ZOOLOGICAL SCIENCE 7: 671–679 (1990)

Instability of the Number of Segments of Unoperated and Regenerated Maxillary Palpi in the Maxillary-Palp-Elongate (*mpe*) German Cockroach Mutant

AKIRA TANAKA and MARY H. ROSS[1]

Department of Biology, Nara Women's University, Nara 630, Japan, and
[1]Department of Entomology, Virginia Polytechnic Institute and
State University, Blacksburg, Virginia 24061, USA

ABSTRACT—Maxillary-palp-elongate (*mpe*) is a mutant modifying the terminal (5th) segment of the wild-type palpus to a variable number of divisions, increasing the total number of segments up to 9. The supernumerary segments sometimes fuse during postembryonic development. The mutant palpi of both sides of the mouth are often asymmetric in length and in the number of segments. The mutant palpus occasionally carries a prominent bristle, never found in wild type. It resembles bristles on legs and occurs exclusively on the 4th segment, a homologous segment to the tibia of legs. The percentage of bristle-bearing palpi increases during nymphal development, and exceeds 50% in the last instar. A few mutant palpi bear more than one bristle on the 4th segment. Amputation experiments were carried out at various levels on *mpe* maxillary palpi. The right palpus was operated in the 2nd instar, and the regenerate was examined in the 4th and 6th instars. Irrespective of amputated levels from the 1st-2nd to the 6th-7th segment, the total number of segments of a regenerated palpus was irrelevant to that before operation. This suggests that the stump does not regenerate new segments according to a "memory" of the original number of segments. The number of segments of a regenerate was also irrelevant to that of the contralateral palpus, which suggests that the stump does not use the contralateral palpus as a "reference" for the number of segments to be regenerated. As shown in unoperated palpi, regenerated segments sometimes fused during subsequent molts. The bristle was occasionally found in the regenerated 4th segment.

INTRODUCTION

Maxillary-palp-elongate (*mpe*) is a simple autosomal recessive in the German cockroach, *Blattella germanica*. The locus lies within a group of closely linked loci on chromosome 9 [1]. This mutant modifies the terminal (5th) segment of the wild-type palpus to a variable number of divisions, increasing the total number of segments up to 9. The mutant palpus often carries a prominent bristle exclusively on the 4th segment, the segment homologous to the tibia of legs. These facts support homology of the maxillary palpus with the leg, and suggest that some distal segments of the mutant palpi correspond to the tarsal segments of legs.

Regeneration experiments with insect appendages have been mainly on the thoracic legs [2]. It is puzzling that regenerated cockroach legs always have tetramerous tarsi and never pentamerous as in the normal legs [3–7], although exceptionally pentamerous after amputation distal to the 2nd tarsomere [8–10]. In this situation, it was of interest to carry out regeneration experiments with the *mpe* mutant, since maxillary palpi are homologous to legs and *mpe* maxillary palpi show a variable number of segments [1]. Here we report (i) further description of *mpe* maxillary palpi focused on the fusion of segments during nymphal development, bilateral differences in the number of segments, and the percentage of bristle-bearing segments, and (ii) regeneration experiments with amputation at various levels on *mpe* maxillary palpi.

Accepted January 10, 1990
Received September 21, 1989

MATERIALS AND METHODS

Observations on mpe maxillary palpi

Maxillary-palp-elongate (*mpe*) is a simple autosomal recessive with full penetrance and viability [1]. Both right and left maxillary palpi were observed in all nymphal instars, from the 1st to the 6th (last) instar. The total number of palpi observed was 1386, thus the number in each instar averaged 231. Two small basal segments were designated as the 1st and the 2nd, and two succeeding longer segments as the 3rd and the 4th segments. The number of segments distal to the 4th varied from 1+ to 4+. "+" denotes that a palpus has an elongated or incompletely-divided segment. The total number of segments hence ranged from 5+ to 8+. In accordance with the total number, the palpi were classified into following seven categories: 5+, 6, 6+, 7, 7+, 8 and 8+. Maxillary palpi with 9 or more segments were not found. No significant sex difference was detected in the number of segments so that the data of both sexes were combined.

Regeneration experiments

Each nymph was raised in a small plastic container (61×43×17 mm high, Sanplatec, No. 2) as previously described [7]. Since the 1st instar was too small to be precisely amputated on the maxillary palpus, the 2nd instar was operated. Prior to amputation, carbon dioxide was introduced into the container for anesthetizing the animal. Right maxillary palpi were amputated with fine scissors at various levels, *i.e.*, between the 1st and 2nd segment, the 2nd and 3rd, the 3rd and 4th, the 4th and 5th, and if available, between the 5th and 6th, and the 6th and 7th segment. These cutting levels were abbreviated to 1–2, 2–3, 3–4, 4–5, 5–6, and 6–7, respectively, in this paper. For the controls, the number of segments were recorded in both befpre-operation right palpi and contralateral left palpi.

Some operated maxillary palpi regenerated their distal segment(s) in the 3rd instar. The regenerating segment(s), however, were rather small and often not so clearly segmented. Then we examined the regenerates in the 4th instar when the segmentation of regenerates became fully recognizable. In order to examine further growth of regenerates, final observation was made in the 6th instar when regeneration was almost completed. Since no significant sex difference was detected in regeneration experiments, the data were again combined.

RESULTS

Fusion of segments during nymphal development

Supernumerary segments found in this mutant were first thought to be retained throughout nymphal development [1]. It has been revealed in this study, however, that the additional segments

TABLE 1. Percentages of segmentation types in *mpe* maxillary palpi

		Instar					
		I	II	III	IV	V	VI
Segmentation type	5+	6.3	7.5	12.6	17.1	19.4	33.2
	6	21.3	16.8	19.1	18.6	25.4	21.7
	6+	28.1	21.6	28.9	36.2	31.7	28.3
	7	22.5	27.4	23.6	12.9	11.9	8.0
	7+	9.4	11.3	8.9	10.0	8.7	7.1
	8	8.1	14.4	6.9	5.2	2.8	1.8
	8+	4.4	1.0				
Av. No. of segments		6.75	6.83	6.59	6.48	6.37	6.20
No. of palpi examined		160	292	246	210	252	226

+ denotes that a palpus has an elongated or incompletely-divided segment and that the value of 0.5 was given to calculate the average number of segments.

sometimes fuse during postembryonic development. Table 1 shows percentages of segmentation types, 5+ to 8+, in each nymphal instar. In the 1st and 2nd instar the percentages of palpi with 7 or more segments were relatively high. After the 2nd instar, the percentages tended to decrease as development advanced. On the other hand, segmentateion type 5+ tended to increase. The average number of segments decreased by about 0.6 during nymphal development. The average reduction was caused by the fusion of segments in some, but not all, palpi during postembryonic development. Fusion took place between the segments distal to the 4th segment, and never between the proximal four segments.

Figure 1 shows various types of *mpe* maxillary palpi (b-h) together with a typical wild-type palpus (a). All specimens are of the 6th (last) instar. The mutant palpi were always longer than wild type, showing typical supernumerary segments (b-d) and various degrees of fusion (e-h). An elongated 5th segment (Fig. 1e) consisted of three distinct distal segments in the 2nd instar. Figure 1f shows an elongated part lying proximal to the last segment. The elongated part consisted of three distinct segments in earlier development, which shows that fusion can take place between intermediate segments. An incompletely-fused distalmost segment in Fig. 1g was two separate segments in the 2nd instar. Another example of incomplete fusion is presented in Figure 1h.

Asymmetry in the number of segments

A particularly interesting characteristic of this mutant is an unequality in the length and the number of segments of the right and left palpi.

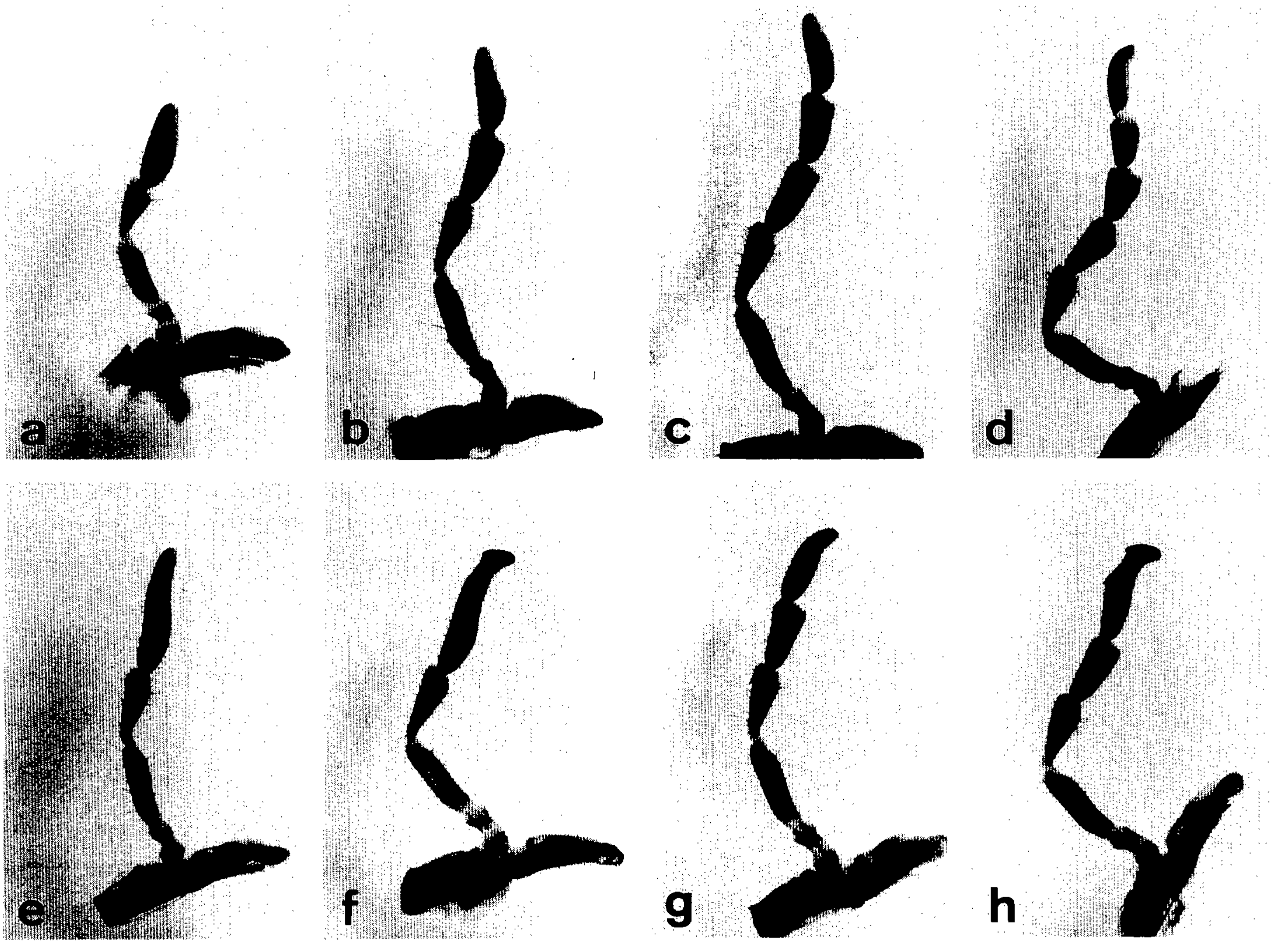

FIG. 1. Various types of maxillary palpi (6th instar). (a) a wild-type palpus showing five typical segments, two small basal and three succeeding longer segments. (b-h) *mpe* palpi: (b) 6-segmented, (c) 7-segmented, (d) 8-segmented with an incipiently-divided 8th-segment, (e) with an elongated 5th segment resulted from complete fusion of three distalmost segments, (f) an originally 8th segment fusing incompletely to an elongated 5th segment, (g) incomplete fusion of two distal segments, and (h) incomplete fusion of three distal segments. (×18)

The palpi are not always symmetrical, differing rather frequently in length and number of segments. Figure 2 shows a correlation of the number of segments between right and left palpi in the 2nd instar. Correlations of the other five instars showed similar tendencies. The correlation was low although significant (r=0.41, p<0.0001). Only about 22% (32/146) of the nymphs had right and left palpi with the same number of segments. Average difference was 0.65, including nymphs with the same number of segments.

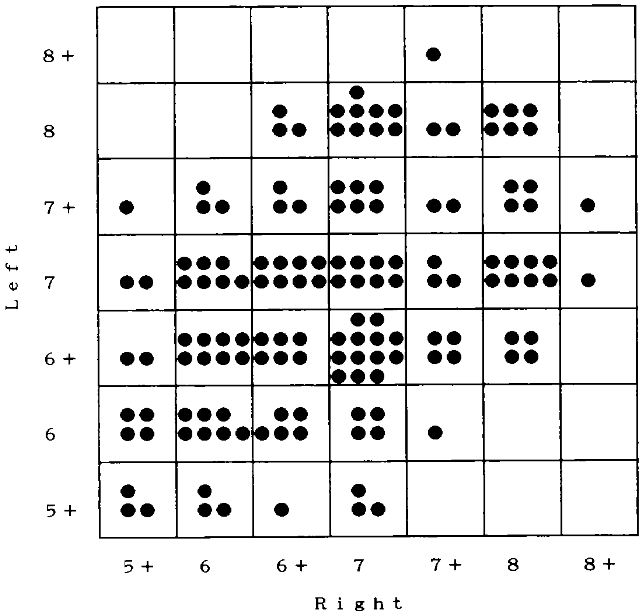

FIG. 2. Correlation in the number of segments between right and left *mpe* maxillary palpi (2nd instar). In this and subsequent figures, "+" denotes that a palpus has an elongated or incompletely-divided segment and that the value of 0.5 was given when correlation coefficient was calculated.

Bristles on maxillary palpi

Another point of interest is the existence of bristles on *mpe* maxillary palpi, since no bristles are found on wild-type palpi. Bristles were found exclusively on the 4th segment of *mpe* palpi. The bristle most frequently appeared as a single bristle as shown in Figure 3a. Double bristles were rarely encountered, either along the same generatrix (Fig. 3b) or around the same level (Fig. 3c) of the 4th segment.

Table 2 shows percentages of bristle-bearing *mpe* palpi in each nymphal instar. No significant difference in the percentage was detected between segmentation types. No bristles were found in new-born nymphs. Bristles first appeared in the 2nd instar, but were very rare. Then the percentage of bristle-bearing palpi gradually increased to become the frequency exceeding 50% in the 6th instar. Palpi with more than one bristle were found only in the 6th instar, *i.e.*, two palpi with double bristles (Fig. 3b, c), and only one palpus with triple brisles.

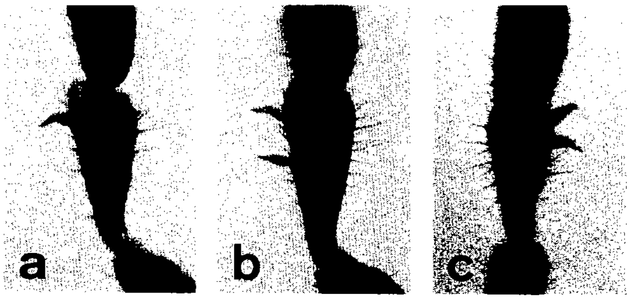

FIG. 3. Bristles found on the 4th-segment of *mpe* maxillary palpi (6th instar). (a) a single bristle, (b) double bristles along the same generatrix, and (c) double bristles across the same level of the segment. (×40)

Regeneration experiments

Regeneration experiments started with 316 nymphs. Out of 316 nymphs, 238 survived until the 4th instar, and 207 until the 6th instar. The number of segments was counted in the 4th and 6th instar and compared with that before operation. Observations in the 4th instar are summarized in Table 3. Changes in the number of segments from the 2nd instar (before operation) to the 4th instar (regenerated) ranged from −3.0 to +2.5. Irrespective of amputated levels, the number of segments in palpi with fewer segments at the time of amputation tended to increase. Conversely, the number tended to decrease in palpi with larger numbers at amputation.

Correlation was analyzed in the number of segments between the 2nd instar palpi before amputation and the 4th instar palpi with regenerated segments (Fig. 4). The data from 1–2 to 4–5 amputation levels were combined in Figure 4 (156 surviving nymphs in total). The data of 5–6 and 6–7 amputation levels were excluded because of lacking 5+, 5+ to 6+ segmentation types at the

TABLE 2. Percentages of bristles on *mpe* maxillary palpi

		Instar					
		I	II	III	IV	V	VI
Segmentation type	5+	0.0	0.0	3.2	19.4	24.5	52.0
	6	0.0	2.0	2.1	12.8	35.9	61.2
	6+	0.0	0.0	2.8	17.1	32.5	53.1*
	7	0.0	1.3	5.2	14.8	23.3	55.6**
	7+	0.0	0.0	0.0	14.3	36.4	56.3
	8	0.0	0.0	5.9	9.1	28.6§	75.0§
	8+	0.0§	0.0§				
	Av.	0.0	0.7	3.3	15.7	31.0	55.3
		(0/160)	(2/292)	(8/246)	(33/210)	(78/252)	(125/226)

Bristle-bearing palpi usually had only one bristle on the 4th segment. In the instar VI exceptionally found were * two palpi with double bristles and ** one palpus with triple bristles on the 4th segment. § denotes that the number of palpi examined was less than 10. In parentheses are shown the numbers of bristle-bearing palpi/total palpi.

TABLE 3. Effects of regeneration on the number of segments of 4th-instar *mpe* maxillary palpi

Amputated level	No. of nymphs	No. of segments before amputation						
		5+	6	6+	7	7+	8	8+
1–2	29	+0.25	+0.25	+0.06	−0.19	−1.00	−1.13	
2–3	37	+0.38	+0.71	+0.17	−0.50	−0.75	−1.00	−2.00*
3–4	40	+1.00*	+0.67	+0.07	−0.22	−0.63	−0.92	
4–5	50	+1.17	+0.95	+0.75	+0.17	−0.08	−0.75	
5–6	50		+0.55	−0.14	−0.71	−1.00	−1.81	−3.00*
6–7	32				−0.71	−1.25	−1.32	

Average changes in the number of segments are shown. 1–2 indicates amputation between the 1st and the 2nd segment, and so on. * Only one nymph was examined.

time of amputation, respectively. The correlation was very low although significant ($r=0.24$, $p<0.01$). Only 37 nymphs out of 156 retained the same number of segments through regeneration. The average difference was 0.69, including nymphs that regenerated the same number of segments.

Another type of analysis was made in Figure 5. The number of segments of regenerated palpi was compared with that of the contralateral unoperated palpi. The data of different amputation levels from 1–2 to 4–5 were again combined. There was no correlation ($r=0.11$, $p>0.1$). Only 29 out of 156 nymphs had the same number of segments between regenerates and contralateral palpi. The

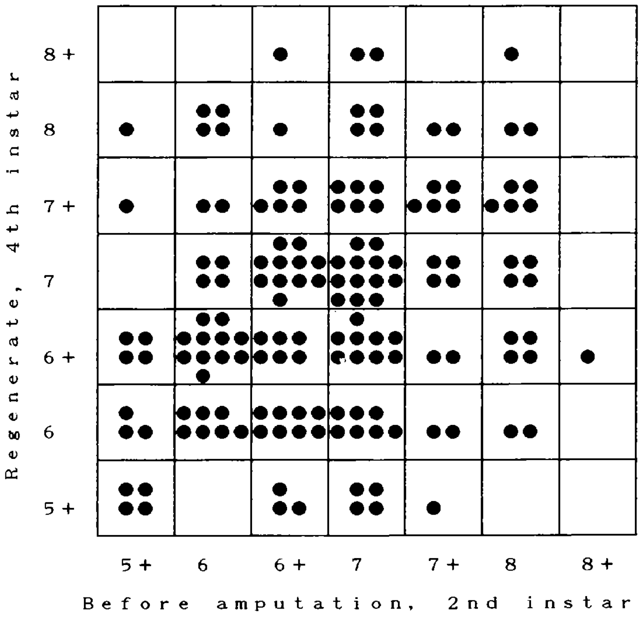

FIG. 4. Correlation in the number of segments between the 2nd instar (before amputation) and the 4th instar (regenerated). For the symbol "+", see Fig. 2.

average difference was 0.77, including nymphs that had the same number of segments in both palpi.

The final examination was carried out on 207 nymphs that survived until the 6th instar (Table 4). Irrespective of amputated levels, the number of segments was mostly unchanged or decreased by 0.5, and less frequently decreased by 1.0 or 1.5 from the 4th to the 6th instar. The average decrease in the number of segments during the two instars was about 0.3, which was close to that of unoperated palpi (Table 1).

Figure 6 shows examples of some right regenerated maxillary palpi together with the left unoperated controls in the 6th instar. Regenerated segments have grown and are almost indistinguishable from unoperated contralateral segments. The right palpus shown in Figure 6a was originally 7-segmented in the 2nd instar. After amputation between the 2nd and 3rd segment (arrow), a 8-segmented palpus was observed in the 4th instar, and a bilobed segment has finally formed in the 6th instar. The right palpus in Figure 6b was 7-segmented and regenerated the same number of segments after operation. The contralateral palpus, also 7-segmented in the 2nd instar, has fused into 6-segments. Figure 6c shows a right palpus, 8-segmented in the 2nd instar, in which the original number of segments was restored after operation and retained thereafter. The left unoperated palpus was also 8-segmented, but three distal segments had fused by the 6th instar. The right palpus in Figure 6d was originally 8-segmented, and did not restore the number until the final instar. In Figure 6e, the right palpus was also originally 8-segmented. After operation the two distalmost segments regenerated in the 4th instar, and were retained throughout following instars. The left unoperated palpus, 8-segmented with a subtle tendency of fusion in the 2nd instar, showed more advanced fusion in the 6th instar.

The percentages of bristles on regenerated maxillary palpi are shown in Table 5. Bristle-bearing palpi usually had only one bristle on the 4th segment. In experiments with amputation levels 1–2, 2–3 and 3–4, the 4th segment was ablated by amputation and later regenerated. In this case, no bristle appeared until the 4th instar. Some palpi later developed a bristle, but the percentage was lower than that of the unoperated palpi even in the

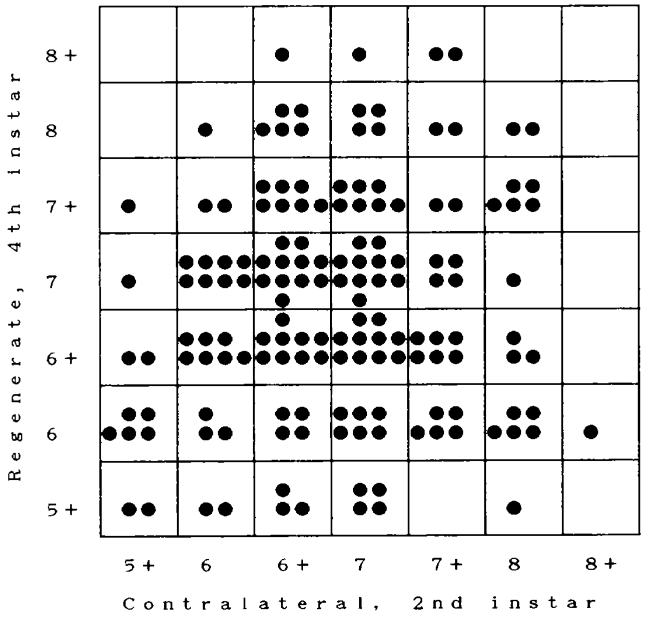

FIG. 5. Comparison of the number of segments between contralateral unoperated palpi (2nd instar) and regenerated palpi (4th instar). For the symbol "+", see Fig. 2.

TABLE 4. Decrease in the number of segments in regenerated *mpe* maxillary palpi from the 4th to 6th instar

Amputated level	No. of nymphs	Decrease in No. of segments					Av. No. of segments Instar	
		0	−0.5	−1.0	−1.5	Av.	IV	VI
1–2	21	10	8	3	0	−0.33	6.50	6.17
2–3	32	14	14	4	0	−0.34	6.56	6.22
3–4	36	22	11	2	1	−0.25	6.75	6.50
4–5	41	19	18	4	0	−0.32	7.07	6.76
5–6	48	22	20	4	2	−0.35	6.32	5.97
6–7	29	16	12	1	0	−0.24	6.40	6.16

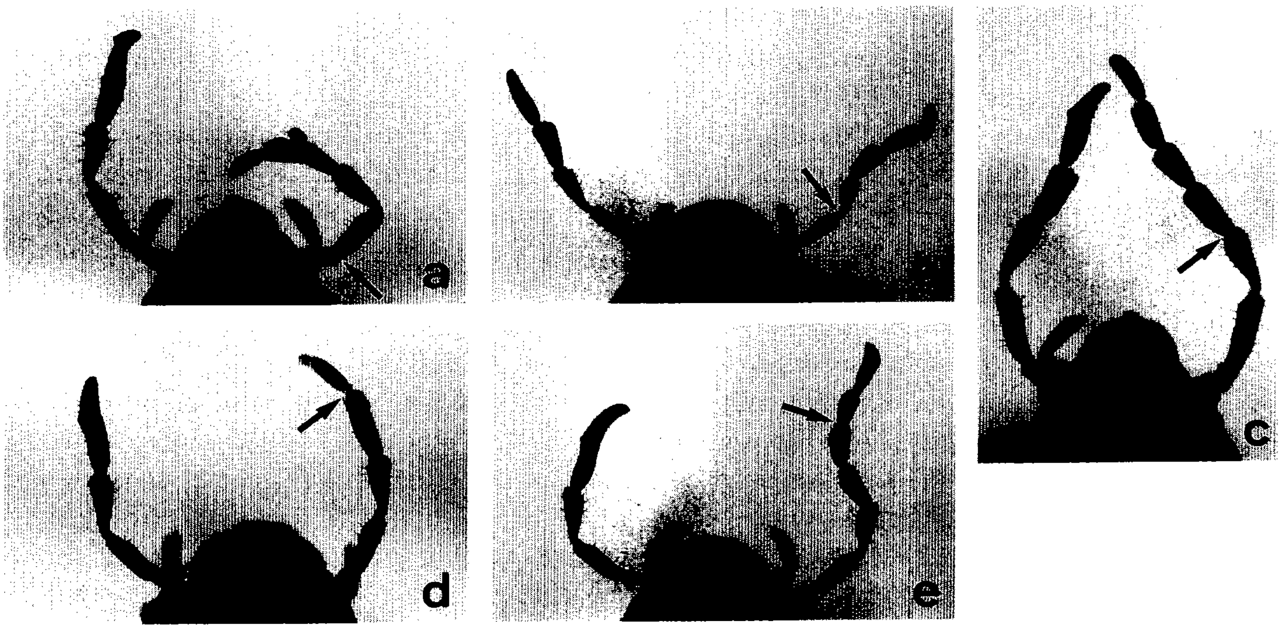

FIG. 6. Examples of regenerated *mpe* maxillary palpi (6th instar). Right maxillary palpi were amputated in the 2nd instar at the indicated levels (arrows): between the 2nd and 3rd segment (a), 3–4 (b), 4–5 (c), 5–6 (d), and 6–7 (e). Left maxillary palpi were unoperated controls. One or two labial palpi are also seen. (a and c, ×16; b and e, ×12; d, ×14)

TABLE 5. Percentages of bristles on regenerated *mpe* maxillary palpi

	Amputated level	Instar IV	Instar VI
4th segment regenerated	1–2	0.0 (0/29)	28.6 (6/21)
	2–3	0.0 (0/37)	28.1 (9/32)
	3–4	0.0 (0/40)	41.7 (15/36)
4th segment unoperated	4–5	10.0 (5/50)	51.2 (21/41)
	5–6	16.0 (8/50)	50.0 (24/48)*
	6–7	18.8 (6/32)	58.6 (17/29)*

* In the instar VI exceptionally found were a few palpi with double bristles (two in 5–6, one in 6–7 amputation) on the unoperated 4th-segment. In parentheses are shown the numbers of bristle-bearing palpi/total palpi.

6th instar. On the other hand, the 4th segment was not eliminated in experiments with amputation levels 4–5, 5–6 and 6–7. In this case the percentage of bristles was similar to that of unoperated palpi both in the 4th and in the 6th instar.

DISCUSSION

Maxillary palpi clearly evolved through the modification of leg-like appendanges [11, 12]. However, legs of wild-type German cockroaches have nine segments whereas maxillary palpi normally have five segments. Prominent bristles occur on the tibia but never on wild-type maxillary palpi. The *mpe* mutant increases the resemblance of maxillary palpi to legs by variable increases in the number of segments up to nine and the presence of a bristle on the 4th segments, a segment presumably homologous to the tibia [1, 11]. The discovery here of double and triple bristles supports homology of the 4th maxillary-palp segment to the tibia. Supernumerary segments are apparently a variable expression of tarsal segments.

The increased resemblance to legs suggests that *mpe* expresses a primitive developmental pathway. It belongs to a group of mutants on chromosome 9 that apparently express primitive traits [1, 13], including prowing (*Pw*) [14, 15], notched sternite (*st*) [16], and stumpy (*sty*) [17]. Although 8+ segments in *mpe* palpi suggested a rare expression of five tarsal segments, four tarsal segments is probably a more primitive trait than five segments. A leg mutant, fused tarsi, has 4-segmented tarsi, *i.e.*, 8-segmented legs [18]. Regenerated cockroach legs also have 4-segmented tarsi [3–7]. It was suggested that archetypical appendages were midleg-like nonspecific forms with 8 segments [6].

Maxillary-palp-elongate (*mpe*) is of interest in that the mutation affects the bilateral symmetry of body plan. The external morphology of cockroaches shows complete bilateral symmetry. The exact likeness between the opposite sides of the body has been verified by high correlation coefficients calculated in the length of appendages of the German cockroach [19]. For example, the correlation coefficients between right and left hindleg ranged 0.86–0.98 in the femur and 0.90–0.99 in the tibia during nymphal instars and adult stage. These very high correlations suggest the existence of a regulatory mechanism to make right and left structures the same in size. The correlation in numbers of segments on right and left *mpe* palpi was exceptionally low (Fig. 2, $r=0.41$). Furthermore, the correlation was even lower when regenerated palpi were compared with the same palpi before operation ($r=0.24$, Fig. 4) or with contralateral unoperated controls ($r=0.11$, Fig. 5).

Why is the number of segments frequently different between right and left in *mpe* maxillary palpi? The fluctuation in the number of segments suggests a deficiency of regulation for bilateral symmetry. We suggest that the increase and instability of the number of segments of *mpe* maxilary palpi is caused by a deficiency of function of the *mpe*+ gene. If so, *mpe*+ not only suppresses the expression of leg-like characteristics of maxillary palpi but also controls the bilateral symmetry in length and segment number of the palpi.

During postembryonic development of the German cockroach, the number of segments increases in antennae and cerci [20], but is unchanged in legs [21] and wild-type maxillary palpi. *mpe* maxillary palpi are the first appendages found where some segments fuse with each other to decrease the number of segments during postembryonic development.

In regeneration experiments of wild-type maxillary palpi, the number of segments remained five after regeneration in *Blabera* [22], and *Blattella* [Tanaka, unpubl.]. This was true with amputation at any levels from 1–2 to 4–5 in *Blattella.* In *mpe* maxillary palpi regeneration, however, the number of segments often changed within the range from 5+ to 8+, including both increases and decreases. Palpi with fewer segments tended to increase the number of segments, and *vice versa* (Table 3). It was first thought that there might be a mechanism averaging the number of segments of regenerated *mpe* palpi. This idea, however, is probably wrong, since not only the correlation between the number of segments before amputation and the number in regenerated 4th instar was very low but also the variation of the latter was as large as that of the former (Fig. 4).

The number of segments of a regenerate was irrelevant to that of the original unoperated palpus. This fact shows that an amputated stump does not regenerate new segments accoring to a "memory" of the original number of segments before amputation. The number of the segments of a regenerate was also irrelevant to that of the contralateral palpus. This likewise shows that the stump does not use the number of segments of contralateral palpus as a "reference" for the number of segments to be regenerated.

Both the increase in the number of segments and the presence of bristles in *mpe* maxillary palpi are characteristics that increase their resembrance with legs. Hence we wondered if there might be a positive correlation between the number of segments and the frequency of bristles. However, we failed to detect such a relationship between the two. Maxillary palpi with more segments did not always show higher frequency of bristles (Table 2). Moreover, the frequency of bristles increased during development whereas the number of segments sometimes decreased. There seemed to be an increase in leg-like characteristics in the segment corresponding to the tibia (4th segment) but a decrease in those corresponding to tarsal segments (tarsomeres). *mpe* is similar to homeotics and, like homeotics, probably controls a battery of genes. Possibly one that controls bristle formation is not "turned off" during post embryonic development, but another controlling segment number is subject to modifiers that cause fusion or less subject to control by *mpe* in later development. In spite of variability of expression, supernumerary segments and bristles are evident during post embryonic development in both unaltered *mpe* and *mpe* regenerates that provide new insight into the characteristics of this mutant and its wild-type allele.

ACKNOWLEDGMENTS

We thank Mrs. Nancy Boles for technical assistance.

REFERENCES

1 Ross, M. H. and Tanaka, A. (1988) Genetic variability in the German cockroach. XII: A third mutant that suggests chromosome 9 carries a highly conserved group of closely linked genes. J. Hered., **79**: 439–443.

2 Bullière, D. and Bullière, F. (1985) Regeneration. In "Comprehensive Insect Physiology, Biochemistry and Pharmacology, Vol. 2 Postembryonic Development". Ed by G. A. Kerkut and L. I. Gilbert, Pergamon Press, Oxford, pp. 371–424.

3 Brindley, H. H. (1897) On the regeneration of the legs in the Blattidae. Proc. Zool. Soc. Lond., **60**: 903–916.

4 O'Farrell, A. F. and Stock, A. (1953) Regeneration and the moulting cycle in *Blattella germanica* L. I. Single regeneration initiated during the first instar. Aust. J. Biol. Sci., **6**: 485–500.

5 Roberts, B. (1973) The relative growth of normal and regenerated legs of the cockroach *Blattella germanica* (L.). Trans. R. ent. Soc. Lond., **126**: 447–461.

6 Tanaka, A., Ohtake-Hashiguchi, M. and Ogawa, E. (1987) Repeated regeneration of the German cockroach legs. Growth, **51**: 282–300.

7 Tanaka, A. and Ross, M. H. (1989) Tibia to femur ratios of unaltered and regenerated legs of the stumpy mutant of the German cockroach. Zool. Sci., **6**: 927–933.

8 Penzlin, H. (1963) Über die Regeneration bei Schaben (Blattaria) I. Das Regenerationsvermögen und die Genese des Regenerats. Wilhelm Roux' Arch., **154**: 434–465.

9 Bohn, H. (1965) Analyse der Regenerationsfähigkeit der Insektenextremität durch Amputations und Transplantationsversuche an Larven der Afrikanischen Schabe *Leucophaea mederae* Fabr. (Blattaria) I. Regenerationspotenzen. Wilhelm Roux' Arch., **156**: 49–74.

10 Bullière, D. (1967) Étude de la régénération chez un insecte Blattoptéroide *Blabera craniifer* Burm. (Dictyoptère). I. Influence du niveau de la section sur la régénération de la patte métathoracique. Bull. Soc. Zool. Fr., **92**: 523–536.

11 Snodgrass, R. E. (1935) Principles of Insect Morphology. McGraw-Hill, New York. pp. 130–156.

12 Matsuda, R. (1965) Morphology and Evolution of the Insect Head. Amer. Entomol. Inst., Ann Arbor. pp. 1–334.

13 Ross, M. H. and Keil, C. B. (1978) Genetic variability in the German cockroach XI. Does chromosome 9 carry remnants of a primitive gene system? J. Hered., **69**: 337–340.

14 Ross, M. H. (1964) Pronotal wings in *Blattella germanica* (L.) and their possible evolutionary significance. Amer. Mid. Natur., **71**: 161–180.

15 Ross, M. H. and Cochran, D. G. (1971) Cytology and genetics of a pronotal-wing trait in the German cockroach. Can. J. Genet. Cytol., **13**: 522–535.

16 Ross, M. H. (1966) Notched sternite: A mutant of *Blattella germanica,* with possible implications for the homology and evolution of ventral abdominal structures. Ann. ent. Soc. Amer., **59**: 473–484.

17 Ross, M. H. (1975) Genetic variability in the German cockroach X. Genetics of pale purple, pearl, and stumpy. J. Hered., **66**: 155–159.

18 Cochran, D. G. and Ross, M. H. (1967) Cockroach genetics. In "Genetics of Insect Vectors of Disease". Ed. by J. W. Wright and R. Pal, Elsevier, Amsterdam, pp. 403–415.

19 Tanaka, A. (1984) Relative growth between femur and tibia in the German cockroach, *Blattella germanica.* Growth, **48**: 278–296.

20 Tanaka, A. and Hasegawa, A. (1979) Nymphal development of the German cockroach, *Blattella germanica* Linné (Blattaria: Blattellidae), with special reference to instar determination and intrainstar staging. Kontyû (Jpn. J. Ent.), **47**: 225–238.

21 Tanaka, A., Ogawa, E. and Ohtake, M. (1986) Relative growth of leg segments of the German cockroach, *Blattella germanica.* Growth, **50**: 273–286.

22 Urvoy, J. et Le Bris, R. (1968) Étude de la régénération des cerques, des palpes labiaux et des palpes maxillaires chez *Blabera craniifer* [Orth. Blattidae]. Ann. Soc. ent. Fr. (N. S.), **4**: 371–383.