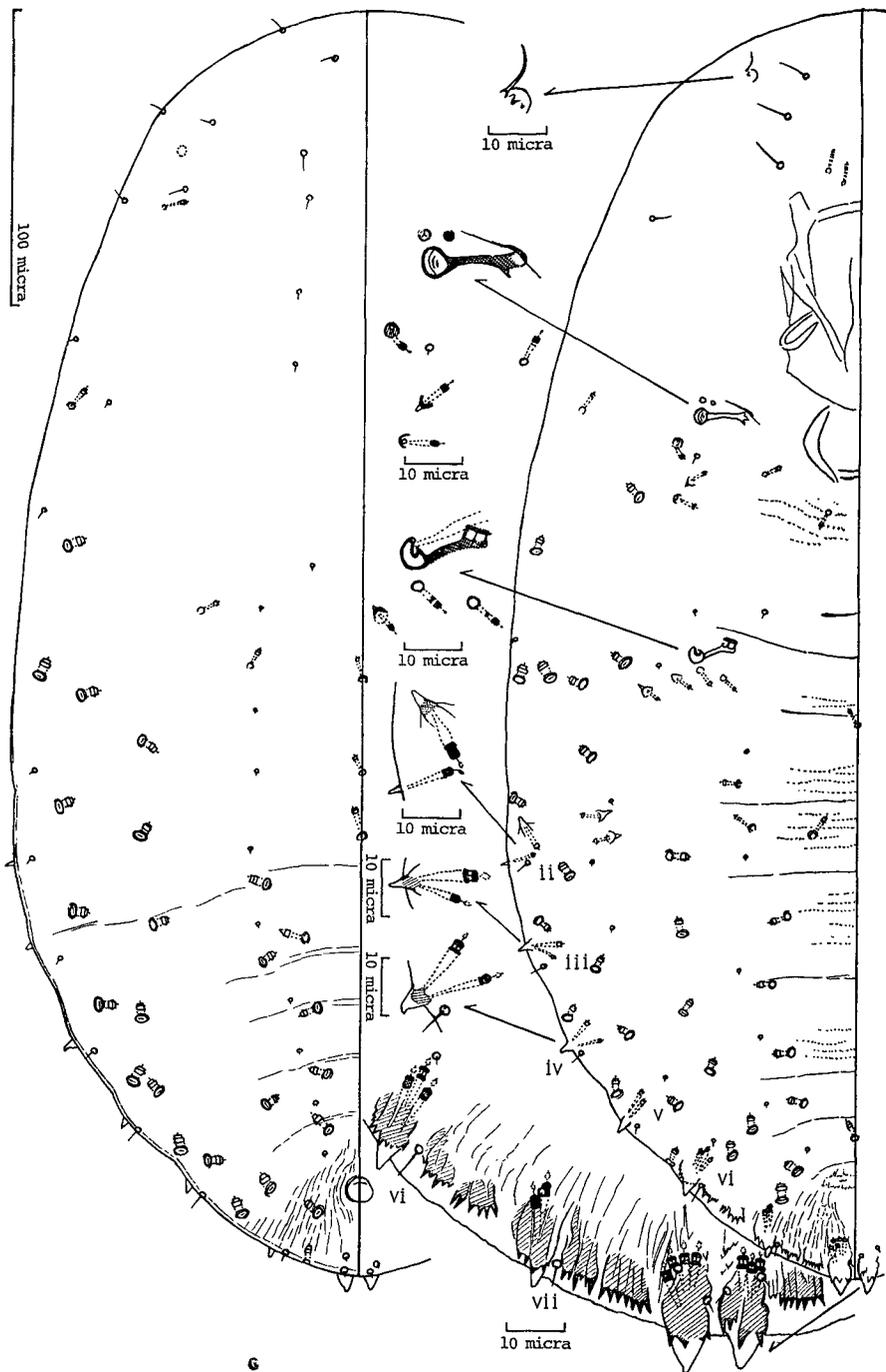


Fig. 15. *Megacanthaspis langtangana*, new species: second instar female. Langtang Valley, Nepal, on *Machilus duthiei*.

Fig. 16. *Megacanthaspis langtangana*, new species: second instar male. Langtang Valley, Nepal, on *Machilus duthiei*.





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Fig. 17. *Megacanthaspis actinodaphnes*: adult female, pygidium. Kagosima, Japan, on *Actinodaphne longifolia*.

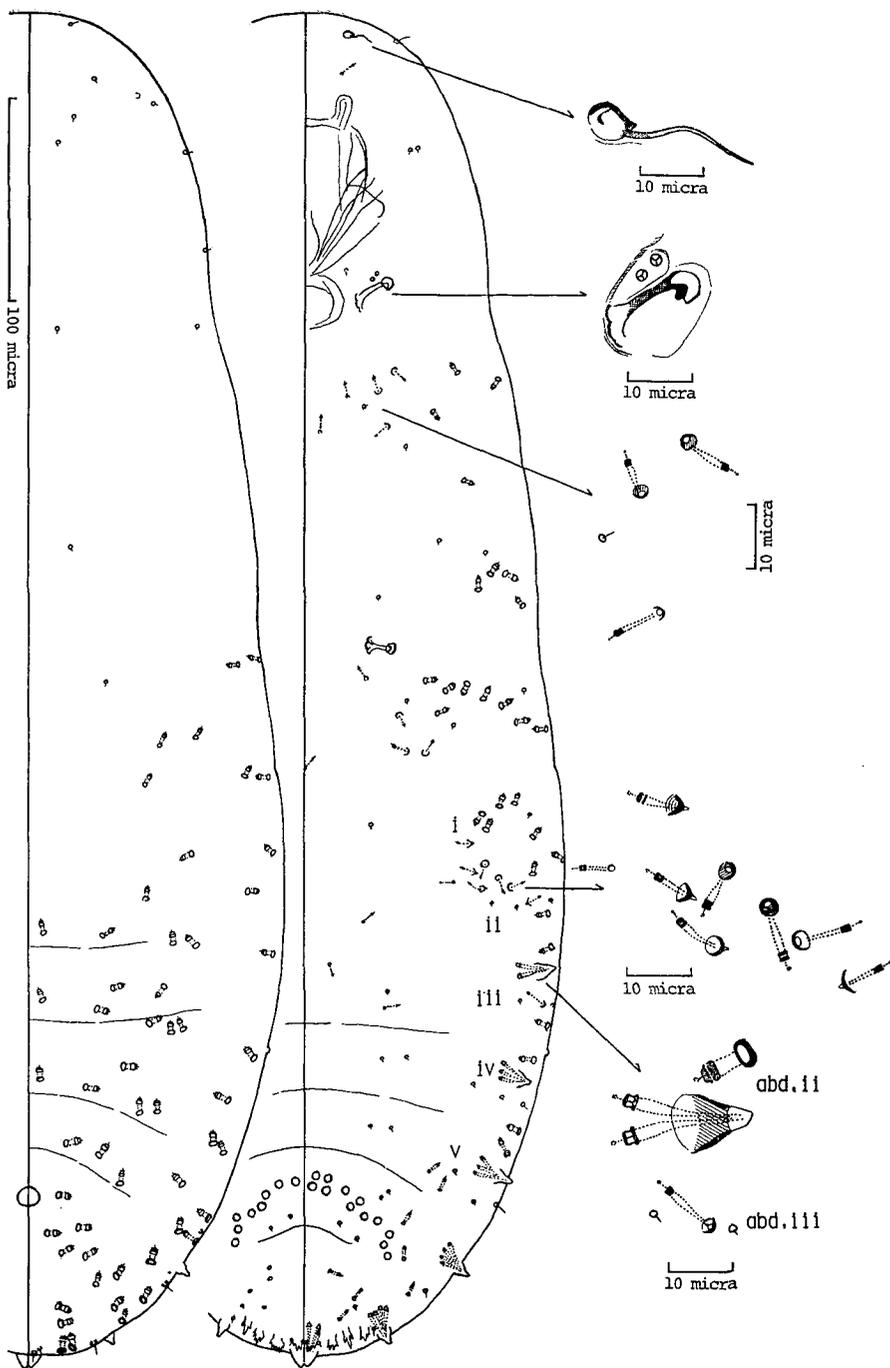


Fig. 18. *Megacanthaspis actinodaphnes*: adult female. Kagosima, Japan, on *Actinodaphne longifolia*.

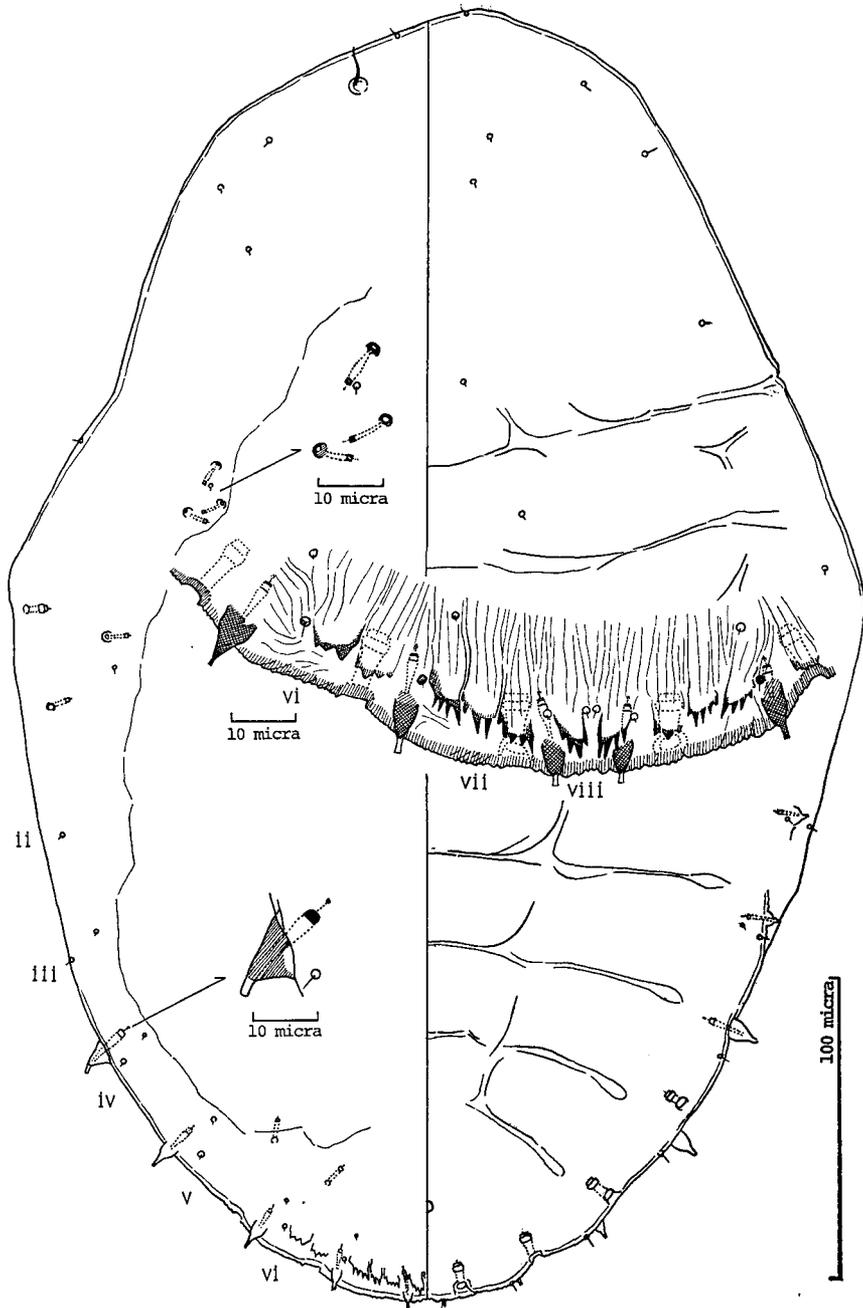


Fig. 19. *Megacanthaspis actinodaphnes*: second instar female, exuvial cast (mouth-parts, pushed back to the posterior extremity of the body, are omitted). Kagosima, Japan, on *Actinodaphne longifolia*.

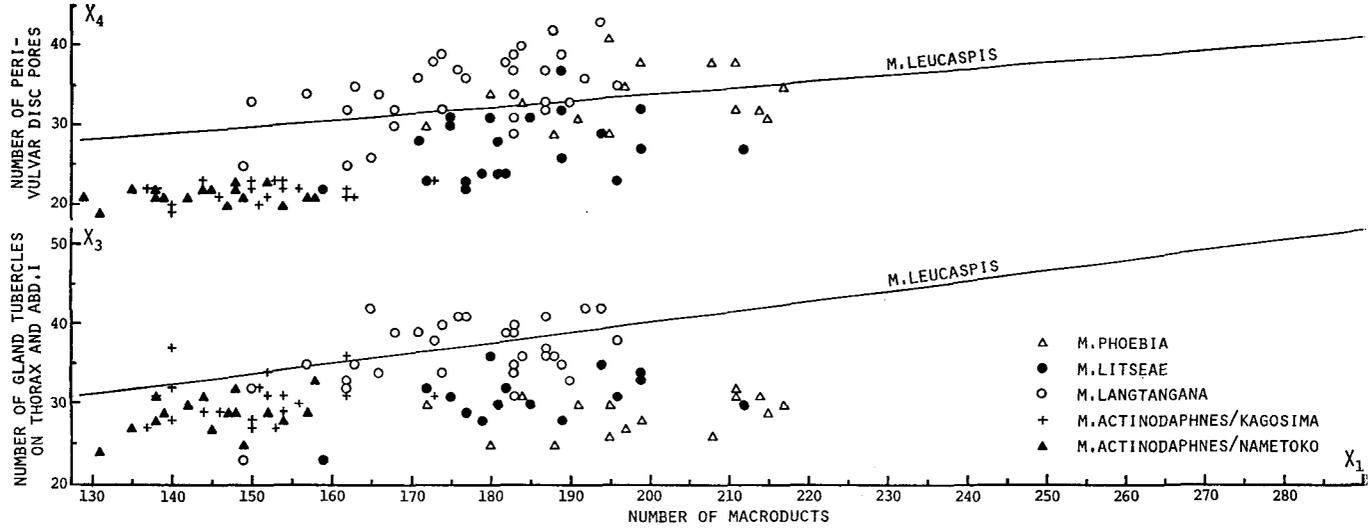


Fig. 20. *Megacanthaspis leucaspis*, *M. phoebia*, *M. litseae*, *M. langtangana* and *M. actinodaphnes*: adult females. Number of gland tubercles on thorax and first abdominal segment against number of macroducts (below); number of perivulvar disc pores against number of macroducts (above). The straight lines drawn for *M. leucaspis* are adopted from Fig. 6.

Fig. 21. Distribution of *Megacanthaspis*, *Thysanaspis* and *Pygalataspis*.

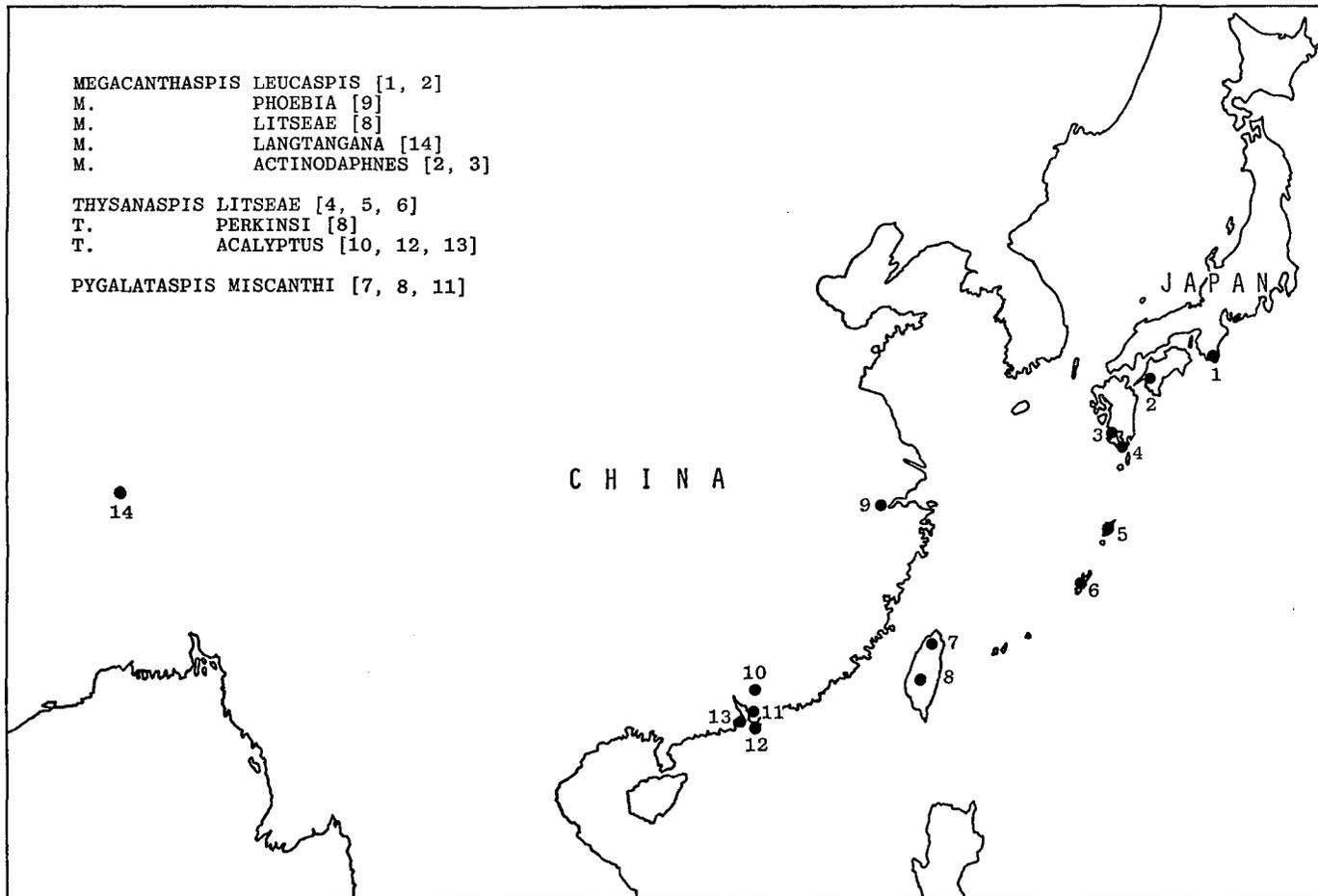




Fig. 22. *Megacanthaspis langtangana*, new species: scales. Completed scales ca. 1.5 mm long in the female and 1.0 mm long in the male. Langtang Valley, Nepal, on *Machilus duthiei*.