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Formation of the monomerous female antenna in *Diaspis echinocacti* (Bouché) 1833 (Rhynchota Diaspididae). I. The second instar antenna

Abstract - Previous authors have described the adult Diaspididae (Coccoidea) antenna as bearing very few or no strutures. But a recent paper demonstrated the full sensory function of the small seta placed on the adult female antenna of *Diaspis echinocacti*. In order to clarify the nature of the female antenna, this paper discusses the question of formation of the uniarticulate second instar antenna as it is tranformed from the six-segmented first instar antenna. Based on interpretation of the results of amputation experiments, the authors hypothesize that the uniarticulate second instar antenna is formed as a result of a fusion of all the articles of first instar antenna. It is suggested that this fusion process is common to all Diaspididae. This study suggests that we should indague on the adult female antenna in others species of *Diaspis* 1828 for joined seta, and eventually to evaluate the importance of the character into the systematic of the taxon. We further suggest that the adult female of other Diaspis species should be examined to evaluate the importance of antennal structures as characters that can be used in systematics.

Key words: Catametabolism, armoured scale, regeneration.

INTRODUCTION

The abrupt transformation that occurs between the first and the second instar female of *Diaspis echinocacti* involves radical changes in the morphology of the antennae (Ben-Dov, 1990a; 1990b; Takagi, 1990) as well as dramatic changes in other structures. This sudden morphological change occurs early in post-embryonic development, giving rise to a second instar that is very different from the crawler. No further reduction occurs between the second and the third stage – the adult (Koteja, 1990).

There are two possible hypotheses for reduction of the antenna in the second instar: (A) loss of distal, intermediate or proximal antennomeres with the second instar monomere being formed from one article of the antenna of crawler and/or (B) fusion of all or some of the first instar antennomeres in various ways or degrees. To determine which of these hypotheses is most likely we decided to investigate the process amputating different parts of the antennae in the crawler. It is important to point out that only part of hypothesis (A) could be tested because it is not possible to amputate intermediate antennomeres of the crawler without also amputating the more distal ones.

The amputation of appendages - parts or whole - is an important chapter in biological research on the regeneration of tissues and appendages in insects (Bullière & Bullière, 1985). However, the experiments here reported are focused on the *non regeneration of wounded parts* so that the rules of regeneration and morphogenesis do not apply to this paper.

Diaspididae offer an ideal experimental system for studying the impact of amputation on first instars because of the peculiar mode of scale cover formation which incorporates the exuvia of the first instar. The scale cover of an experimentally altered second instar contains the exuvia of the amputated first instar which is available for examination to check details of excision in each experiment. There is no question that the crawler exuvia incorporated in the scale cover developed into the altered second instar.

We make the basic and obvious assumption that the antenna of the crawler is homologous to the antenna of the second instar and that the former is transformed into the latter during the moulting process.

MATERIAL AND METHODS

Mass rearing

All the observations were made using crawlers of *D. echinocacti* that were mass-reared on cladodes of prickly pear [*Opuntia ficus-indica* (L.) Mill.] growing in our laboratory at room condition (Rose, 1990).
The colony was started from crawlers collected in the field.

Antenna excision

Antennomere amputations were made using a dissecting binocular microscope and a tungsten scalpel made by the authors. To avoid damage from shaky hands a Plasticine hand-support was used next to the dissecting microscope.

Just fixed crawlers was chosen for amputation; this stage was identified because the crawlers were not walking anymore and there was still no wax secretion. This was important because during the moult the antennal tissues are retracted into the body and they wouldn't have been cut during amputation.

Experimental specimens were labelled with consecutive number drawn directly on the host plant.

Surrounding crawlers were removed to avoid any question about the identity of a particular specimen at the time of the recovery. Notes were made in a lab book recording the antennomere that was cut from the specimen identified by the number etched on the host plant next to the feeding crawler.

Specimen preparation and specimen tracking

The occurrence of the moult between the first and second instar was detected by the appearance of a new white wax secretion around the perimeter of the crawler. As soon as the second instar secretion was completed each specimen was collected with its scale cover and placed in a numbered methacrylate vial. The second instar and the scale cover (including the first instar exuvia) from each methacrylate vial were left soaking overnight at room temperature in a mixture of Sodium Hydroxide (NaOH, 25 gr.), Sodium laurylsulphate (CH3(CH2)11OSO3Na, 25 gr.), hand dishwashing liquid soap (25 ml.) and distilled water (up to 500 ml.). A small cut was made on one side of the second instar body. The NaOH mixture was replaced several times in order to remove all of the tissues and to clean the cuticle of the first exuvia.

Second instars, their associated scale covers and first instar exuvia were processed in a numbered vial. Each specimen was mounted on a slide with its associated exuvial skin. Other mounting procedures are suggested in Wilkey (1990, table 1.5.1.1, pag. 348) starting from step 4 onward.

Drawings and photomicrographs were taken using phase contrast microscopy. The tables are collages from several pictures taken at different focal plains.

Results are reported based on the number of cut antennal segments. Three experiments bear letters instead of numbers because they were part of a previous study that was reported in a poster (Porcelli & Di Palma, 2000). Missing numbers in the experimental series are because the specimen was a male, there was overcrowding of crawlers and we lost track of the amputated specimen, or the specimen died. Second instar males were not used in the experiments.

Results (Table 1)

Case “C” (Fig. 1)
First instar.

The exuvial cast was lost during slide-mounting procedure, so this description is based of the sketch prepared during amputation.

Almost all of the right antenna was cut away, the first (proximal) antennomere remained.

Second instar.

The right antenna was absent. The fovea antennalis is the only indication of where the antenna should be located.

The left antenna was fully developed and normal.

48 (Fig. 2)
First instar.

The distal antennomere of the left antenna was amputated but the remaining antennomeres show signs of extensive stretching especially between the second and the third antennomeres, where a strain seems to occur. In other words the antenna seems cut two times, but with a part, composed of three segments, still connected with the exuvia by a small tatter of cuticle.

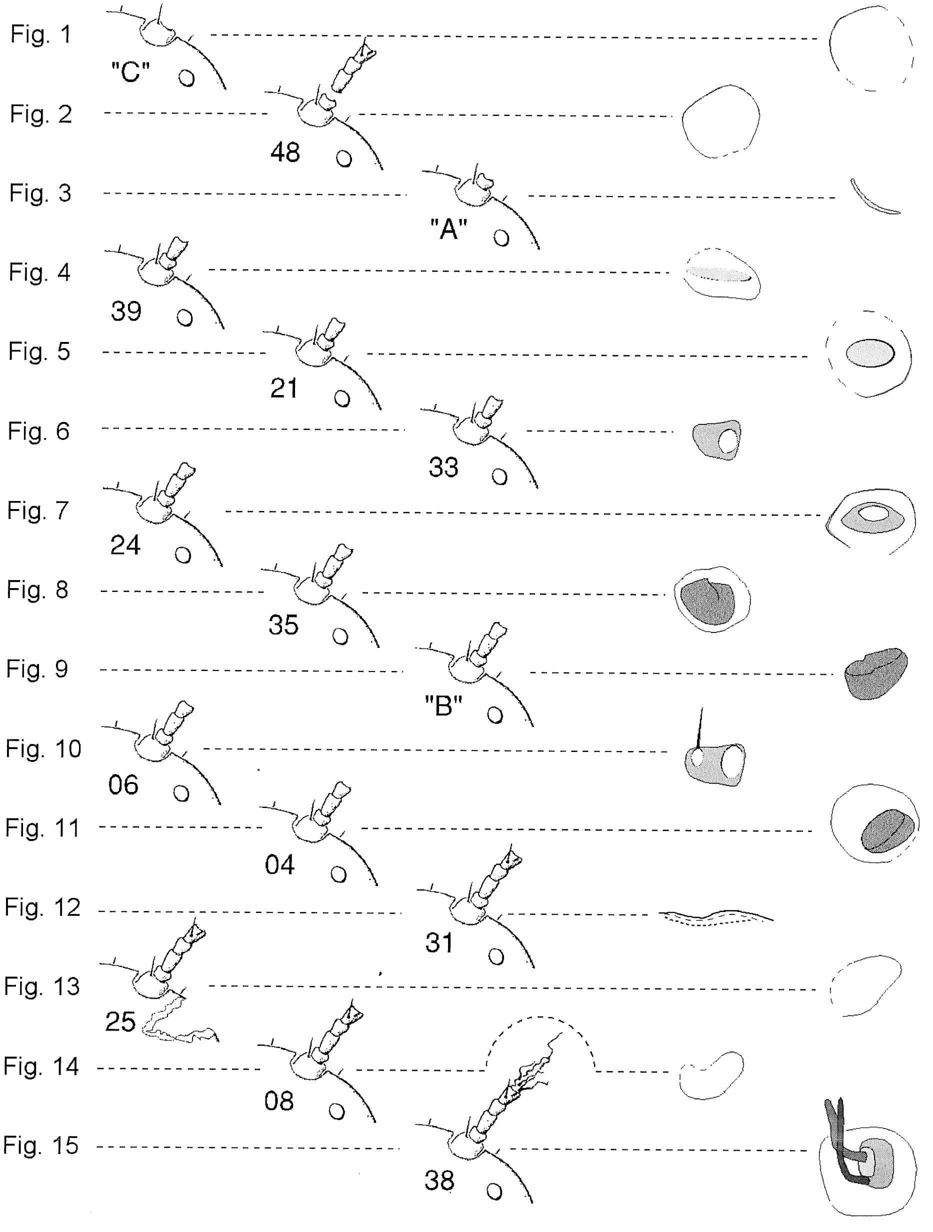

Table 1 - Comprehensive table of the performed experiments. The single experiments are sorted according to the number of cut antennomeres, starting from the distal – top – up to the proximal ones - bottom. The numbers report to the original mark on the cladode identifying the crawler at the time of amputation and so the numbering system in the "Results" section.

Table 1 – Results of experiment summarised by number of amputated antennal segments.

Fig. No.	**Exper. No.**	**Segments amputated**	**Others damaged**	**Antennal segment**	**fovea**	**pegs**	**seta**
1	C	5	no	no	yes	no	no
2	48	4	no	no	small	no	no
3	A	4	no	small	yes	no	no
4	39	3	no	small	small	no	no
5	21	3	no	small	small	no	no
6	33	3	no	small	no	no	no
7	24	2	yes	small	small	no	no
8	35	2	yes	small	yes	no	no
9	B	2	no	small	yes	no	no
10	6	2	no	small	no	no	Small (tricoid)
11	4	2	yes	yes	yes	no	no
12	31	1	yes	no	yes	no	no
13	25	1	yes	no	yes	no	no
14	8	1	yes	no	yes	no	no
15	38	3 (crushed)	no	yes	yes	yes	Abnor.

Second instar.

The left antenna was absent except for an inconspicuous fovea antennalis. The right antenna was normal except the antennal fovea was difficult to see because of heavy sclerotization.

Case "A" (Fig. 3)
First instar.

The distal 4 antennomeres of the right antenna were amputated. There was no sign of stretching or curling on the remaining two antemomeres as a result of the amputation procedure.

Second instar.

The right antenna was reduced to a short undifferentiated sclerotized line. The position on the prosoma and the boundaries of the antennal fovea confirm that the described part is actually the remains of a badly shaped antenna.

The left antenna was normal. The seta was thick and arose from two roots both inserted into the only antennomere. Two slender pegs were also visible at more than 600 enlargements. The whole antenna was in the antennal fovea.

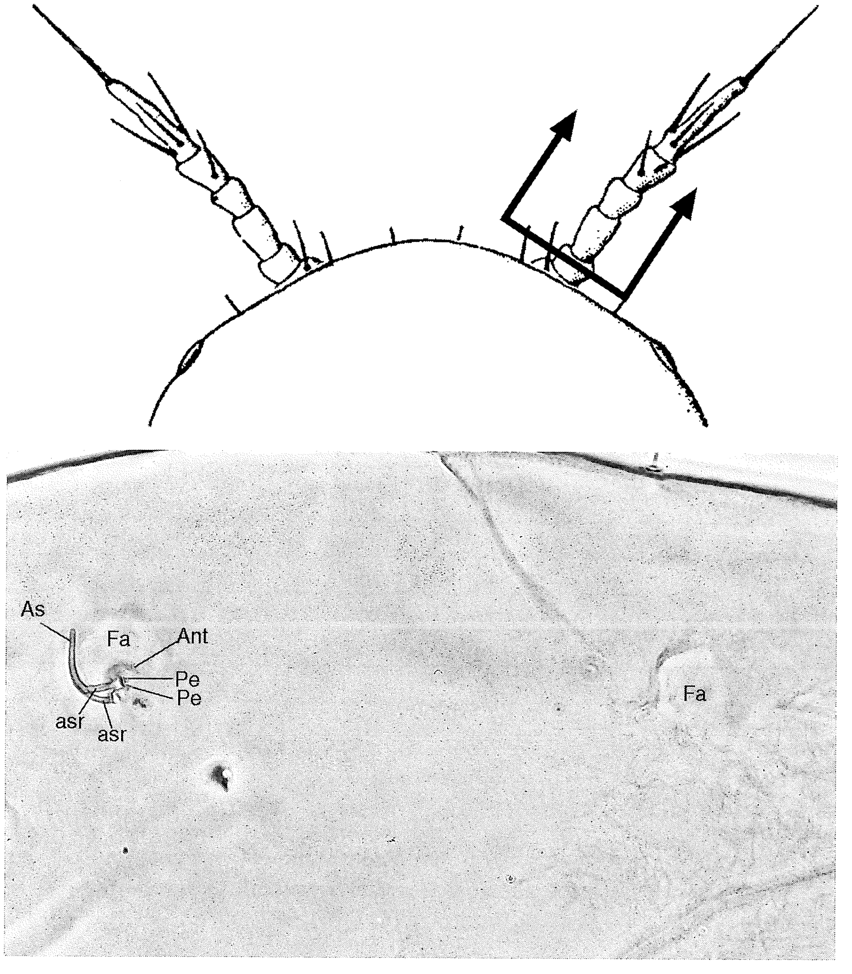

Fig. 1 - Result of experiment "C": cut antenna on right side. First instar at the top, corresponding second instar at the bottom. Ant: antennomeres; Fa: antennal fovea; As: antennal seta: asr: antennal seta roots; Pe: pegs.

39 (Fig. 4)

First instar.

The distal three antennomeres of the right antenna were amputated. The remaining three antennomeres showed no sign of stretching as a result of the amputation process.

Second instar.

The right antenna was reduced into a small, undifferentiated sclerotized patch that has no resemblance to an antenna except for its position and inconspicuous antennal fovea.

The left antenna is normal.

Fig. 2 - Result of experiment 48: cut antenna on left side. First instar at the top, corresponding second instar at the bottom. Fa: antennal fovea.

21 (Fig. 5)
First instar.

The distal three antennomeres of the left antenna were amputated. The remaining antennomeres showed no sign of stretching or curling as a result of the amputation process.

Second instar.

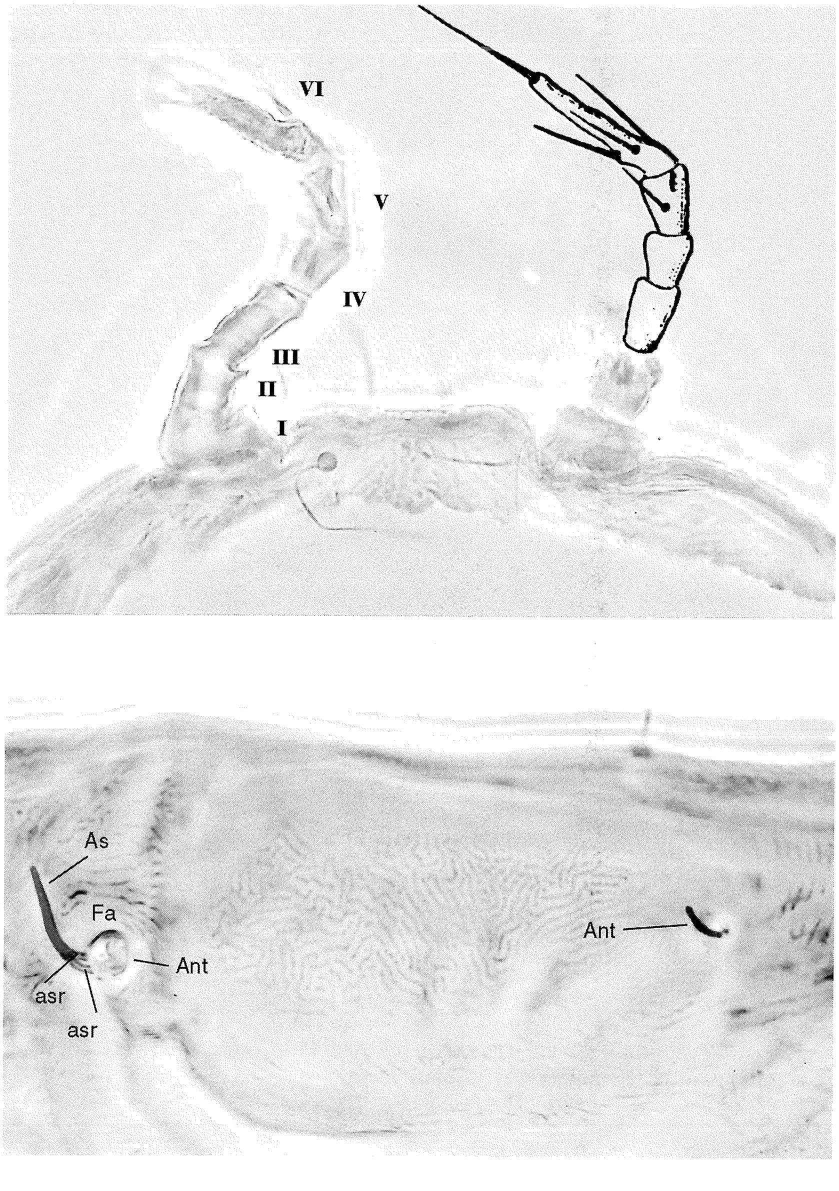

Fig. 3 - Result of experiment "A": cut antenna on right side. First instar at the top, corresponding second instar at the bottom. Ant: antennomere; Fa: antennal fovea; I to VI: antennomeres from first to sixth; As: antennal seta: asr: antennal seta roots.

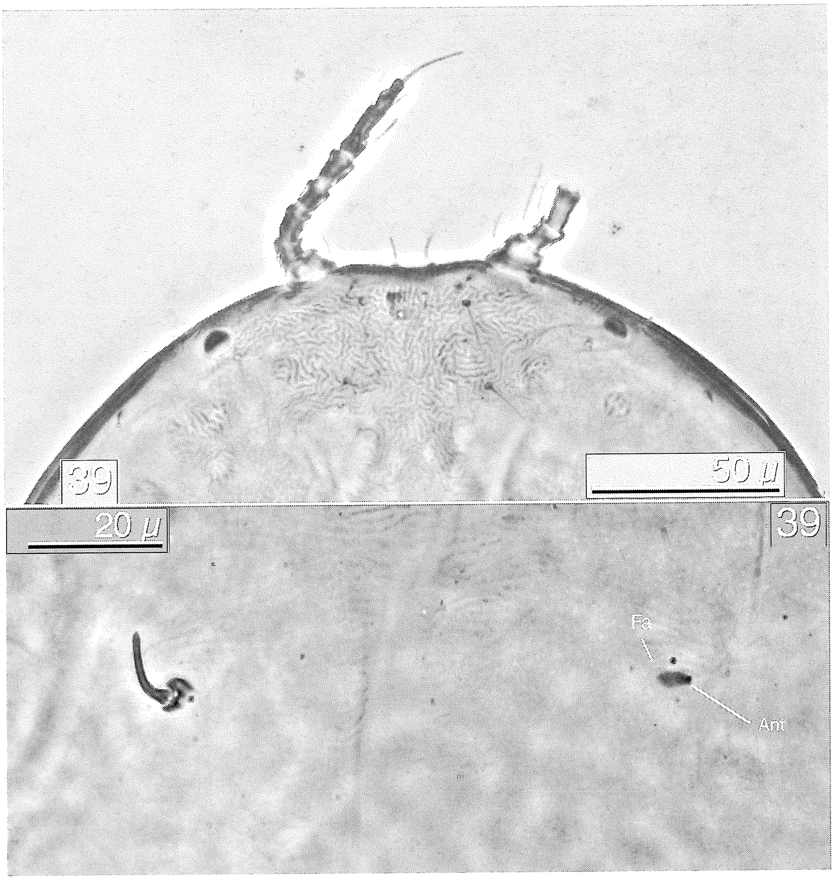

Fig. 4 - Result of experiment 39: cut antenna on right side. First instar at the top, corresponding second instar at the bottom. Ant: antennomere; Fa: antennal fovea.

The left antenna was made of a smaller than normal antennomere with no sign of the seta or pegs. The antennal fovea were barely perceivable.

The right antenna is fully shaped and normal.

33 (Fig. 6)

First instar.

The distal three segments of the right antenna was amputated. The residual three basal antennomeres showed few signs of stretching as a result of the amputation process.

Second instar.

The right antenna was represented by a small sclerotized plate without a seta, pegs,

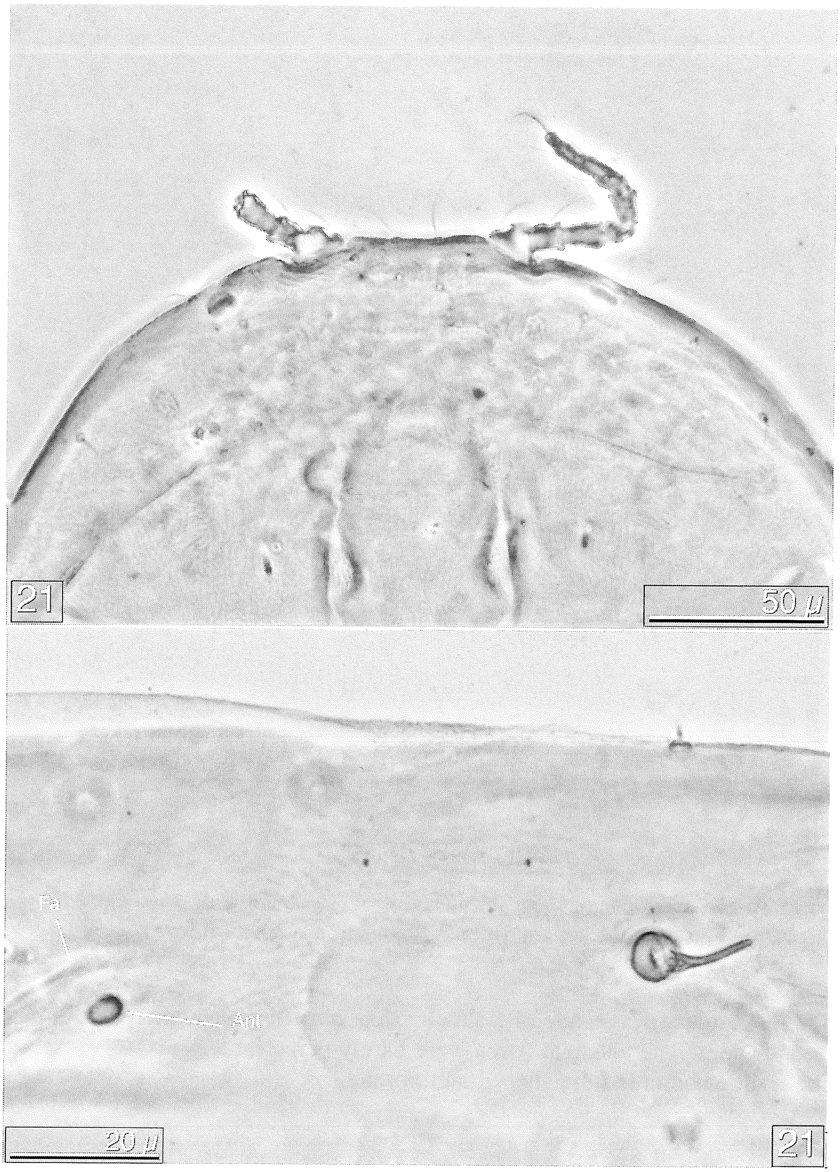

Fig. 5 - Result of experiment 21: cut antenna on left side. First instar at the top, corresponding second instar at the bottom. Ant: antennomere; Fa: antennal fovea.

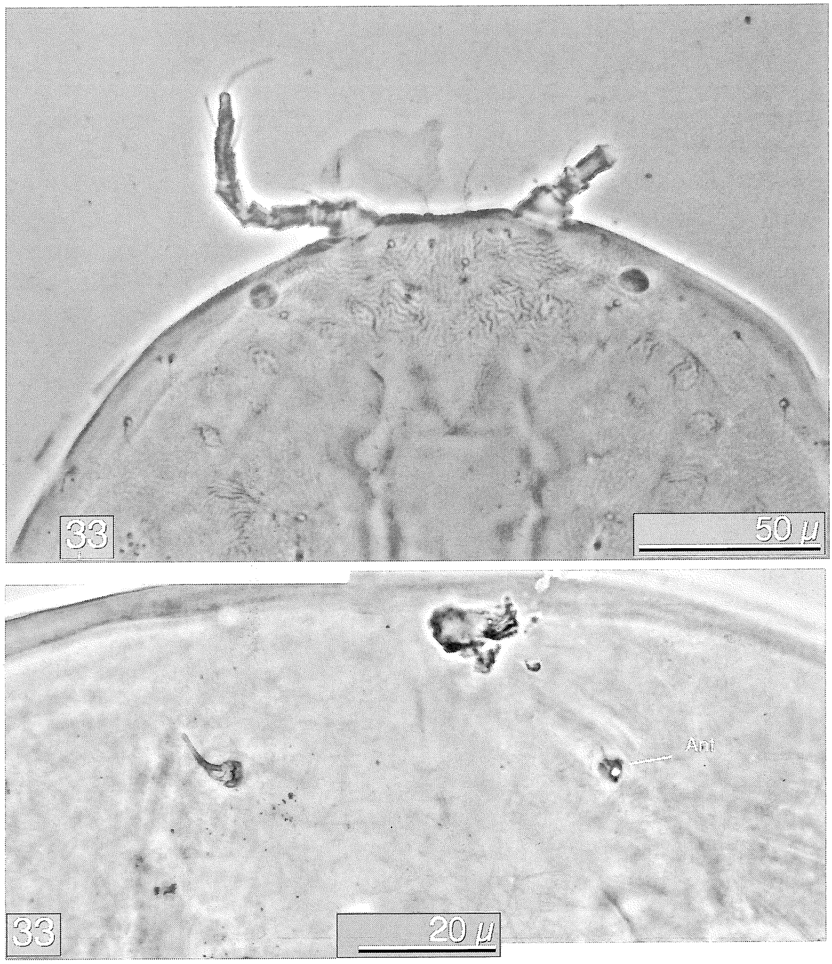

Fig. 6 - Result of experiment 33: cut antenna on right side. First instar at the top, corresponding second instar at the bottom. Ant: antennomere.

or antennal fovea. The left antenna was normal and showed the confluence of the two roots joining the single antennal seta.

24 (Fig. 7)
First instar.

The distal two antennomers of the left antenna were amputated. Some sign of stretching or curling were perceivable as a result of the amputation process.

Second instar.

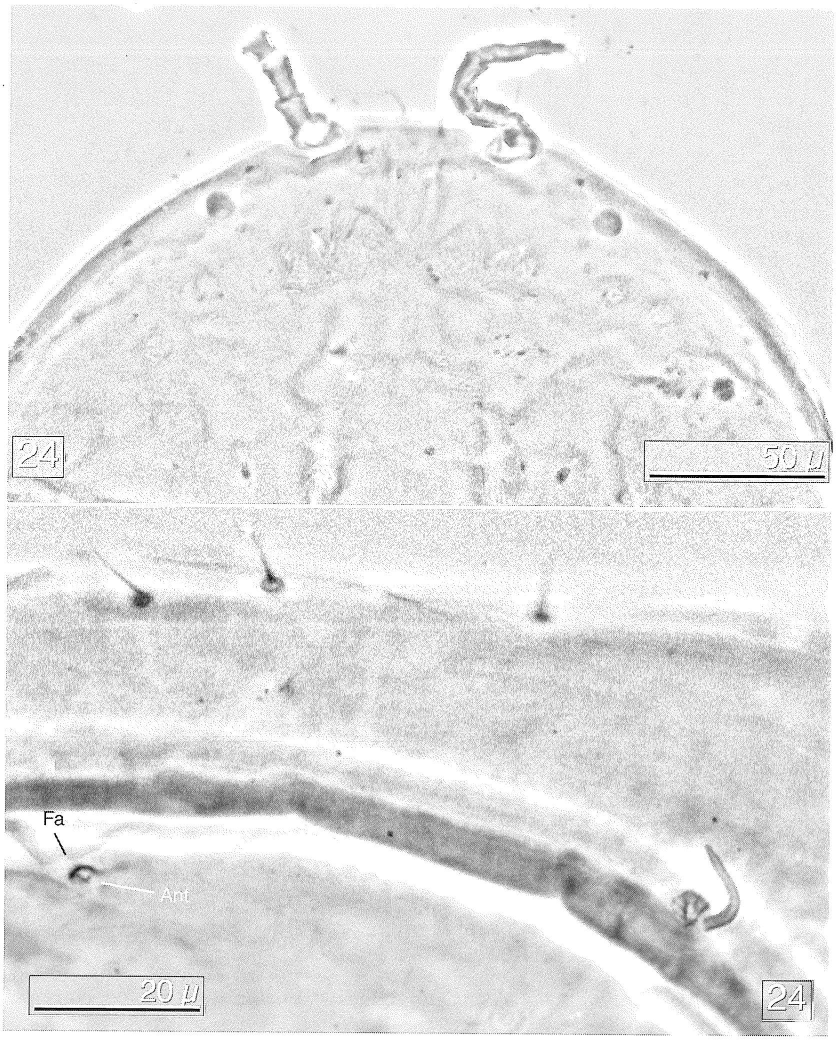

Fig. 7 - Result of experiment 24: cut antenna on left side. First instar at the top, corresponding second instar at the bottom.

The left antenna was reduced to a small sclerotized area on the cuticle with no sign of setae or pegs. The antennal fovae was barely recognizable. The right antenna was normally shaped but some parts were hidden because this specimen was about to moult to the adult female and so more sclerotized than normal. The antennal fovea was scarcely visible because of the sclerotization.

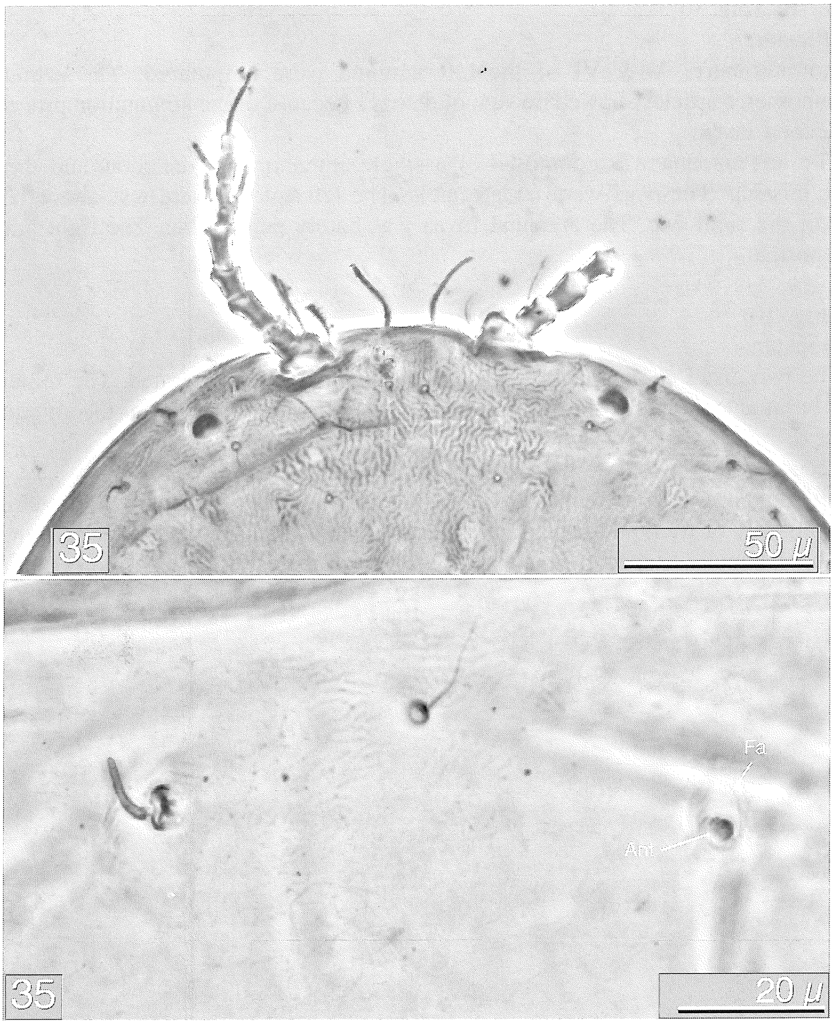

Fig. 8 - Result of experiment 35: cut antenna on right side. First instar at the top, corresponding second instar at the bottom. Ant: antennomere; Fa: antennal fovea.

35 (Fig. 8)
First instar.

The distal two antennomeres of the right antenna were amputated. The remaining four antennomeres showed signs of stretching as a result of the amputation process.

Second instar.

The right antenna was represented by the dome-shaped antennomere without a seta or pegs and was lying in the antennal fovea. The left antenna was normal.

Case "B" (Fig. 9)
First instar.

Antennomeres V & VI of the left antenna were amputated. The remaining antennomeres articles showed no sign of damage because of the amputation procedure.

Second instar.

The left antenna was composed of a single antennomere: the roots and the seta were missing. The pegs were undetectable. The left antennomere was about 1/2 the size of the right one. The antennal fovea was barely perceivable. The right antenna was normal.

06 (Fig. 10)
First instar.

The two distal antennomeres of the right antenna were amputated. The remaining four basal antennomeres showed some sign of stretching as a result of the amputation process.

Second instar.

The right antenna was represented by a small antennomere bearing a short rectilinear seta possibly of trichoid shape. The antenna fovea was not obvious. The left antenna was not normally shaped. The antennomere was of the expected size and position but

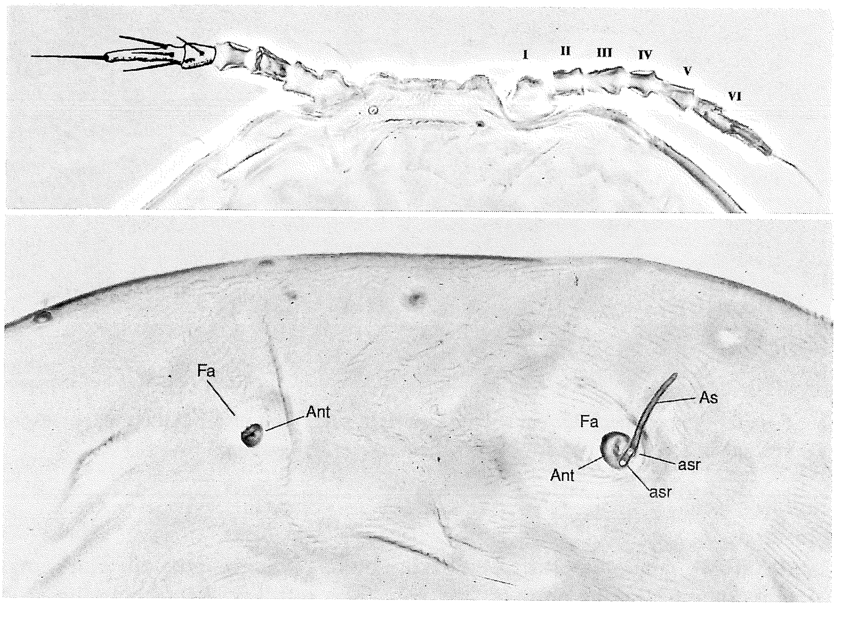

Fig. 9 - Result of experiment "B": cut antenna on left side. First instar at the top, corresponding second instar at the bottom. Ant: antennomere; Fa: antennal fovea; I to VI: antennomeres from first to sixth; As: antennal seta: asr: antennal seta roots.

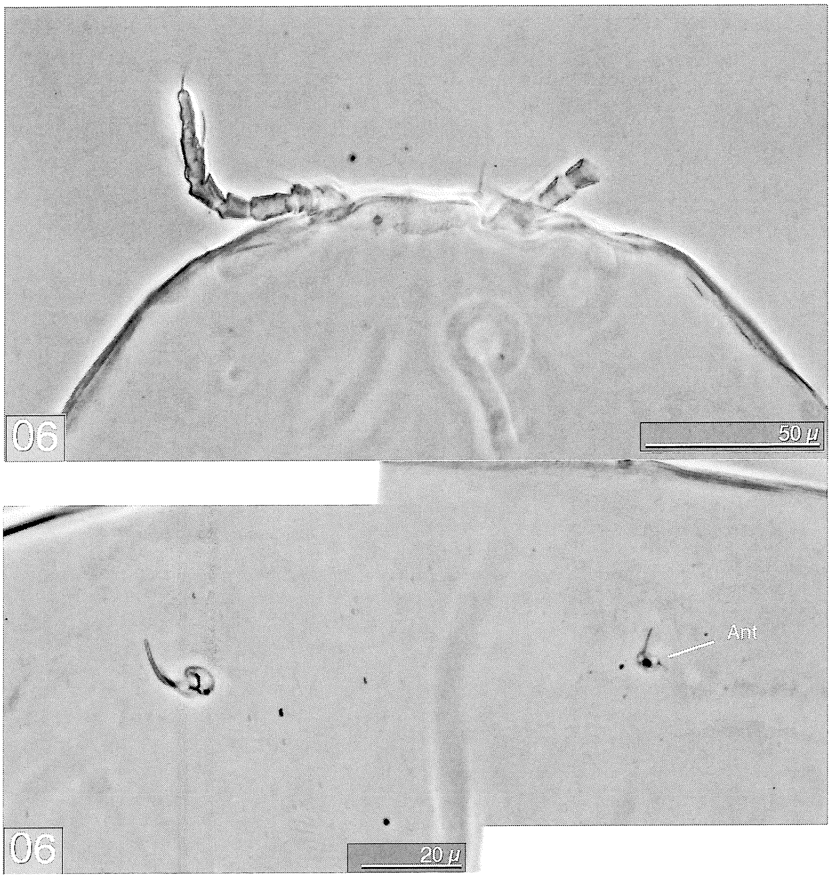

Fig. 10 - Result of experiment 06: cut antenna on right side. First instar at the top, corresponding second instar at the bottom. Ant: antennomere.

it bore two arched setae of chaeticum appearance instead of the usual two rooted single seta. The antenna fovea was not obvious.

04 (Fig. 11)
First instar.

The two distal antennomeres of the left antenna were amputated. The residual antennomers showed some curling and stretching resulting from the amputation procedure.

Second instar.

The left antenna was made up of a fully shaped, single antennomere but the seta

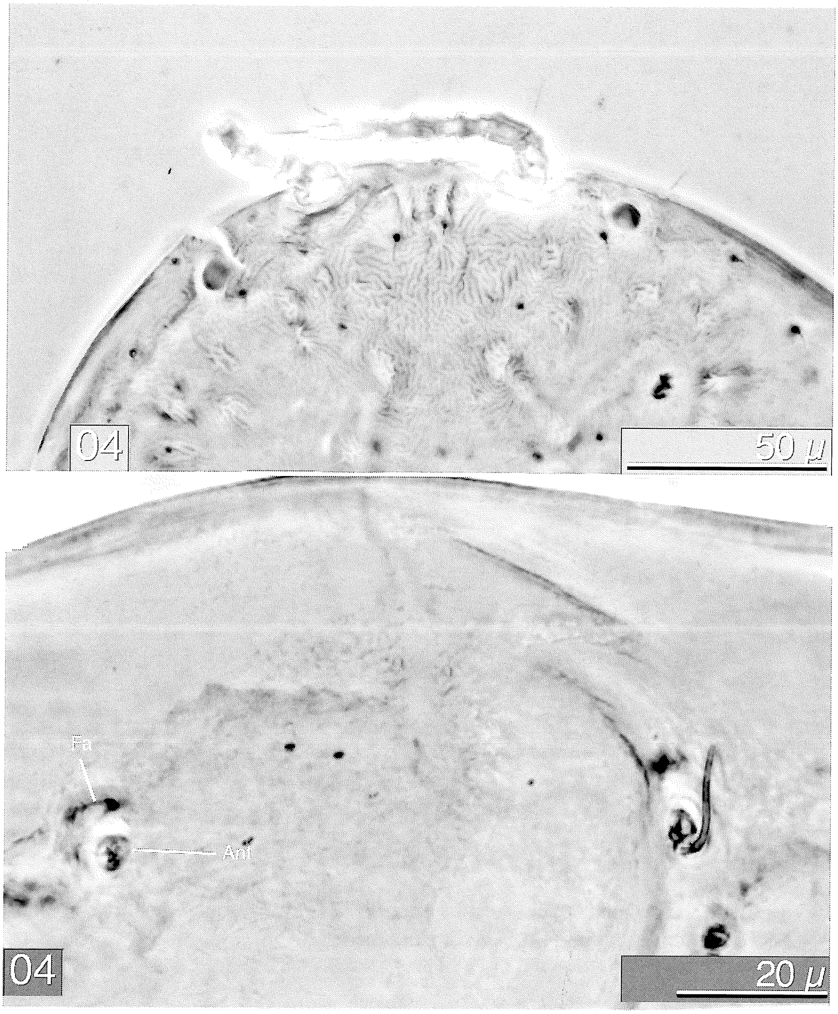

Fig. 11 - Result of experiment 04: cut antenna on left side. First instar at the top, corresponding second instar at the bottom. Ant: antennomere; Fa: antennal fovea.

and pegs were completly absent. The right antenna was normal with the fovea antennalis better developed than around the left antenna.

31 (Fig. 12)
First instar.

The distal antennomere of the right antenna was amputated. Clear signs of stretching were apparent on the remaining segments as a result of the amputation process.

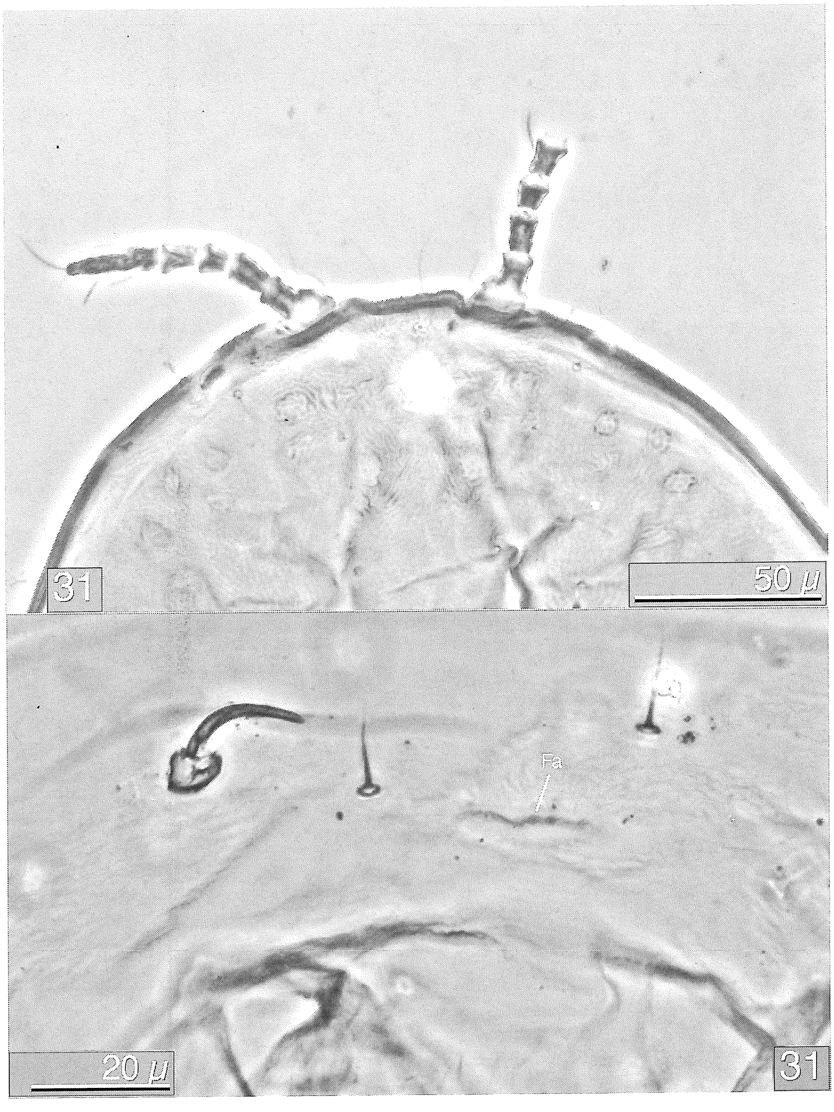

Fig. 12 - Result of experiment 31: cut antenna on right side. First instar at the top, corresponding second instar at the bottom. Fa: antennal fovea.

Second instar.

The right antenna was absent except that a small difference in the cuticular texture was detected. The left antenna was normal except the antennal fovea was faintly visible because the specimen was teneral.

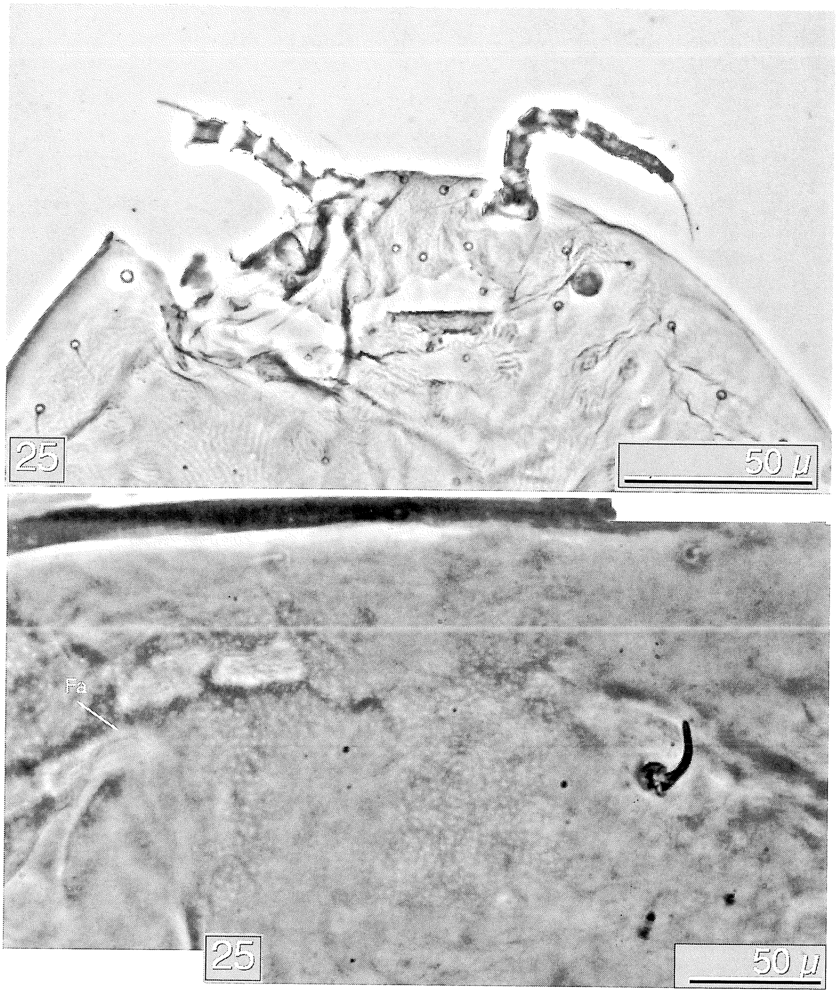

Fig. 13 - Result of experiment 25: cut antenna on left side. First instar at the top, corresponding second instar at the bottom. Fa: antennal fovea.

25 (Fig. 13)
First instar.

The distal antennomere of the left antenna was amputated but extensive damage also was caused to the region near the left eye. Clear signs of stretching were evident on the five remaining antennomeres, mainly on the intersegmental membrane between the fourth and the fifth antennomeres.

Second instar.

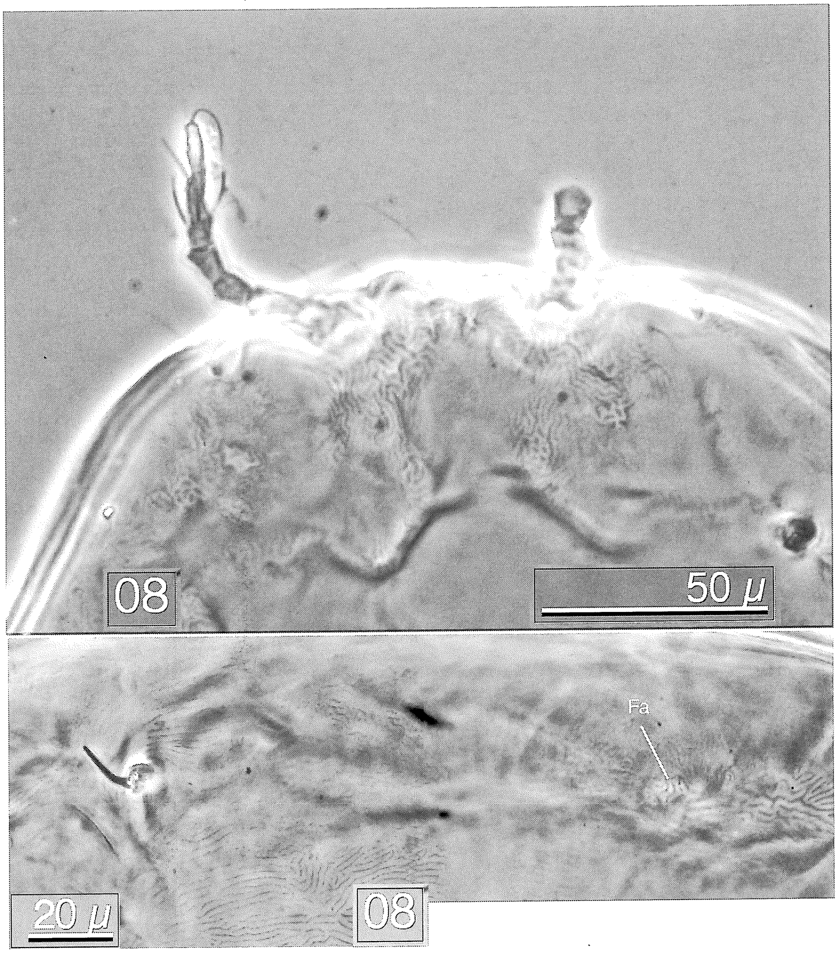

Fig. 14 - Result of experiment 08: cut antenna on right side. First instar at the top, corresponding second instar at the bottom. Fa: antennal fovea.

The left antenna was absent with only a faint depression in the cuticle marking the place usually occupied by the antenna. The right antenna was normal except that it was placed in a faint antennal fovea. Despite the large wound near the eye on the first instar, the specimen survived and moulted normally.

08 (Fig. 14)
First instar.

The distal antennomere of the right antenna was amputated. The proximal five antennomeres showed signs of stretching and curling as a result of the amputation process.

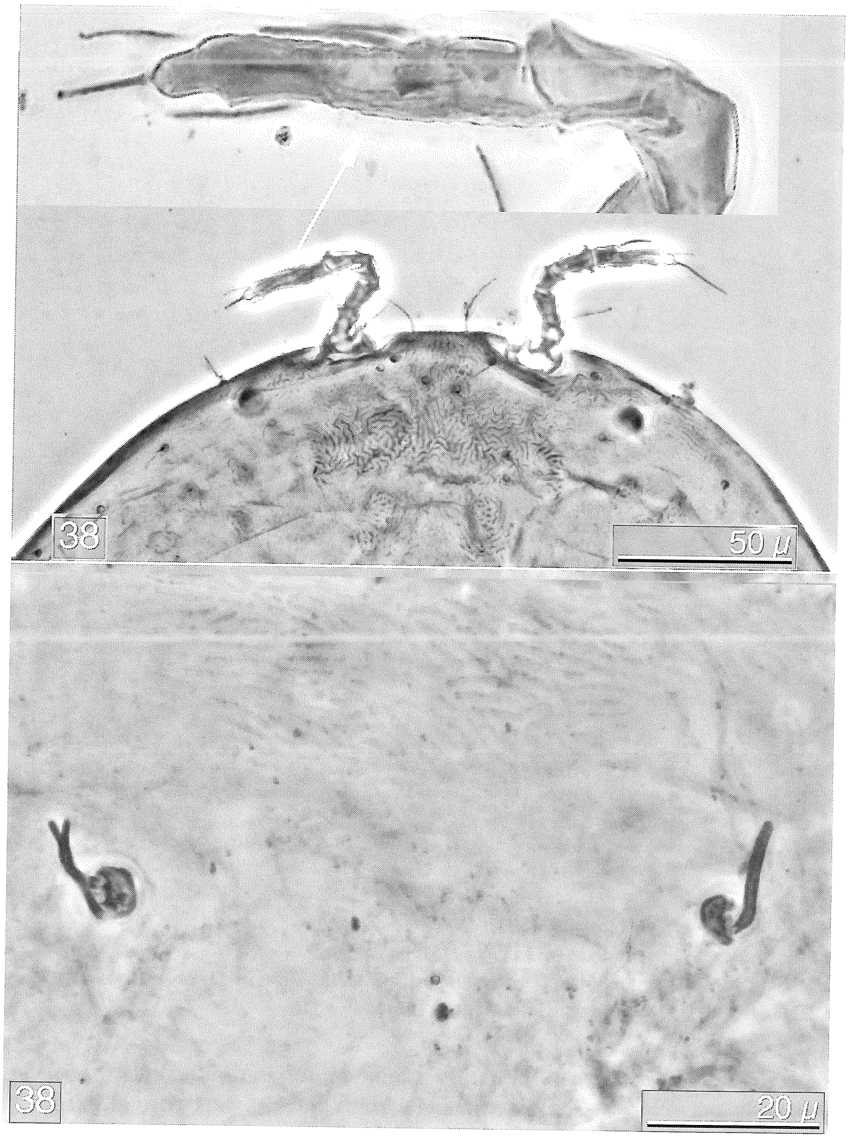

Fig. 15 - Result of experiment 38: smeared antenna on left side. First instar at the top, corresponding second instar at the bottom. Arrow points to an enlargement of the smeared antennomeres.

Second instar.

The right antenna was absent; only a light abnormality in the cuticular structure suggested the possible remnants of the antenna. The left antenna was normally formed and shaped.

38 (Fig. 15)

First instar.

The three distal antennomeres of the left antenna were not amputated, but were smeared.

Second instar.

The left antenna from the smeared three distal antennomeres resulted in a normal antenna except the joining of the two setae to form the single sensillum chaeticum is incomplete. The roots soon join into a single stalk normally but they diverge at the apex. The right antenna is normal.

DISCUSSION AND CONCLUSION

The fact that a damaged crawler antenna results in a damaged second instar antenna demonstrates that the second instar monomerous antenna is homologous with the six-segmented antenna of the crawler. Homology between the antennae of the two instars was postulated as experimental background and it is here accepted as valid based on the results of our experiments.

On the base of this knowledge it makes sense to clarify the list of reduction mode by antennomere loss we can demonstrate, on the antennae, during the first moult. We can experimentally demonstrate only the loss of distal antennomere: being actually impossible to cut off intermediate or proximal article leaving others connected with the crawler's body. So we can verify only the "distal antennomere loss" hypothesis, being impossible to set up a proper experiment to check the "intermediate or proximal antennomere loss" hypothesis. It is possible to verify the "joining process" hypothesis in the case that the joining involves more than one antennal articles because we have resolution of at least one antennomere during the cut. So we can test only two hypothesis on the basis of the described facts, the second instar antenna is: (a) the result of the loss of distal antennomere(s); (b) the result of a joining process involving some antennal articles. Both processes occur at the time of first moult.

Regarding the first hypothesis, "distal antennomere loss", this means that the second instar antenna is made up from cells pertaining to the basal antennomeres. The second instar antenna resulting from the artificial ablation of the distal antennomere clearly speaks against it. To accept that the monomerous antenna is the result of the natural loss of the distal antennomnere, means that the artificial cut of the distal antennomere could not produce changes (or very few) in respect to the second instar antenna. In other words the amputation of the distal antennomere should produce none or few effects in order to verify the "distal antennomere loss" hypothesis. This is definitely not what we observe.

Ablation of the distal antennomeres results in a range of effects from the occurrence of no second instar antenna to an antenna made up of the only antennomere (cases: 31, 25, 08, 04). Of special interest is case 38: the smeared distal antennomere results into a misshapen second instar antennal seta. If the second instar antenna had been the result of the mere basal articles of the crawler's antenna, the damage on the distal article would have resulted into no changes of the morphology of the descending second instar antennal seta. On the basis of the exposed analysis we rejects the "distal antennomere loss" hypothesis in that the distal antennomeres is responsible for the antennal seta and pegs (see case 38).

Regarding the second hypothesis, "joining process", this means that the second instar antenna is made up from all crawler's antennomeres joined and melted together. The second instar antenna resulting from the artificial cut of the antennomeres, clearly speaks in favour of it. To accept that the monomerous antenna is the result of the natural joining of all the antennomere, means that the artificial cut of the antennomeres from the basal one to the distal could produce changes, in respect to the second instar antenna, proportional to the inflicted wound. In other words the more the antennomeres are cut the more effects we should observe in order to verify the "joining process" hypothesis. This is definitely what we observe. Ablation of the antennomeres results in a range of effects going from the occurrence of no second instar antenna to an antenna made up of the only antennomere (cases: 21, 33, 24, 35, "B", 06 "C", 38) depending on the number of cut articles.

The correspondence among the level of amputation and the resulting structure and size of the second instar antenna is noteworthy. Again of special interest is the case 38: the smeared distal antennomere results in a deform second instar antennal seta. Hence the second instar antennal seta is the result of distal antennomeres only (or mainly). The damage on the distal antennomeres should result in morphological changes of the corresponding parts of the descending (second instar) antenna.

On the basis of the exposed analysis we accept the "joining process" hypothesis. On the basis of the fact that a sclerotized remnant of the antenna is formed even when the apical segment or apical 4 segments are amputated gives strong support to the hypothesis of segment fusion. It also is clear that the apical segment of the crawler antenna is important and is the source of the peg and at least part of the seta.

Three other considerations merit mention

There were several examples of second instar antenna that did not adhere to the pattern demonstrated by other experiments namely n° 31, 25, 08 and 48.

First: we suggest that more damage occurs than is evident when examining the amputated antenna. The real damage of the tissues can be harder than the damage seen on the cuticle of the cut antenna. This can clearly occur because of the more or less pronounced, and impossible to check, drying of the exposed tissue surface and for stretching and curling also. This can explain the not so clear-cut results in the case of a more-damaged-than-expected second instar resulting antenna (cases: 31; 25; 08 and 48).

Second: accepting the over damage of the crawler's antenna, it could be difficult to admit that the damage reaches the basal antennomere. In this case at least some second instar antennal parts should be expected in the case of terminal abbreviation. The evidence of no vestige of antenna is another proof against the "distal antennomere loss" hypothesis. More, the damage of intermediate antennomere is not in contrast with the experiment results if the "joining process" hypothesis is accepted. In other words the seta is missing because of terminal antennomere amputation and antennal article is missing because of the intermediate article damage during the experimental cut.

Bielenin *et al.* (1995) report observation about the post-embryonic development of *Quadraspidiotus ostreaeformis* (Curtis) drawing the "predetermined cell of the second generation of antennae" just at the base of the "empty envelope of instar I larva antenna after tissue atrophy" at fig. 2 (page 18). Accepting that the described process at the time of moulting is almost the same, one can argue that a late cut of the crawler's antenna will result into a fully developed second instar antenna because the "predetermined cell" stays untouched. This is contrary to the observation: there are only over effects among observations, never any under effects. The evidences mean that the cell involved into the second instar antenna building are touched – and cut away or killed – in all reported cases. Also the crawler's age at the time of the cut is far from the first moult (Oetting, 1984) and, so, far from the internal reorganization of the tissue devoted to the grow of the second instar antenna. One more induction of the "joining process" hypothesis.

On the other side of the coin a normal second instar antenna never results from an operated one (no matter how small is the cut part). Thus it makes us able to coarsely describe the importance - in building the second instar antenna - of the distal crawler's antennomeres.

A further proof in favour of the importance of the distal antennomeres and against the "distal antennomere loss" hypothesis is that nothing descents leaving only the basal antennomere. So that: "The more distal are the articles on the first instar antenna the more important they became on the morphology of the descending second instar antenna". This fact seems true in *Diaspis echinocacti* but could be not so true in other tribes of Diaspididae.

Few notes are possible about the descent of single sensilla on the second instar antenna: the only possible hypothesis is that the single seta descents, at least, from two setae of the chaeticum shape on the distal article of the crawler's antenna. In the same manner the two coeloconic pegs on the distal antennomere are possibly homologous with those on the single second instar antenna. But of this we can have some evidences only.

Two arguments are missing in this discussion: the functional importance of the studied parts and the origin of the antennal fovea region: both are besides the scope of this paper. The first – the function – involves a full morpho/functional description of the first instar antenna of *Diaspis echinocacti* crawlers female with an accurate account of the sensory nature and fate of each seta or sensillum; the second – the nature of the fovea – belongs to the gross anatomy of both the crawler and the adult female. In the meantime the only reasonable inference we can formulate is that mechanoreceptors on the crawler antenna are lost preferentially instead of chemoreceptors (Porcelli, 1999) during the joining process.

In synthesis the amputation of the distal antennomere (without damaging the others more proximal) never results in a normal antenna but gives the basal antennomere only. So, the apical distal segment is not alone responsible for the antenna of the second instar. The apical segment alone is responsible mainly of the seta of second instar antenna, in fact smeared crawler distal antennal article results in the only misshapen seta, leaving the antennomere pretty normal. This is a further proof of the role of other antennal articles in building the second instar antenna. The sub-apical antennomeres have importance in building up the second instar antennal article. This evidence derives from the existence of the sole antennal tubercle if the distal antennomere is amputated so that the tubercle must result from more proximal antennal segments.

Concluding, the *Diaspis echinocacti* antenna is a monomerous antenna descending from the six-segmented crawler's antenna, by a joining a fusion process occurring at the time of the first moult. In our opinion the results here presented occur throughout the Diaspididae and provide evidence about the antennal reduction process. This early reduction, changing deeply the morphology of the antenna, may suggest the identification of the post-embryonic development scheme for Diaspididae as Catametabolic (Grandi, 1945; 1969; Porcelli, 2001, in press) instead of Neotenic as actually reported (Ben-Dov, 1990a; 1990b; Koteja, 1990; Takagi, 1990). But to do this, we need that a similar deep early reduction will be demonstrated for the entire body plan. The future could reserve us to map and describe the crawlers antenna of a Diaspidine as a whole in comparison with the antenna of the second instar and the adult female, also attempting single-seta-burning experiment by LASER light to collect proofs about the fate of single antennal sensilla.

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