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**ANOTHER MODE OF LIFE IN ARMoured SCALE INSECTS
(STERNORRHYNCHA: COCCOIDEA: DIASPIDIDAE)**

By SADA0 TAKAGI

Abstract

TAKAGI, S., 2022. Another mode of life in armoured scale insects (Sternorrhyncha: Coccoidea: Diaspididae). *Ins. matsum. n. s.* 78: 27–56, 15 figs.

Thecatosoma, n.g., is proposed and *T. caudatum* (type-species), *T. verticale*, *T. auriculatum*, *T. gracile*, and *T. crenatum*, n.spp., are described from eastern tropical Asia (Palawan; Malaya; Borneo). The adult females of these scale insects are peculiar in having at maturity the head, all the thoracic segments, and the first abdominal segment coalescent to form an elongate sheath-like structure or ‘theca’, which is heavily sclerotized on the dorsal surface and along the body margin on the ventral side. They represent the ‘thecate’ mode of life, which is associated with ovoviviparity, the theca supplying a space with a tough cover for eggs developing into the nymphal stage within the maternal body. Excepting the formation of the theca, *Thecatosoma* is very similar to *Unaspis*, and should have originated from the latter. *T. auriculatum* in the pre-thecate state of the adult female is even undistinguishable from *Unaspis* and, in addition, finds a very similar species in *Unaspis*. These facts suggest the possibility that *Thecatosoma* is not a distinct genus but an aggregate of thecate forms of *Unaspis*, these forms being not necessarily closely related to each other. However, *Thecatosoma* as represented by the five species has the morphological variation much broader than in *Unaspis* in spite of the much fewer species. These species as a whole should not be the same as *Unaspis* in some biological aspects and, accordingly, in evolutionary potential, further species being expected to show a broader variation.

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Preface

I started this study 26 years ago, but soon bumped against a wall or the insufficient material. At that time I was unable to decide whether Thecatosoma is a good genus or a mere aggregate of thecate forms of Unaspis. I stopped the study and decided to wait for further material. Until to-day, I have found no additional material helpful for approaching the question, and I think there will be no chance to advance my study even in a few years hereafter.

The paper published here, therefore, remains ambiguous as to the taxonomic status of Thecatosoma. This tentative genus, however, may be worthy of publication in view of adaptive body reformation in association with ovoviviparity.

INTRODUCTION

The females of the scale insect family Diaspididae have three instars. The first instar is the only stage that has well-developed legs and antennae; it produces crawlers for dispersal and settlement. The third instar is the adult stage. In the greater part of the family, it has a span much longer than in the preceding instars, makes the greatest amount of body growth among the instars (thus showing that this female stage is neotenic [see *Males* at the conclusion of this section]), and completes the construction of the test (scale; scale cover). In its incipiency, the test is composed mainly of the exuvial casts of the first and second instars (so that ‘di-aspid’); in the adult stage, it is much enlarged in accordance with the body growth, being made of abundant wax filaments produced from secreting organs (tubular ducts in various sizes, numbers, and arrangements) and cemented together by excreta expelled from the anal opening, and being constructed, in the great majority of cases, by the oscillatory or rotatory movements of the body with the pivot fixed on the prosoma, which probably serves as a large sucking-disc (sometimes reinforced with small suckers, a number of spiny setae, spinous antennal tubercles, and so on). The second instar is little more than a transitional stage from the first instar to the third; it is similar to the adult female, but much smaller in size and much simpler in structure than the latter. Many groups of armoured scale insects have evolved all along this mode of life, which, therefore, is *the ordinary diaspidid mode*.

It is probably usual in this mode that the female cleans her test-constructing spot on the host plant by the use of the trullae, which work like little knives or saws in co-operation with her body movement. In some diaspidids belonging to various taxa, this behaviour has given rise to another behaviour—burrowing under the upper epidermal layer of the plant body, and *the burrowing mode* has brought some further modifications in behavioural and morphological traits. An unusual case of such modifications is the formation of a familial or matrifilial burrow, which is inhabited not only by the female but also by males, probably her sons, and these males grow to the adult stage in the burrow (Takagi, 2003). Such a burrowing may be comparable to gall-inhabitation, but the known gall-inducing diaspidids are limited, and our knowledge as to *the gall-inhabiting mode* in the Diaspididae is still meagre (in this connection, see Takagi, 2007, for cases occurring in the gall-inhabiting coccoid family Beesoniidae).

In other forms scattered in the family, the second-instar female makes the largest amount of growth among the instars. The adult female makes no growth in body size, staying within or below the enlarged exuvial cast of the second instar and, thus, appearing to be under the protection of the latter. These forms, therefore, have been known as pupillarial, representing *the pupillarial mode*.

Though rare and peculiar, cases are also known where the adult females are not covered with any test or nymphal exuvial cast, thus representing *the ‘denudative’ mode*. The most conspicuous characteristic of diaspidids inhabiting galleries constructed by ants in living plants is the absence of covering test (Ben-Dov, 1990). Another case is known in the bamboo-associated odonaspidine *Batarasa lumampao*. The adult female of this species, living on the plant surface, is almost devoid of wax-secreting ducts on the ‘caudal disc’ of the pygidium, thus forming no distinct test; individuals of this stage are crowded closely together on the node of the host stem (where branches grow out), standing on the head, growing to become rather plump, and having their pygidia exposed to the outside of the colony; this species is probably ovoviviparous (Takagi, 2009). It is expected that

their colony is regularly visited and attended by ants.

Another mode of life, which, so far as I am aware, has been unrecorded in literature, is treated in this paper. For explaining it, the noun '*theca*' (a container such as case, sac, sheath, etc.) and the adjective 'thecate' (*thecatus*: having a theca) are adopted, and the compounds 'pre-thecate', 'early-thecate', and 'full-thecate' are used. A new genus is proposed primarily on the basis of two new species, with three other species, also new, added to the genus. The adult females of these five species have the head, the three thoracic segments, and the first abdominal segment all united together to form a sheath-like theca at full growth and in forming a poor test instead. They represent the '*thecatomatic*' or '*thecate*' mode of life.

Males. It should be added that the male insects of the family have five instars: the first instar produces crawlers; the second is primarily devoted to growth exclusively, forming a test along with the growing immobile body or (in a part of the family) by making a little of body movement; the third or the fifth represent the stages of prepupa, pupa, and adult, the last stage being principally provided with well-developed antennae and legs and with a pair of membranous wings on the mesothorax and a pair of halteres on the metathorax.

Abbreviations (in the descriptions and figures of the species). The abbreviations 'prth', 'msth', and 'mtth' stand for the pro-, meso-, and metathorax; 'abd I' to 'abd VIII' for the first to eighth abdominal segments.

Depositories of the holotypes. The holotype of the type species is deposited in the collection of the Museum of Natural History, University of the Philippines at Los Baños, Laguna, the Philippines; the holotypes of the other four species are deposited in the Entomology Division, Forest Research Institute of Malaysia, Kepong, Kuala Lumpur, Malaysia. Specimens of pre-thecate adult females, especially those in good condition, are available not in all the five species, so that full-thecate adult females with the pygidium not retracted, at least not wholly, into the theca [see 1·1., 1) *Theca formation*] are adopted for the holotypes. In fact, the five species are easily distinguishable from each other by comparing their thecae.

1. *THECATOSOMA*, n.g.

The genus is described first on the basis of *T. caudatum* (the type-species) and *T. verticale*, these two being 'starting forms' or 'starters', and then three other species are added and described in comparison with the starters. This genus belongs to the tribe Diaspidini, and is closely related to the genus *Unaspis* MacGillivray, 1921.

Type-species. *Thecatosoma caudatum*, n.sp.

1·1. Adult female

1) *Theca formation*. The pre-thecate body is fusiform, with the prepygidial postsomatic segments well lobed laterally. In the process of growth, the body and especially the meso- and metathorax become elongated; the cephalothorax thus elongated and the first abdominal segment gradually change in outline and sclerotization, and ultimately form a coalescent structure or theca. The completed theca is shaped like an elongate sheath with parallel or subparallel lateral margins, with no trace of the segmental lobes, and heavily sclerotized on the dorsal surface; the ventral surface is

much less sclerotized, even remaining membranous on the first abdominal segment, except a narrow zone along the body margin, which is also thickly sclerotized. The sclerotization of the theca begins at an early stage of the body growth (when the prepygidial postsomatic segments are well lobed laterally) and becomes heavier during the growth, while the second and succeeding abdominal segments remain membranous (except for the originally sclerotic pattern of the pygidium) and little changed in shape. It seems that these membranous segments of the abdomen are retracted partly or wholly into the theca during or after the release of nymphs produced by ovoviviparity.—2) *Antennae*. Each antenna is represented by a thickened and fleshy seta, which arises on the bottom of a vase-shaped dermal pocket, there being no tubercle to bear it. (In a few specimens of *T. caudatum*, an elongate thickened process, probably the antennal tubercle persisting abnormally, has been found near the base of the antennal seta.) It seems that the exterior surface of the pocket is provided with a short minute duct or a pair of such ducts leading to and opening on the interior side of the pocket near the base of the seta. (All these antennal structures are observable in pre-thecate specimens.)—3) *Median gland spine*. A gland spine occurs between the median trullae, with a pair of long filiform microducts (thus suggesting that it has originated from a pair of gland spines fused together).—4) *Macroducts on the pygidium*. The pygidium is provided with marginal macroducts of uniform size occurring on the fourth to seventh abdominal segments and with other dorsal macroducts not numerous and scattered broadly in the space extending from the marginal area of the fourth abdominal segment to the probable seventh abdominal segment (which should be represented by a narrow area arising from the base of the second trulla and extending anteriorly along the midline supposed on the pygidium); these scattered macroducts are generally distinctly smaller than the marginal macroducts, but one of them, situated just in front of the marginal macroducts of the sixth abdominal segment, is as large as the latter.—5) *Trullae (pygidial lobes)*. The pygidial margin is provided with three pairs of trullae, of which the lobes and lobules are all well represented. The median trullae are distinctly non-zygotic, with a gland spine between them as stated in 3), a little sunken into the apex of the pygidium, divergent, and serrate on the mesal margin. The second and third trullae are bilobulate. On the ventral surface, each median trulla and the mesal lobules of the lateral trullae are provided basally with a pair of slender scleroses, which are convergent anteriorly and, on the median and second trullae, much elongated.—6) *Marginal gland spines*. Besides the median gland spine mentioned in 3), single marginal gland spines occur on the fifth to eighth abdominal segments.—7) *Lateral wax-secreting organs*. Short gland spines and small macroducts occur laterally on the fourth and preceding abdominal segments.

The description above is based on the ‘starters’ [see the opening of 1. *Thecatosoma*, n.g.]. Three other species, *T. auriculatum*, *T. gracile*, and *T. crenatum*, agree with the starters in forming a theca, and are treated as members of the genus. Although the individuals available in the latter two of the three species are not sufficient for study, all these species probably undergo the same theca-forming process as that described in item 1) above. On the other hand, the three species have each antennal seta associated with no dermal pocket: in *T. auriculatum* it arises on a tubercle (as usual in the family) and in *T. gracile* and *T. crenatum* it appears to be associated with a shallow dermal depression, there being no tubercle to bear it. Moreover, these three species are provided with no gland spine between the median trullae. They appear, therefore, to be significantly different from the starters concerning items 2) and 3). *T. auriculatum* has dorsal

macroducts scattered on the pygidium as in the starters but more numerous, and none of these macroducts is particularly enlarged in size, so that the agreement is not complete concerning item 4); *T. gracile* and *T. crenatum* have no macroducts scattered on the dorsal surface of the pygidium (on which the marginal macroducts persist and are well represented), and in this character they are plainly different from the other three species (the starters and *T. auriculatum*). Concerning the trullae, item 5), *T. auriculatum* differs from the other species in having the median trullae nearly parallel to each other and little sunken basally, and *T. gracile* and *T. crenatum* are characterized in having the median trullae apparently smaller than the second, with the pair of slender basal scleroses much shortened, and the third trullae replaced with serrate processes. Concerning item 6), *T. crenatum* differs from the other species in having no marginal gland spine on the fifth and sixth abdominal segments. Concerning item 7), *T. gracile* and *T. crenatum* appear to differ from the others in the occurring pattern of lateral gland spines and macroducts, but in the available samples observations on these organs have not been complete. None of the five species described in this paper is provided with perivulvar disc pores except for occasional rudimentary occurrence. (In the descriptions of individual species below, no mention is made as to the rudimentary occurrence, if ever, of this organ. In the family, the presence and absence of these disc pores are sometimes observed among congeneric species. In the case of *Thecatosoma*, there should be a causal connection between their absence and the thecate mode [see 3. Biological significance of various modes of life].)

Test. In the five species referred to the genus, the full-grown adult female is coated with a pale wax cover, which is a size larger than the body and so thin as to show the dark-coloured theca through it. (All this suggests that the body makes no movement when forming the test and that the production of wax is very limited.)

1·2. Nymphal stages

In all the five species, the second-instar females are provided with four single marginal macroducts on each side of the pygidium, which occur on the fourth to seventh abdominal segments. The median and second trullae are well represented and similar in shape to those in the adult females. The third trullae are reduced in development and serrate, variously according to species. No gland spine is found between the median trullae even in *T. caudatum* and *T. verticale*.

The second-instar males have been available in four species and those of three species, *T. caudatum*, *T. auriculatum*, and *T. crenatum*, are figured in this paper. In the three species, they do not agree especially in the marginal processes occurring around the abdomen, but they may belong to a large basic type of the stage in the Diaspidini, showing its variations. (*T. verticale* in this stage, represented by a few specimens in poor condition, is similar to *T. caudatum* in the marginal processes, differing in the occurring pattern of submedian dorsal macroducts.)

The first-instar nymphs of the five species agree in having five-segmented antennae. In other characters, too, they are uniform except for the occurrence of elongate marginal setae around the body in *T. crenatum*.

2. RECOGNITION OF SPECIES

2.1. *Thecatosoma caudatum*, n.sp.

Fig. 1: pre-thecate adult female, teneral. Fig. 2: early-thecate female and fully formed thecae (outlines); second-instar female, exuvial cast (outline; apical margin of pygidium); first-instar female, exuvial cast (antenna). Fig. 9: second-instar male.

Material examined. Collected in Maasin Forest, Brooke's Point, Palawan Is., on *Semecarpus* sp., Anacardiaceae, 22.VIII.1993. Males and females occurring on both surfaces of leaves, females mainly along veins and margin. Mounted specimens examined: 15 pre-thecate, 1 early-thecate, and 26 full-thecate adult females (numbers of wax organs: based on the pre-thecate individuals); 7 second-instar males; exuvial casts of both sexes.

Recognition characters (adult female). *Theca* about 3.2–3.8 times [$n=10$] as long as wide when fully formed, usually broadly rounded on head margin, broadly rounded or almost truncate on posterior end. *Antennae* each represented by a thickened and fleshy seta arising on the bottom of a vase-shaped dermal pocket and projecting outside for its larger part. *Anterior spiracles* each with 4–7 disc pores. *Trullae* in 3 pairs, with lobes and lobules well represented in all the pairs. Median trullae separated from each other basally by a space narrower than one of them, a little sunken into apex of pygidium, divergent, serrate on diverging mesal margins, each basally with a pair of long slender scleroses, which are convergent anteriorly and to be united together, the united part curved sideways. Second trullae bilobulate, with lateral lobule somewhat smaller; both lobules rounded apically, serrate on lateral margin; mesal lobule basally with a pair of long slender scleroses, which are convergent anteriorly but not united together; lateral lobule smaller, basally with a pair of much shorter scleroses. Third trullae with lobules similar to those of the second, a little smaller; mesal lobule with shorter basal scleroses; lateral lobule with no basal scleroses. *Pygidial margin* with 3 low and broad finely serrate prominences on abd V; 2 similar prominences on IV. *Marginal gland spines* occurring between median trullae and on abd V–VIII, all single. *Lateral gland spines* on abd I–IV; 2–10, usually 5 or 6, on I; 3–5 on II and III each; 2, occasionally 3, on IV. *Marginal macroducts* of uniform size 6 on each side of pygidium, single on abd IV and VII, double on V and VI. *Dorsal macroducts* scattered broadly on pygidium from marginal area of abd IV to abd VII, 8–12 on one side, distinctly smaller than marginal macroducts except for one occurring anteriorly to the marginal macroducts of abd VI and as large as the latter; 1 or 2 small submarginal macroducts occasionally on abd III. *Lateral macroducts* occurring on abd I–III, 3–6 on I and also on II, 3–7 on III; 1–3 occasionally on posterolateral corner of mtth, much reduced in size. *Microducts* abundant on ventral surface of mtth especially on lateral lobe.

Remarks. This species is very similar to *T. verticale* [see 2.2, *Remarks*].

2.2. *Thecatosoma verticale*, n.sp.

Fig. 3: pre-thecate adult female, teneral. Fig. 5, A–D: fully formed thecae (outlines); second-instar female, exuvial cast (outline; apical margin of pygidium).

Material examined. Collected in Taman Bako, Sarawak, northern Borneo, on *Ormosia* sp., Leguminosae, 14.X.1991. Males and females occurring on upper surface of leaves, females mainly along margin. Mounted specimens examined: 4 pre-thecate,

1 early-thecate, and ca.50 full-thecate adult females (numbers of wax organs: based on the pre-thecate individuals); several second-instar males (all in poor condition owing to parasitism and other reasons); exuvial casts of both sexes.

Recognition characters (adult female). *Theca* ca.3.6–5.0 times [$n=10$] as long as wide when fully formed; lateral margins subparallel, usually slightly curved outwards on one or both sides (sometimes curved on both sides and symmetrically, making the whole theca narrowly fusiform); vertex with a pair of rounded protuberances or 'humps' laterally; posterior end (posterior margin of abd I) rounded. *Vertex* in pre-thecate body, too, with humps (though they may not always be clearly visible). *Antennae* each represented by a thickened and fleshy seta arising on the bottom of a vase-shaped dermal pocket and projecting outside for a certain apical part. *Anterior spiracles* each with 3–7 disc pores. *Trullae* in 3 pairs, with lobes and lobules well represented in all the pairs. Median trullae separated from each other by a space as wide as one of them, a little sunken into apex of pygidium, divergent, more or less serrate on diverging mesal margins, each basally with a pair of long slender scleroses, which are convergent anteriorly to be united together, the united part gently curved sideways. Second trullae bilobulate, with lateral lobule a little smaller, both lobules rounded apically, obscurely serrate on lateral side, mesal lobule basally with a pair of slender scleroses, which are convergent anteriorly; lateral lobule smaller, basally with no distinct slender scleroses. Third trullae similar to the second, smaller; mesal lobule basally with a pair of short scleroses. *Pygidial margin* with 3 low and broad finely serrate prominences on abd V; 2 similar prominences on IV. *Marginal gland spines* occurring between median trullae and on abd V–VIII, all single. *Lateral gland spines* on abd I–IV; 5–8 on I, 5–7 on II, 5 or 6 on III, 2, occasionally 3, on IV. *Marginal macroducts* of uniform size 6 on each side of pygidium, single on abd IV and VII, double on V and VI. *Dorsal macroducts* scattered broadly on pygidium from marginal area of abd IV to abd VII, 11–13 on one side, distinctly smaller than marginal macroducts except for one occurring anteriorly to marginal macroducts of abd VI and as large as the latter; 1 small submarginal macroduct on abd III. *Lateral macroducts* 4–6 on abd I and also on II, 5–7 on III; 3–7 on mtth, variable in size.

Remarks. *Thecatosoma verticale* is very similar to *T. caudatum* [2:1], but it is peculiar in having a pair of rounded protuberances or humps on the vertex. It seems that the humps are fairly stable in occurrence, and they are clearly visible especially in full-thecate individuals. This species differs from *T. caudatum* also in several other characters: the shorter antennal setae, the stable occurrence of lateral macroducts on the metathorax, and the wider interlobular space of the median trullae. These differences are subtle, but they may support the view that the two are different species. (These two species show a clear difference in the occurring pattern of submedian dorsal macroducts in the second-instar males.)

2.3. *Thecatosoma auriculatum*, n.sp.

Fig. 4: early-thecate adult female. Fig. 5, E–H: thecae (outlines); second-instar female, exuvial cast (outline; apical margin of pygidium). Fig. 10: second-instar male.

Material examined. Collected at 2 localities in Malaya and from 3 species of plants belonging to the family Celastraceae. At Hutan Simpan Mencali, Kuala Rompin, Pahang, on *Lophopetalum floribundum*, Sample 1, and on *Kokoona reflexa*, Sample 2, 17.VIII.1990; At Anak Chelong, Perlis, on *Salacia* sp., 13.XI.1991, Sample 3. Males

and females occurring on lower surface of leaves, females mainly along veins. Mounted specimens examined: 2 full-thecate adult females from Sample 1; 15 full-thecate adult females, several second-instar males, and exuvial casts of both sexes from Sample 2; 2 pre-thecate (poor in condition), 1 early-thecate (with cephalothorax slightly sclerotized dorsally), and 19 full-thecate adult females (numbers of wax organs: based mainly on the early-thecate individual and partly on the pre-thecate ones), 5 second-instar males (generally not good in condition), and exuvial casts of both sexes from Sample 3. Holotype: from Sample 3.

Recognition characters (adult female). *Theca* 3.5–4.7 times [$n=10$] as long as wide when fully formed, more or less broadening posteriorly, with eyes produced laterally, and with posterior end (posterior margin of abd I) truncate; head dorsally with a pair of elongate clusters of many minute and irregular fissures. *Antennae* each represented by a thick seta arising on a tubercle. *Anterior spiracles* each with 3–5 disc pores; posterior spiracles each with 1 disc pore. *Trullae* in 3 pairs, with lobes and lobules well represented in all the pairs. Median trullae separated from each other by a space a little narrower than one of them, parallel to each other, basally not sunken into apex of pygidium, each lobe roundish apically. Lateral trullae with each lobule contracted basally; third trullae a little smaller than the second. Median trullae and mesal lobules of lateral trullae each basally with a pair of long slender scleroses converging anteriorly. *Pygidial margin* with 3 finely serrate prominences on abd V; posterior angle of abd IV also finely serrate. *Marginal gland spines* occurring on abd V–VIII, all single; no gland spine between median trullae. *Lateral gland spines* on abd I–IV, 12–15 on I, 5–9 on II, 3 or 4 on III, 2 on IV; 1 small gland spine present or absent on mtth. *Marginal macroducts* of uniform size 6 on each side of pygidium, single on abd IV and VII, double on V and VI. *Dorsal macroducts* of distinctly smaller size scattered broadly on pygidium from marginal area of abd IV to abd VII, 18 or 19 on one side; 1 submedian and 3–5 submarginal macroducts, the latter arranged in a row, on abd III; 1–3 submarginal macroducts on II. *Lateral macroducts* on mtth and abd I–III, 9–12 on mtth, 10–13 on abd I, 6–8 on II, 4 or 5 on III. *Microducts* abundant in a cluster on lateral lobe of mtth; strewn along margin of msth.

Remarks. There is no reason to exclude this species from *Unaspis* so far as the generic assignment is based on the morphological traits of the adult female other than the formation of a theca. The problem here may be concerned with the biological significance of the thecate mode of life and its consequence in evolution [see 3. Biological significance of various modes of life].

2.4. *Thecatosoma gracile*, n.sp.

Fig. 6: full-thecate adult females (outlines of thecae; pygidium and other features); second-instar female, exuvial cast (outline; apical margin of pygidium).

Material examined. Collected on Bukit Bauk, Terengganu, Malaya, on *Cleistanthus glaucus*, Euphorbiaceae, 10.VIII.1990. Females occurring on lower surface of leaves, especially on midrib; no male tests were found. Full-thecate adult females, 34 individuals in total and some of them with exuvial casts, were mounted. Holotype with pygidium wholly produced from theca and with abd I and II retracted into theca; 2 other females with pygidium produced for most part.

Recognition characters. *Theca* slender, 6.8–9.3 times [$n=10$] as long as wide when fully formed; vertex rounded; posterior end (posterior margin of abd I) truncate; anterior extremity (area enclosed approximately by vertical margin) transparent (not dark-

coloured), the other dorsal surface of the theca sclerotized and dark-coloured. *Antennae* each represented by a thick seta arising from a shallow dermal depression, there being no tubercle to bear the seta. *Anterior spiracles* each with 1 disc pore. *Trullae* in 2 pairs. Median trullae basally sunken into apex of pygidium, each with base intruding into pygidium with a short process pointed at anterior end; separated from each other by a space as wide as one of them, divergent, serrate on diverging mesal margins. Second trullae bilobulate, the mesal lobule distinctly larger than the lateral, both lobules much broader than median trulla, broadly roundish on apical margin; mesal lobule basally with a pair of slender scleroses converging anteriorly to be fused together and then to be united with a fusiform sclerosis; lateral lobule basally with or without rudimentary convergent slender scleroses. *Marginal gland spines* occurring on abd V–VIII, all single. *Lateral gland spines* 2–4 on abd III, conical; probably occurring also on anterior segments (not clearly discernible in the examined specimens). *Marginal macroducts* well represented, single on abd VII, single or double on IV, double on V and VI. *Dorsal macroducts* of smaller size absent on pygidium. *Lateral macroducts* occurring on mtth and abd I–III, a few on mtth, ca. 11–14 on abd I and II combined, 2 on III.

Remarks. This species is easily recognizable in having a slender theca, which is also peculiarly characterized in the head transparent at the anterior end. On the other hand, it is hardly distinguishable from the species described below (*T. crenatum*) by the use of pygidial characters, while the latter, too, has a remarkable theca, which is elaborately crenate on the lateral margins.

2.5. *Thecatosoma crenatum*, n.sp.

Fig. 7: adult female, thecate but not fully. Fig. 8: adult female, pre-thecate (lateral macroducts); full-thecate (outline of theca); second-instar female, exuvial cast (outline; apical margin of pygidium); first-instar female, exuvial cast (antennae; parts of body margin). Fig. 11: second-instar male.

Material examined. Collected at Sepilok Laut, Sabah, northern Borneo, on *Cleistanthus* sp., Euphorbiaceae, 2.XI.1988, Sample 1; in Taman Bako, Sarawak, northern Borneo, on *Sarcotheca* sp., Oxalidaceae, 15.X.1991, Sample 2. Females occurring on both surfaces of leaves, often on lower surface and on midrib and margin; males on lower surface of leaves. Mounted specimens examined: 1 pre-thecate and ca.120 thecate adult females (fully or not fully), 2 second-instar males, and male and female exuvial casts from Sample 1; 7 pre- or early-thecate and ca.80 full-thecate adult females, with exuvial casts of some of them, from Sample 2. (The present study is based mainly on Sample 1 and the pre- and early-thecate adult females from Sample 2. In general, the available specimens of the pre- and early-thecate adult females and the second-instar males are not good in condition). Holotype from Sample 1.

Recognition characters. *Theca* ca.3.0–3.9 times [$n=10$] as long as wide when fully formed, rounded on both anterior and posterior ends, subparallel and elaborately crenate on lateral margins. *Antennae* each represented by a thick seta arising from a shallow dermal depression, there being no tubercle to bear it. *Anterior spiracles* each with 1 or 2 disc pores. *Trullae* in 2 pairs. Median trullae basally sunken into apex of pygidium, each with base intruding into pygidium with a short process pointed at anterior end; separated from each other by a space narrower than one of them, divergent, serrate on diverging mesal margins. Second trullae bilobulate; mesal lobule distinctly larger than the lateral and much broader than median trulla, both lobules broadly roundish on apical margin;

mesal lobule basally with a pair of slender scleroses converging anteriorly to be fused together and then to be united with a fusiform sclerosis. *Marginal gland spines* 3 on each side of pygidium, occurring on abd VII and VIII and also on IV. *Lateral gland spines* 1 on abd I–III each. *Marginal macroducts* well represented, 7 on each side of pygidium usually or normally, 2 on abd IV–VI each, 1 on VII. *Dorsal macroducts* of smaller size absent. *Lateral macroducts* on abd I–III, 1 or 2 opening dorsally and 1 or 2 occurring ventrally on I, 1–3 on II and 2 or 3 on III ventrally, the ventral macroducts each opening at apex of a small process protruding from lateral margin of segment.

Remarks. This species is very similar to *T. gracile* in the characters of the trullae and in having no dorsal macroducts scattered on the pygidium. It is, however, remarkably different not only from *T. gracile* but also from the other known species in having the theca elaborately crenate on the lateral margins. The biological significance of such a peculiar structure of the theca is not understandable in the present state of our knowledge.

In this species, the first-instar nymphs of both sexes are provided with long marginal setae around the body probably for wind-dispersal.

3. BIOLOGICAL SIGNIFICANCE OF VARIOUS MODES OF LIFE

The ordinary diaspidid mode of life prevails in the family Diaspididae, a very successful group in the Coccoidea. 'The difficulty encountered in the chemical control of these insects is largely due to the presence of a scale cover whose chemical properties of hardness and impermeability provide an effective barrier against contact toxicants.' (Foldi, 1990). The chemical control, a recent human factor, has proved the protective potential of the covering against some natural factors, too. Natural enemies may be supposed to be among such factors. In reality, however, parasitic and predatory insects are often very effective in controlling diaspidids as well as other coccoids which have no particular covering.

Here I adopt the view that the primary and main rôle of the diaspidid female test should be for maintaining a relatively stable micro-environment in the space under the waxy cover, probably concerning moisture above all, and in this way for protecting not only the adult female but also the deposited eggs and newly hatched crawlers, the next generation, in particular. Provided other conditions are the same, broader coverings may be more effective for performing that rôle. In fact, a shift to the construction of a broader, ultimately circular, female test is an evolutionary trend observable in parallel among diverse groups of the family. It should be added, however, that the reverse change, from a broad test to a narrower one, also takes place according to circumstances (Takagi and Tippins, 1972). Not only the manner but also the occurrence and cessation of body movement in test construction may change not unidirectionally.

Matsuda (1927) made a detailed study on the test formation in an aspidiotine scale insect ('*Chrysomphalus aonidum*'), of which the female test represents a circular type. (He summed up the results by the use of some drawings on one plate, of which a copy is made in this paper [Appendix II, Fig. 15]). His study and a few others made thereafter by himself and other authors show how laborious the construction of a female test in the ordinary diaspidid mode is. It involves clockwise and anticlockwise movements of the body repeated so many times, production of wax filaments and excretion of anal substance both in co-operation with the body movements, repairs of the ceiling of the test under construction, and so on. All this should be common to the construction of female

tests in the ordinary mode, whether they are circular or narrow. Needless to say, such a work is maintained so far as it is adaptive. Whenever the ecological circumstances are changed and the adaptive value is lost, it will be ceased.

The other modes of life—burrowing, gall-inhabiting, denudative, pupillarial, and thecate modes—apparently all started from the ordinary diaspidid mode directly or ultimately in origin. They agree in their success in lightening or sparing by their respective ways the female's work devoted to test construction. The burrowing and gall-inhabiting modes, and some cases of the denudative mode, have arisen from the changes of their inhabiting sites into some covered or closed spaces on the host plants. The case of *Batarasa lumampao* should be associated with ovoviviparity (no oviposition accordingly) and may be maintained by a crowding of female individuals in a narrow half-closed space on the host plant and regular attendance by ants.

The pupillarial and thecate modes should have required some morphogenetic changes for their arising. The pupillarial forms are broadly scattered in the family, so that the necessary morphogenetic change should have occurred frequently. However, it is not clear under what circumstances it took place.

The thecate mode of life is very rare so far. The only known thecate genus *Thecatosoma* is closely related to *Unaspis*. In the latter genus, as marked (though not general) tendencies, the adult females have the test ridged medially, the perivulvar disc pores reductive in number, rudimentary, or obsolete, and the cephalothorax and first abdominal segment sclerotized dorsally at full growth. What these tendencies suggest may be as follows: first, the females of *Unaspis* species (probably many species) do not make any movement when forming the test (thus shaping on the test a median ridge, which reflects the arrangement of dorsal macroducts on the pygidium); secondly, they are not oviparous but ovoviviparous (so that having the perivulvar disc pores poorly represented or obsolete [these disc pores in their normal function are to powder eggs with wax probably at the time of oviposition; in scanning electron microscopy, they produce wax rings, which are so minute as to make the wax powder]); thirdly, they protect eggs, which develop into the nymphal stage within the maternal body, by making the dorsal body surface of a sclerotized cover.

Thecatosoma arose undoubtedly from *Unaspis* through the morphogenetic change of the cephalothorax and basal abdominal segment into a theca or a sheath-like coalescent structure, which should be a much firmer container for eggs developing within the maternal body, thus representing a reformation of the adult female body in association with ovoviviparity. This is well shown by one of the known species, *T. auriculatum*, which does not differ from *Unaspis* species in every respect except for the formation of the theca in the last period of growth. It seems certain that *Thecatosoma* could not arise without the biological attributes of *Unaspis*, which provided some preceding conditions indispensable for the appearance of the former. This supposition may even cause a doubt about the distinctness of *Thecatosoma* from *Unaspis*. However, *Thecatosoma* as represented by the five known species has the morphological variation much broader than in *Unaspis* in spite of the much fewer species. The species of *Thecatosoma* as a whole should not be the same as *Unaspis* in some biological aspects and, accordingly, in evolutionary potential, further species being expected to show further variations.

4. Taxonomic treatment of thecate species

The five species of *Thecatosoma* are divisible into three sorts. *T. caudatum* (type-species) and *T. verticale* belong to the first sort, which are characterized in having each antennal seta arising from the bottom of a deep dermal pocket, there being no tubercle to bear it (at least normally [see 1·1. Adult female]), and in possessing a distinct gland spine between the median trullae. Another sort is represented by *T. auriculatum*, which does not differ from *Unaspis* species except for the formation of the theca. The third consists of *T. gracile* and *T. crenatum*; these species have each antenna represented by a seta not arising on a tubercle (as in the first sort) but lying on a shallow dermal depression; they possess no macroducts on the pygidium except for the marginal ones, which are well represented; and they have only two pairs of trullae. These three sorts appear to be distinct from each other, there being no intermediate or connective forms, while each of them shows an unmistakable resemblance to *Unaspis* in some of their characters.

In a possible interpretation, which may suppose an extreme case, the three sorts should represent different lineages originated from *Unaspis* species independently, and the thecate development of the body should be an infrageneric phenomenon of *Unaspis*, occurring frequently within the genus [see Appendix I]. In another possible interpretation, which may be a routine thinking, they are fragments from a broader group, and there should be unknown forms which connect the three sorts into a single lineage. In any case, the available thecate species are too few to proceed further with the taxonomic treatment of them.

In concluding this paper, several matters should be mentioned. 1) *T. auriculatum* apparently represents an incipient form of *Thecatosoma*, the pre-thecate adult female of this species being closely similar to '*Unaspis acuminata*' [see Appendix I]. 2) The occurrence of the antennal seta in a deep dermal pocket in *T. caudatum* and *T. verticale* may be an adaptation to the incorporation of the head in the theca. 3) In *T. gracile* and *T. crenatum* each antennal seta lies in a shallow dermal depression, which may represent another adaptation and, on the other hand, an evolutionary step preceding the development of a dermal pocket. 4) *T. gracile* and *T. crenatum* have no small dorsal macroducts scattered on the pygidium. *T. caudatum* and *T. verticale* have the small dorsal macroducts on the pygidium apparently decreased in number. On the other hand, they have a submarginal macroduct on each side of the sixth abdominal segment enlarged and as large as the marginal macroducts. This condition suggests the possibility that, in the latter two species, pygidial wax filaments are largely or wholly produced by these marginal and submarginal macroducts. 5) The occurrence of a gland spine between the median trullae in *T. caudatum* and *T. verticale* may be of atavistic nature. It is probably a phenomenon parallel to the occurrence of a gland spine between the median trullae in *Chionaspis caudata* Vea et al. (2012) concerning the underlying genetic and developmental mechanisms. 6) I once asked why the Conchaspidae (constructing remarkable tests) were so poorly represented in contrast with the Diaspididae. Scanning electron microscopy made on five species of *Conchaspis* occurring in tropical Asia revealed a substantial difference in the internal structure of the tests between the two families, and I concluded that the difference in the manner of test construction should have taken part in the causation of the difference in evolutionary diversification between these families (Takagi, 1992; 1997).

APPENDIX I: *THECATOSOMA AURICULATUM* AND '*UNASPIS ACUMINATA*'

Excepting the formation of the theca, there is no reason to exclude *Thecatosoma auriculatum* from *Unaspis*. I have found in my collection many samples of *Unaspis* which are closely similar to the pre-thecate stage of *T. auriculatum*. Figures of the adult female (Fig. 12) and the second-instar male (Fig. 13), drawn from one of the samples, are given here for comparison with *T. auriculatum* (Fig. 4, Fig. 10). I am inclined to believe that the sample belongs to *Unaspis acuminata* (= *Chionaspis acuminata* Green), the type-species of *Unaspis*. Green (1899) redescribed the species, and Pl. XLV in his redescription is copied here for comparison (Fig. 14). [I have failed to find reliable descriptions and figures of *Unaspis acuminata* in later publications.]

In a foregoing part of this paper I have tried to settle the problem of the generic distinctness of *Thecatosoma* from *Unaspis* on the basis of a biological viewpoint [see 3. Biological significance of various modes of life]. However, the combination of *T. auriculatum* and '*U. acuminata*' [identified rather tentatively] suggests the possible occurrence of further combinations of closely similar species which are divided into *Thecatosoma* and *Unaspis*. When such combinations really exist, the theca formation will be no more than an infrageneric phenomenon of *Unaspis* and *Thecatosoma* will be no taxonomic unit in any sense. The problem of the thecate species concerning their evolutionary relationships and our taxonomic treatment still wait for the discovery of further material [see 4. Taxonomic treatment of thecate species].

APPENDIX II: MATSUDA (1927) ON TEST CONSTRUCTION

Matsuda (1927) made a detailed study on the test formation, especially on the construction of the female test, in the aspidiotine scale insect '*Chrysomphalus aonidum*', in Formosa (Taiwan). He planted a *Citrus* sapling (ca.15cm tall) in a pot (21cm in diameter) somewhat apart from the centre of the pot, and released about 20 crawlers on the leaves; he fixed on the pot a microscope ($\times 60$) combined with a camera lucida. Observations with this device were made indoors day and night; at intervals, the whole device was removed outdoors to be put in the sun for keeping the sapling alive.

In his preliminary observation, Matsuda noticed that a wet point appeared on the dorsal surface of the female test under construction, making the point translucent, and after a short time (about one minute) another wet point appeared at another position nearby. He interpreted this phenomenon as the expelling of the anal substance which shifted its position in association with the movement of the female body in test construction.

He started his observations on the seventh of August, 1927. The main task was to trace wet points appearing on the test with occasional interruptions and to record their positions with the use of the camera lucida. The enlarging of the test represented by the increasing diameter stopped on the seventeenth of September, and on the twentieth the leaves fell off the sapling.

His text is written in Japanese, with 22 tables of data. He summed up the results of his observations in six pieces of drawings on one plate with explanations in English. In this paper, his drawings are copied in Fig. 15 and his explanations are transcribed below.

Explanations of the drawings in Fig. 15:

Fig. 15. Drawings from Matsuda (1927): a summing-up of his study on test formation in '*Chrysomphalus aonidum*'. 1: female scale (E: exuviae, R: rings on scale). 2: male scale (E: exuviae, R: rings on scale). 3: pygidium of adult female (a: anal opening, L: lobes, S: spinnerets, t: thickenings, V: vulva, W.P.: wax pores). 4: female and its scale upturned (a: body, b: scale, c: posterior end of scale, d: excretion from wax pores indicating moving of female from c). 5: apex of pygidium extruding out of margin of scale; arrows indicate the direction of movement. 6: formation of scale in one female; the numbers indicate the date Sept. 1 to 17, 1927 (a: first moulting, b: second moulting, c: scale of second larval instar; arrows indicate the direction of movement). [It is conceivable from his paper and especially from Drawing 6 (there being no detailed explanation by him) that the recorded positions of wet points should have connected together successively to make a circular line every day, and also that the female body should have grown in the night-time without making movement under nocturnal conditions (no light; declining air temperature).]

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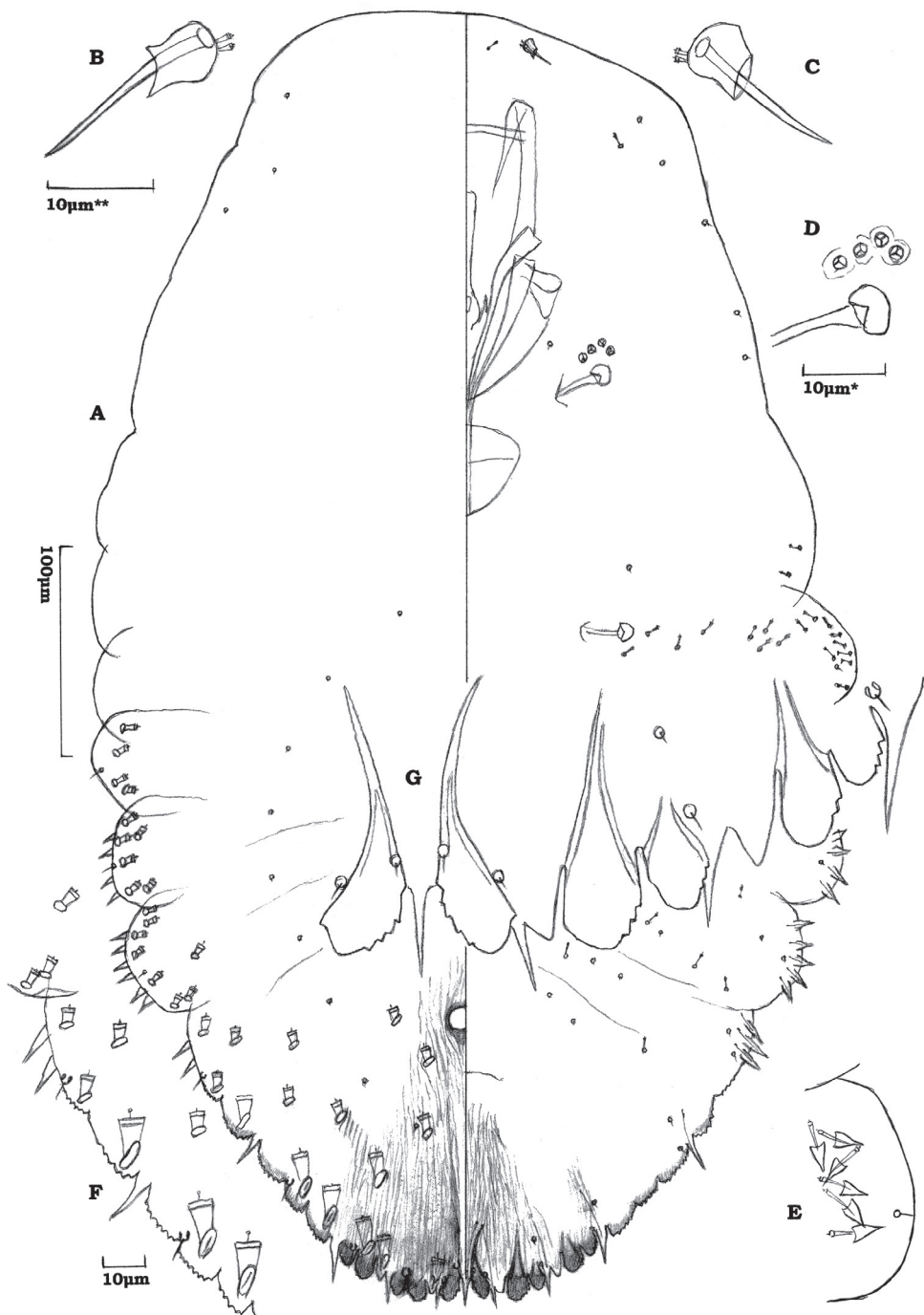


Fig. 1. *Thecatosoma caudatum*. Adult female, pre-thecate, teneral. B, C: antenna; D: disc pores associated with anterior spiracle; E: gland spines on lateral lobe of abd I, ventral surface; F: abd IV, V, margin, dorsal surface; G: trullae, ventral surface. Scale bars: 10µm, for E, F; 10µm*, for D; 10µm**, for B, C, G; 100µm, for A.

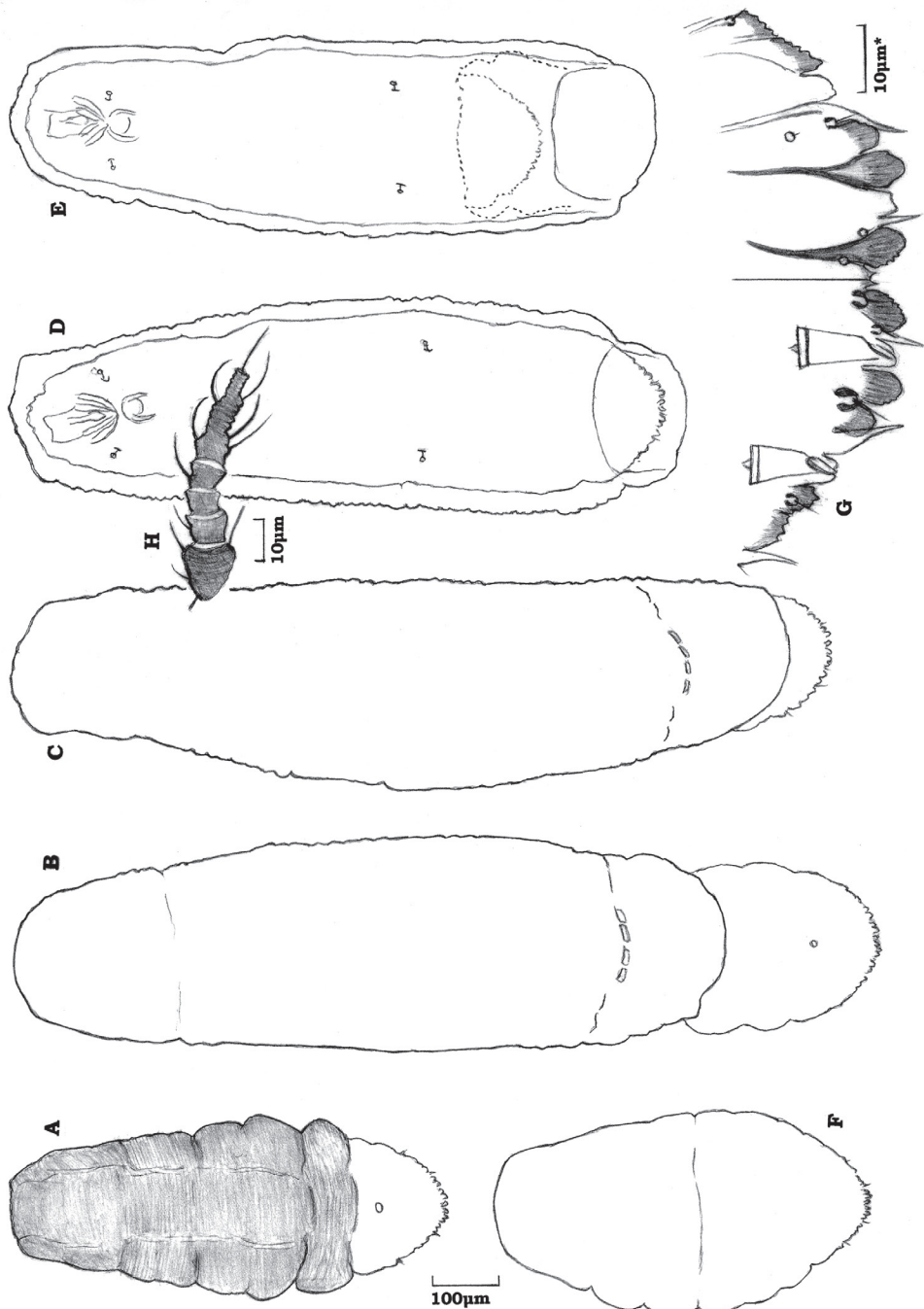


Fig. 2. *Thecatosoma caudatum*. A–E: adult female, outline; A: early-thecate, dorsal surface; B–E: full-thecate; B, C: dorsal surface; D, E: ventral surface; F, G: second-instar female, exuvial cast; F: outline; G: pygidial margin, apex; H: first-instar female, exuvial cast, antenna. Scale bars: 10µm, for H; 10µm*, for G; 100µm, for A–F.



Fig. 3. *Thecatosoma verticale*. Adult female, pre-thecate, teneral. B, C: antenna (B represented by 2 setae probably abnormally); D: anterior spiracle; E: pygidial margin, ventral surface. Scale bars: 10µm, for B–E; 100µm, for A.

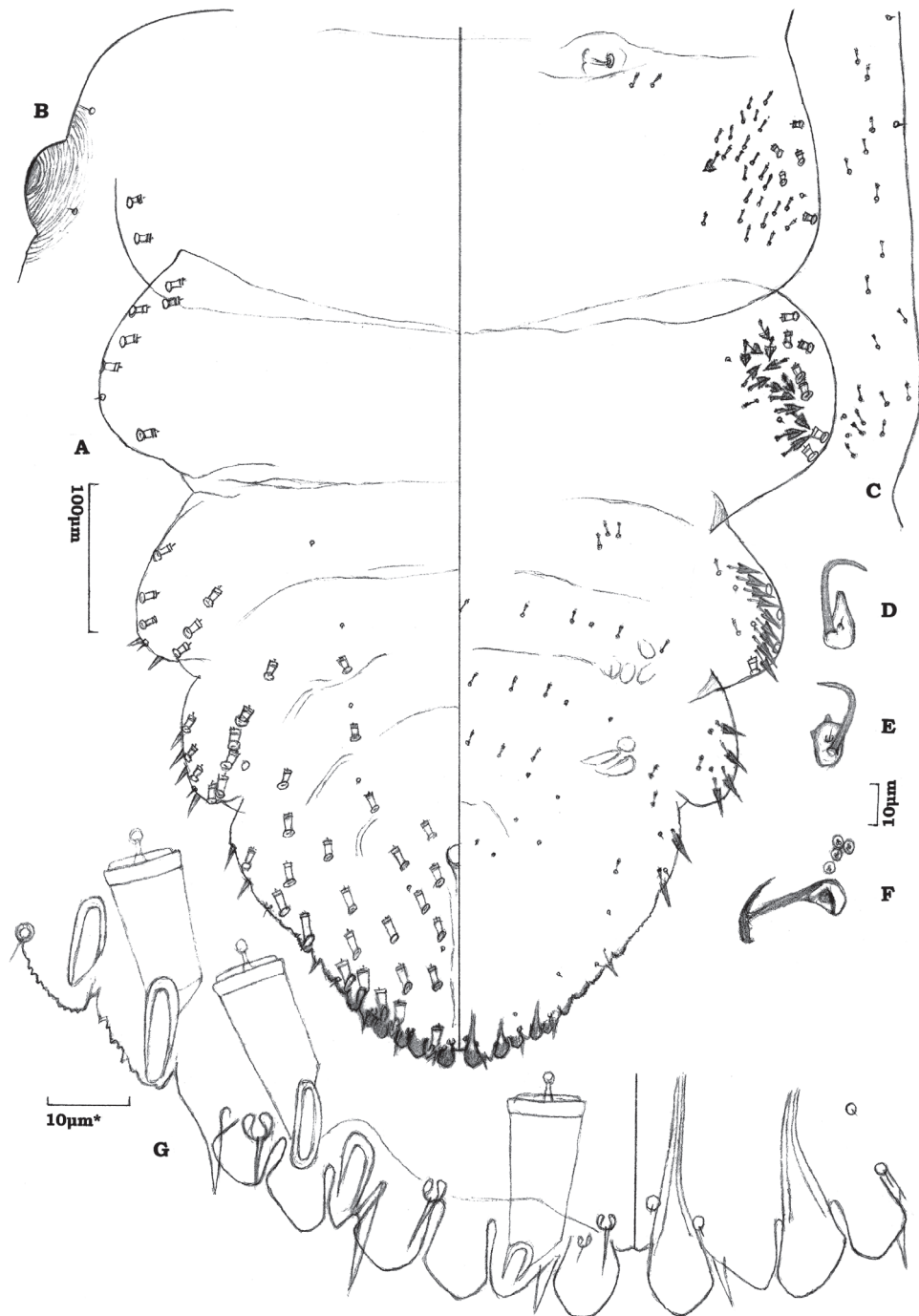


Fig. 4. *Thecatosoma auriculatum*, Sample 3. Adult female, pre-thecate. A: postsoma; B: eye; C: msth, margin, ventral surface; D, E: antenna; F: anterior spiracle; G: trullae. Scale bars: 10µm, for D–F; 10µm*, for G; 100µm, for A–C.

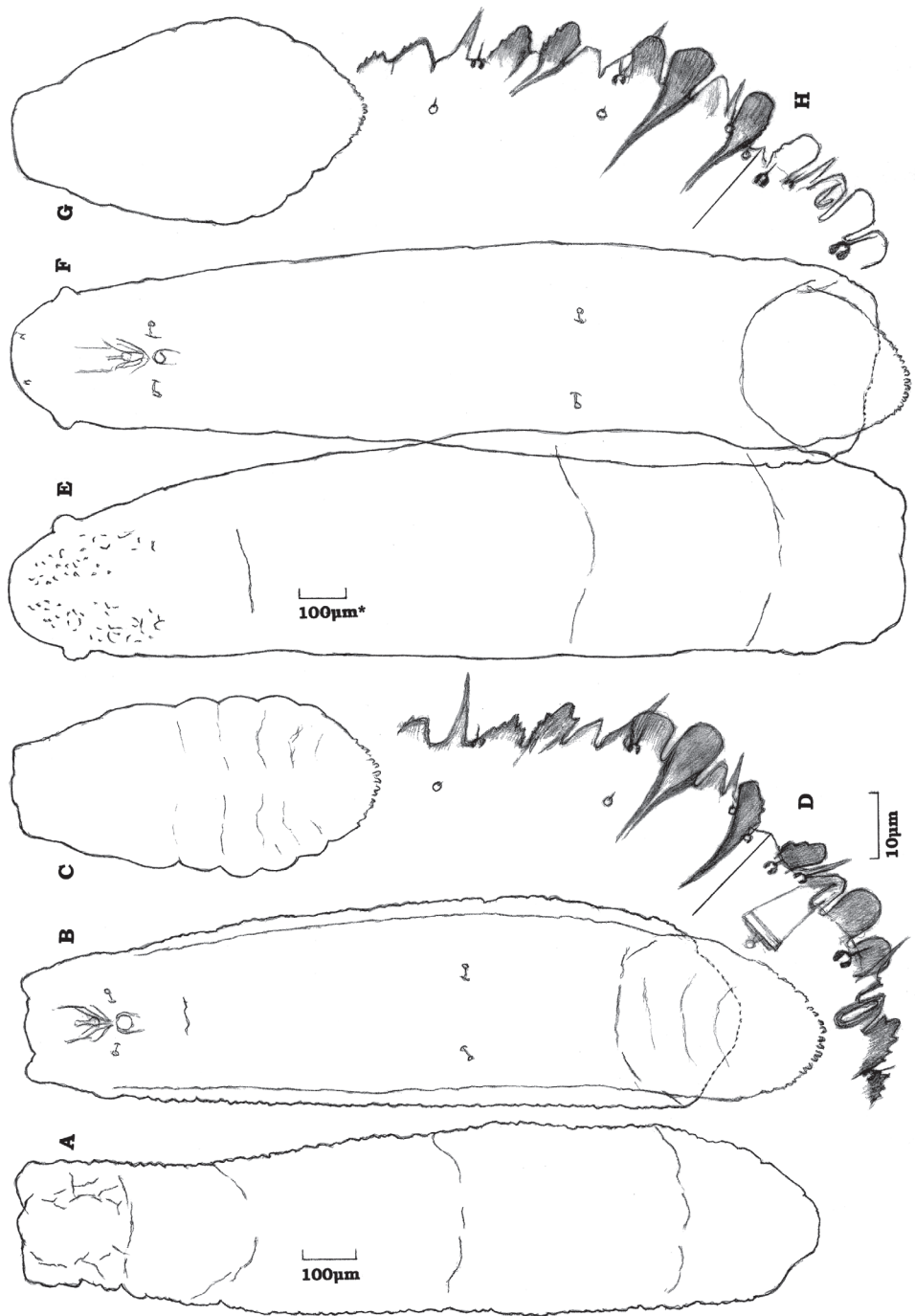


Fig. 5. A–D. *Thecatosoma verticale*. A, B: adult female, full-thecate, outline; A: dorsal surface; B: ventral surface; C, D: second-instar female, exuvial cast; C: outline; D: pygidial margin, apex. E–H. *Thecatosoma auriculatum*, sample 2. E, F: adult female, full-thecate; E: dorsal surface; F: ventral surface; G, H: second-instar female, exuvial cast; G: outline; H: pygidial margin, apex. Scale bars: 10µm, for D, H; 100µm, for A–C; 100µm*, for E–G.

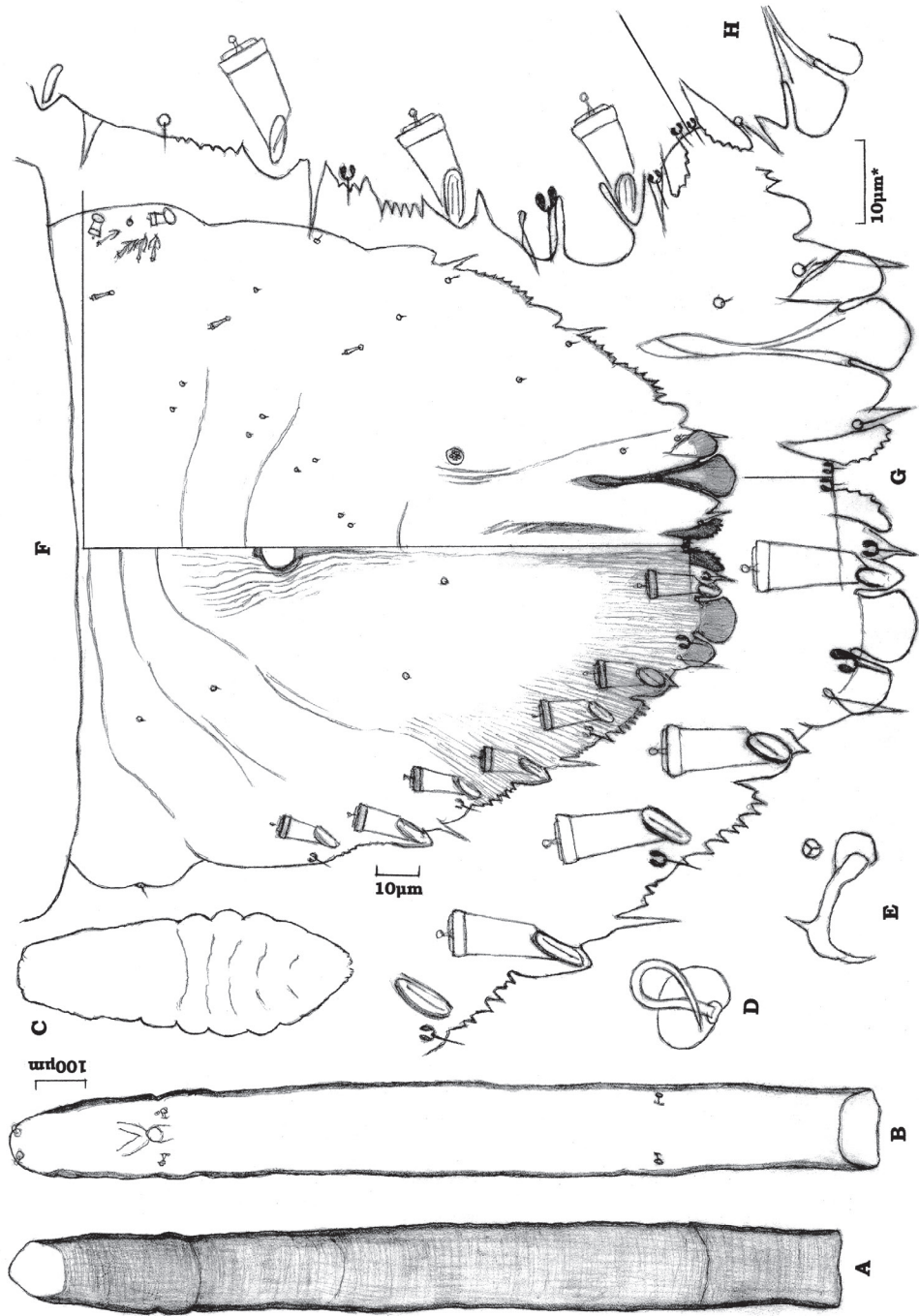


Fig. 6. *Thecatosoma gracile*. A, B, D–G: adult female, full-thecate; A, B: theca; A: dorsal surface; B: ventral surface; D: antenna; E: anterior spiracle; F: pygidium (produced from theca); G: pygidial margin, apex; C, H: second-instar female, exuvial cast; C: outline; H: pygidial margin, apex. Scale bars: 10µm, for D–F; 10µm*, for G, H; 100µm, for A–C.



Fig. 7. *Thecatosoma crenatum*, Sample 1. Adult female, nearly full-thecate. A: theca, outline (with pygidium produced); B: antenna; C: anterior spiracle; D: abd II, III, lateral lobe, ventral surface; E: pygidium (produced from theca); F: pygidial margin, apex. Scale bars: 10µm, for E; 10µm*, for D, F; 10µm**, for B, C; 100µm, for A.

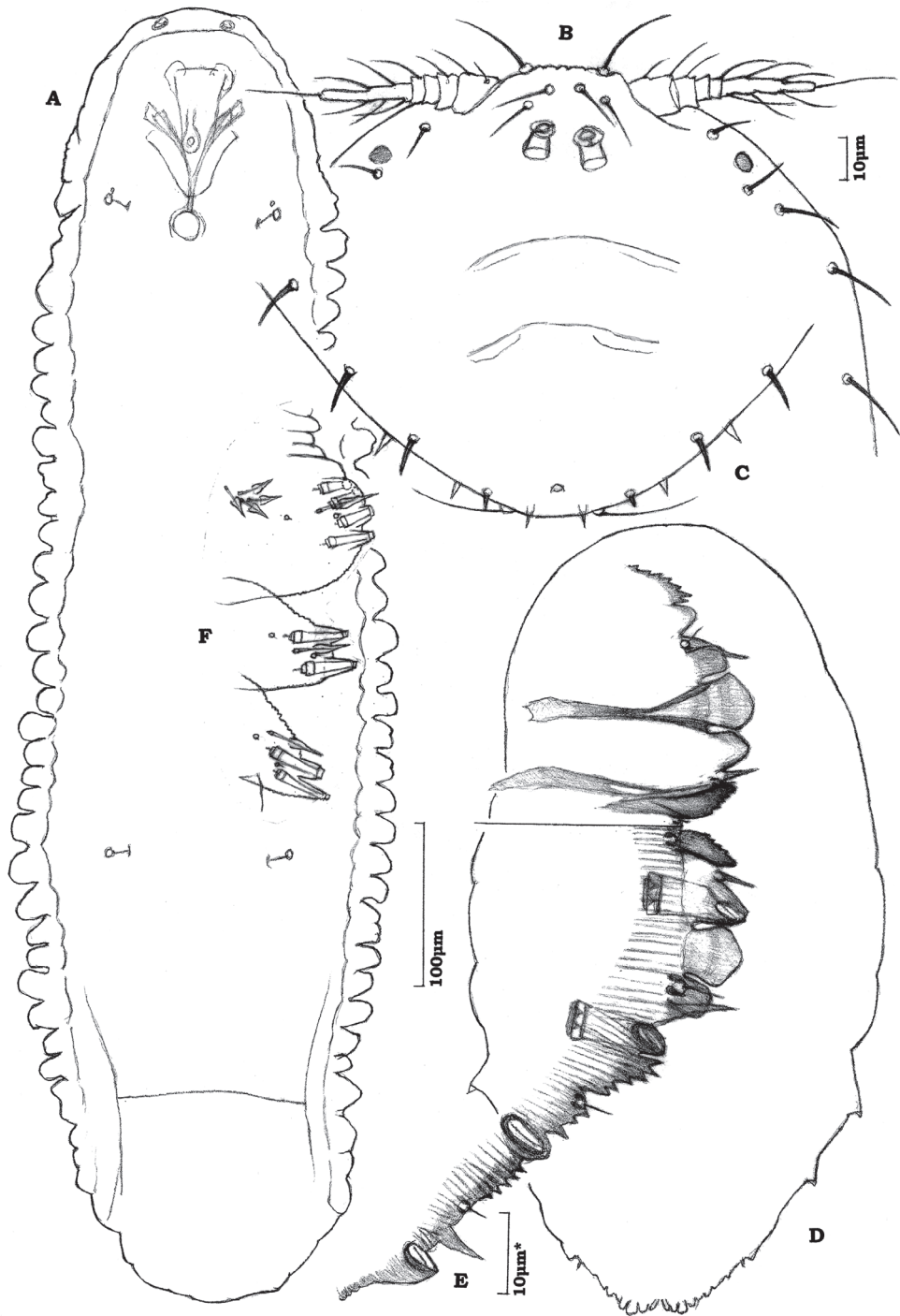


Fig. 8. *Thecatosoma crenatum*, Sample 1. A: adult female, theca, ventral surface; B, C: first-instar female, exuvial cast; B: head; C: posterior end; D, E: second-instar female, exuvial cast; D: outline; E: pygidial margin; F: adult female, pre-thecate, abd I-III, lateral lobes, ventral surface. Scale bars: 10µm, for B, C, F; 10µm*, for E; 100µm, for A, D.

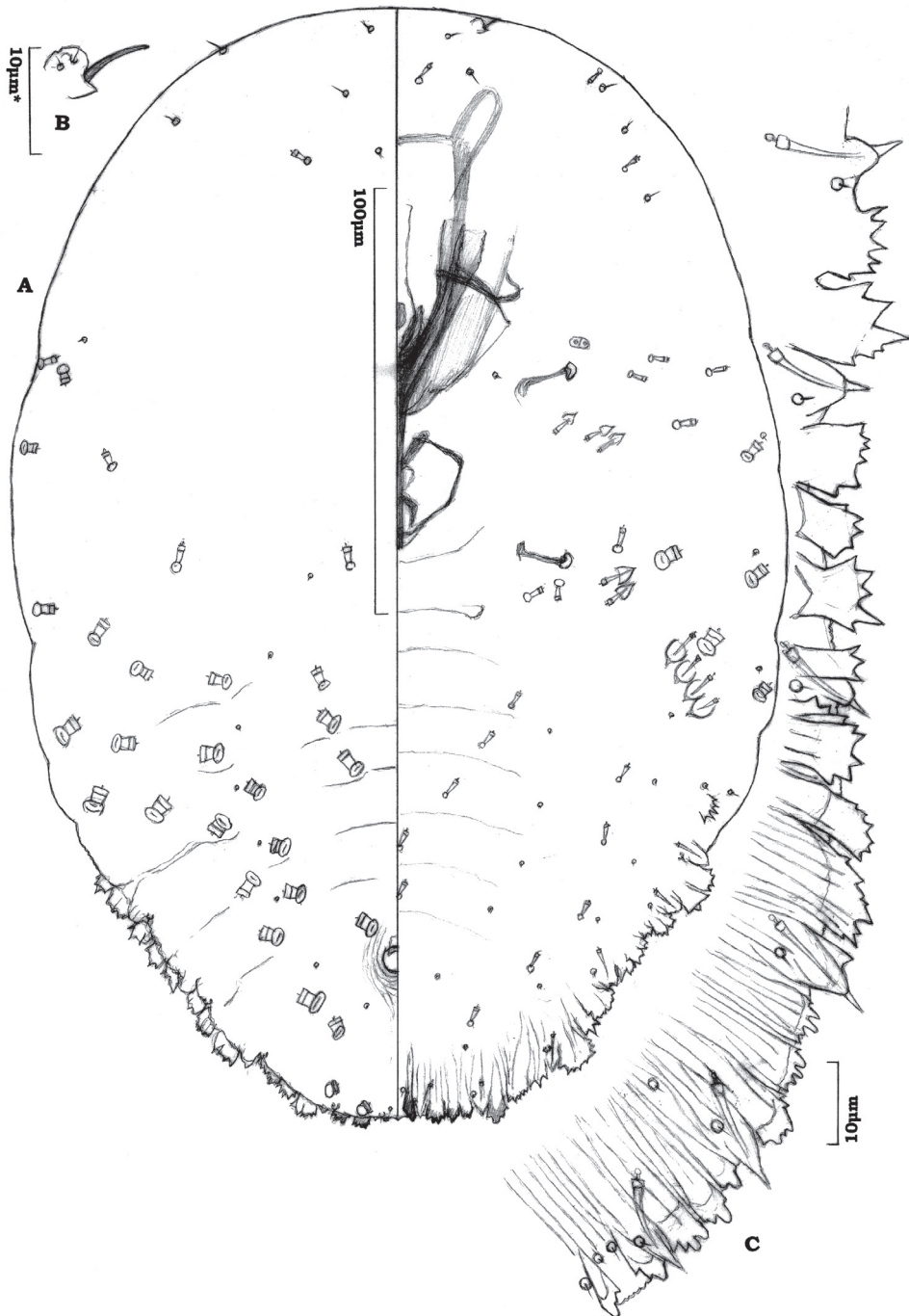


Fig. 9. *Thecatosoma caudatum*. Second-instar male. A, B: teneral; B: antenna. C: growing individual, processes on body margin, ventral surface. Scale bars: 10µm, for C; 10µm*, for B; 100µm, for A.



Fig. 10. *Thecatosoma auriculatum*, Sample 3. Second-instar male. B: antenna; C: processes on body margin, ventral surface; D: margin of abd IV, V, dorsal surface. Scale bars: 10µm, for C, D; 10µm*, for B; 100µm, for A.

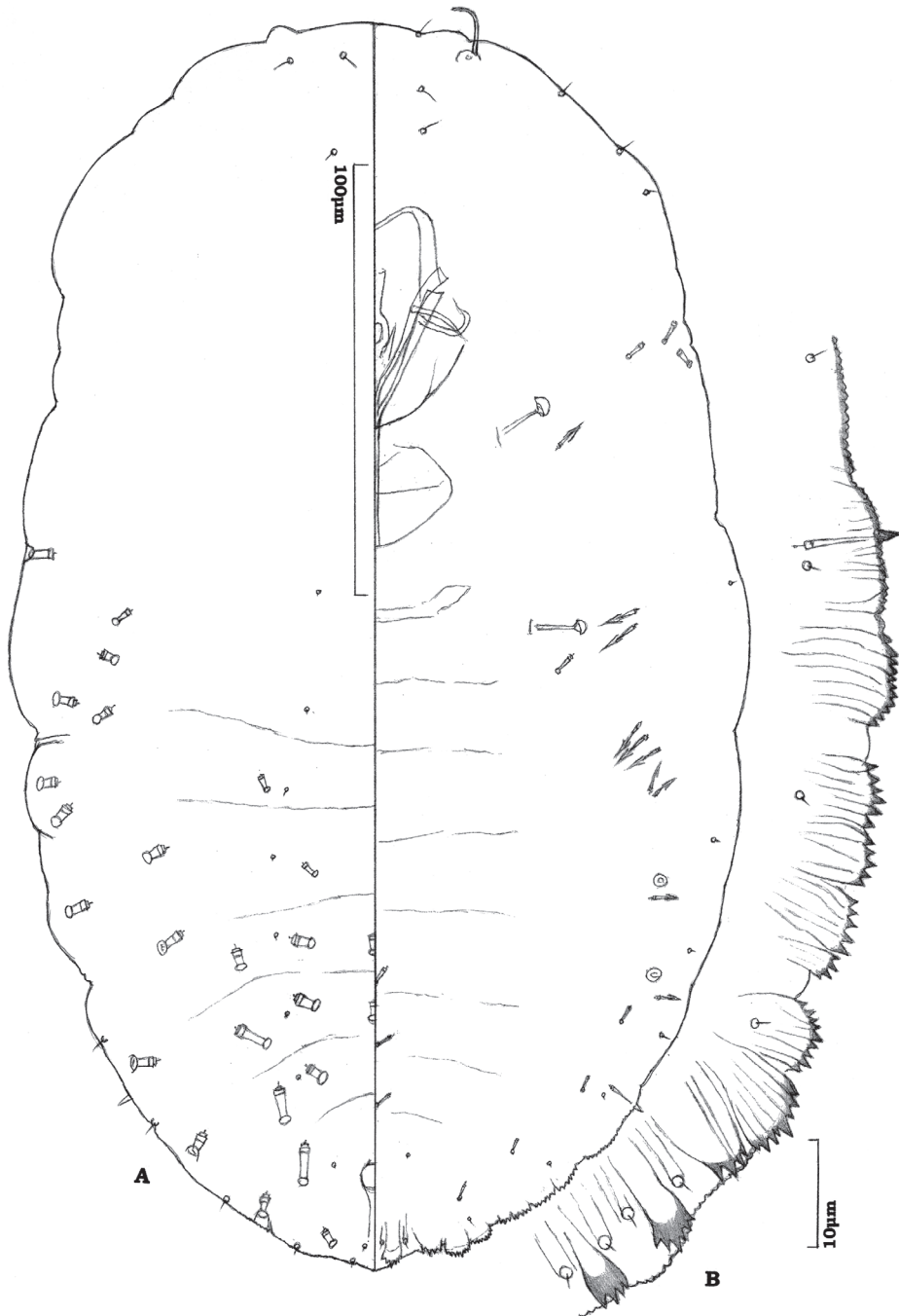


Fig. 11. *Thecatosoma crenatum*, Sample 1. Second-instar male. B: processes on body margin, ventral surface. Scale bars: 10µm, for B; 100µm, for A. [Drawing A may not be complete owing to the condition of the specimen.]

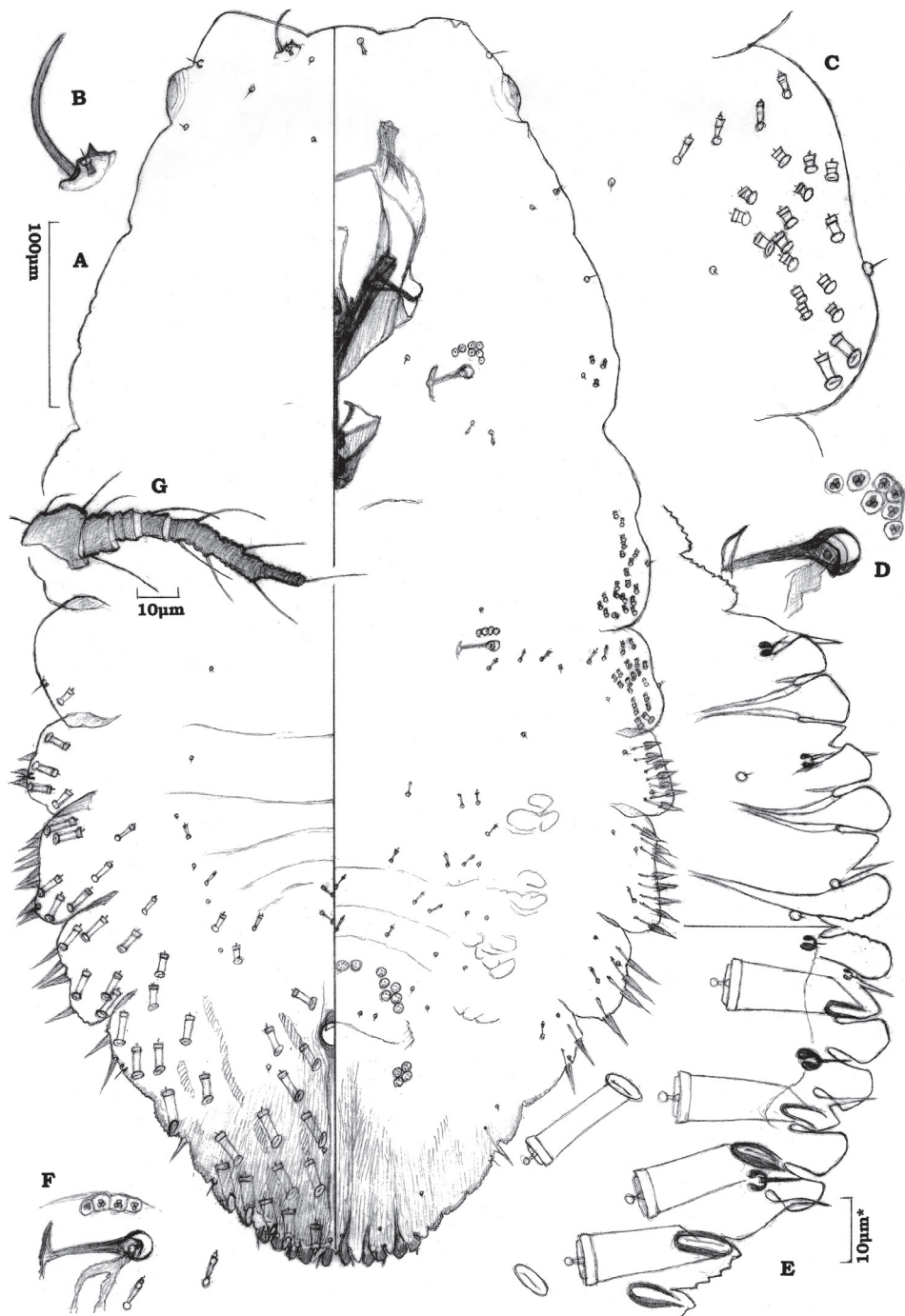


Fig. 12. '*Unaspis acuminata*' [tentative identification]. Dhoni Forest, Palghat, Kerala, alt. ca.400m, on *Hydnocarpus* (?) sp., leaf., 7.XII.1978. Adult female, teneral. B: antenna; C: mth, lateral lobe, ventral surface; D: anterior spiracle; E: pygidial margin, apex; F: posterior spiracle. G: first-instar female, exuvial cast, antenna. Scale bars: 10µm, for G; 10µm*, for B-F; 100µm, for A.

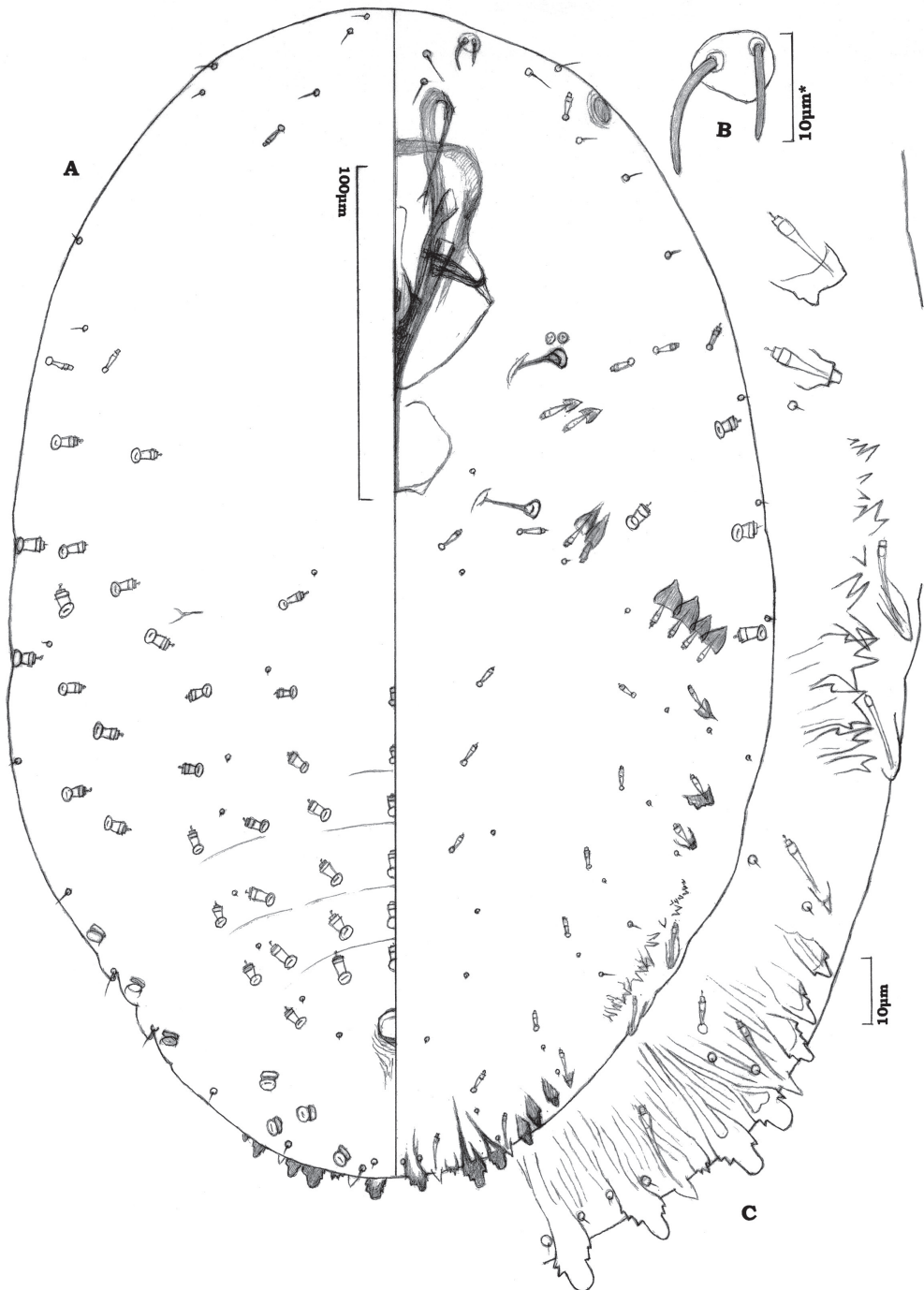


Fig. 13. '*Unaspis acuminata*'. Same sample as the adult female in Fig. 12. Second-instar male. B: antenna; C: marginal processes on body margin, ventral surface. Scale bars: 10µm, for C; 10µm*, for B; 100µm, for A.

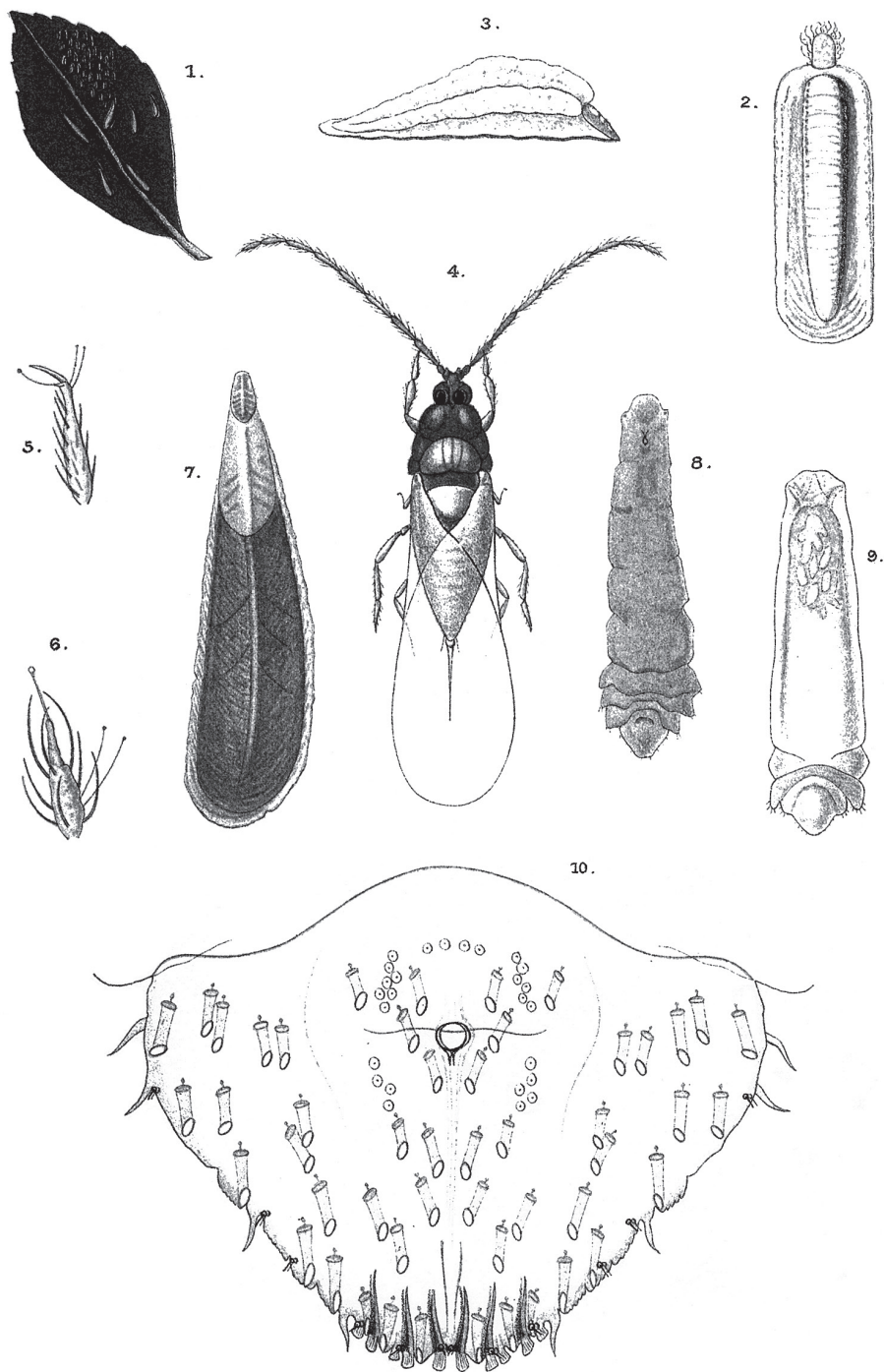


Fig. 14. *Chionaspis acuminata* in Green (1899), Pl. XLV. Pundaluoya, Ceylon. 1: leaf with insects *in situ*. 2, 3: male puparium; 2, dorsal view; 3, side view. 4–6: adult male; 5, foot; 6, terminal joint of antenna. 7: female puparium, dorsal view. 8–10: adult female; 8, ventral view; 9, older example, dorsal view; 10, pygidium.

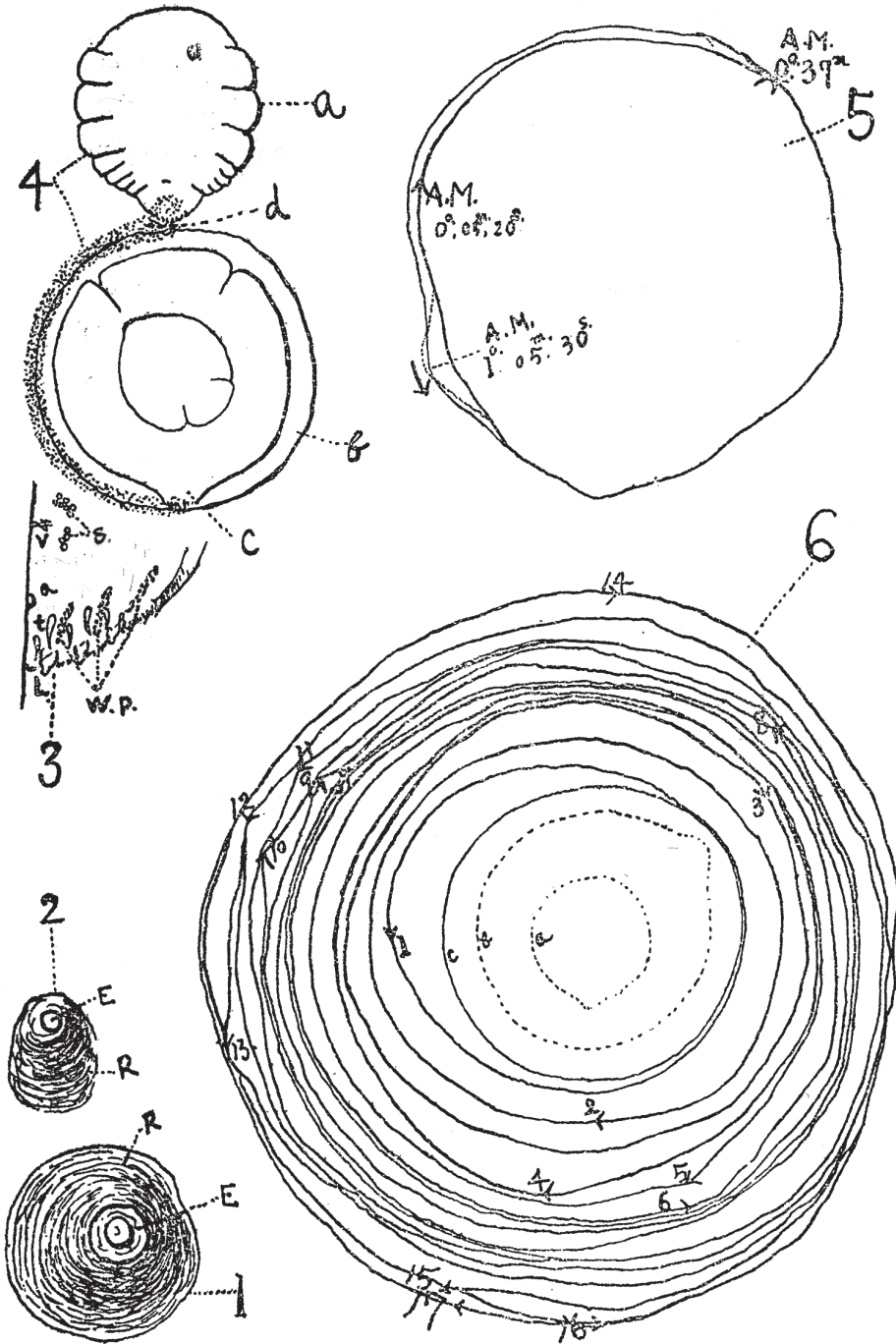


Fig.15. Drawings from Matsuda (1927). His explanations of the drawings are translocated for space to the end of the section 'Appendix II. Matsuda (1927) on test construction'.