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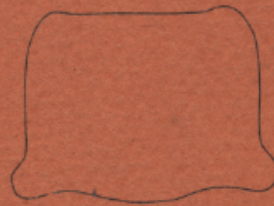
# TRIBOLIUM

Information Bulletin

8



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March 1965

MATERIAL CONTRIBUTED BY WORKERS ON TRIBOLIUM  
AND OTHER COLEOPTERA

DEPARTMENT OF GENETICS, UNIVERSITY OF CALIFORNIA  
BERKELEY, CALIFORNIA

TRIBOLIUM INFORMATION BULLETIN

Number 8

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Editor: A. Sokoloff, Department of Genetics,  
University of California, Berkeley, California

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#### NOTE

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FOREWORD

The present issue of TIB, it would seem at this writing, will far exceed in length previous issues of the bulletin. This undoubtedly reflects the increased use of *Tribolium* in genetic and ecological research for the last few years, and a recognition on the part of contributors of the necessity of this bulletin as a means of exchanging information.

Again it is a pleasure to acknowledge the fine cooperation of contributors in submitting their material on time. It would greatly facilitate my task and speed up the publication of TIB if contributors would follow instructions closely in regard to the identification of each of the items submitted with their institutions, and the forwarding of bibliographies in typewritten pages not to exceed the length of a 3 x 5" reference card so that I may paste these bibliographies directly, instead of having to cut them up in strips to fit the cards.

The assistance of Mrs. Marjorie Hoy in proof-reading the copy prepared by Mrs. Mary Jo Rawlins is gratefully acknowledged.

The publication of TIB-8 was made possible by USPHS grant GM-08942.

A. SOKOLOFF

Berkeley, California  
March, 1965



EDITOR'S RANDOM NOTES

Once again it has been necessary to include a long list of wild type and mutant stocks available at Berkeley. In part this is prompted by the fact that from time to time we get requests for information of mutants available. It is far easier to produce a few more copies of these pages while the material is at the printer than having to thermofax a separate stock list everytime a request arrives. Furthermore, one of the functions of the Stock Center should be to provide up-to-date information not only of the various mutants available, but also their linkage relationships. In view of the fact that this is one of the few laboratories in which such work is being carried out, a periodic revision of these stock lists appears to be mandatory.

\* \* \* \*

It is gratifying to the writer to have witnessed the rapid growth of this bulletin. The first issue was only an announcement of its creation. No. 2 reproduced the bibliography on Coleoptera compiled by Dr. Thomas Park and included four notes. No. 3 included a description of the biology (and listed equipment used in the rearing) of Tribolium, and 10 research notes. The number of research, technical and teaching notes increased to twenty in the fourth issue, and it appeared that the number of such notes would stabilize at around 30 (there were 29, 36 and 30 notes in issues 5-7 of the bulletin, respectively). This, however, appears to be far from the case, since the present issue includes about 50 notes, and many of these are rather lengthy. Of interest, also, is the "rash" of mutants described. Up to 1958, half a dozen or so mutants were known in Tribolium castaneum and T. confusum. In 1960, eleven new mutants were reported in these two species and Latheticus oryzae; in 1961, eighteen; in 1962, twenty-eight; and in 1963, twenty-two. In the last two years, however, a total of 135 mutants in various Coleoptera (but the majority in Tribolium) have been found! Most of these have appeared spontaneously, and the majority are mutants which are new, i.e., not allelic to previously described mutations. This despite the fact that it takes most Coleoptera kept in laboratories over a month to complete their life cycle at room temperature, and without a particularly intensive effort in looking for mutants.

As I indicated last year, the large number of mutants available poses a problem on what to do with them. They are far too numerous for any one laboratory to handle. In view of the fact that the 10 linkage groups in T. castaneum appear to have been identified, and that in T. confusum the nine linkage groups will soon bear easily identifiable markers, it is earnestly hoped that geneticists having graduate students will take advantage of this material, available for distribution without restriction, and assign their students the task of determining their linkage relationships. We are willing to send this material to anyone anywhere in the world (and extraterrestrially if we can find a means of getting this material to

interested parties). Having had a first-hand acquaintance with these beetles I can highly recommend their use in genetic research and teaching. The fact that these organisms have not been investigated genetically has an intrinsic interest and such studies sometimes provide unexpected interesting results. Furthermore, some genes affect major taxonomic characters (see, for example, illustration on the cover and a note on pleiotropic effects of sex-linked and autosomal genes in *Tribolium* in this issue of TIB). Besides, within the family Tenebrionidae or even within the genus *Tribolium* there has already been a long period of evolution, the species having diverged to the point where hybridization is impossible. Hence, the material is highly suitable for comparative genetic studies, especially since, of the few mutants already known in *Tribolium* and *Latheticus*, a number exhibit similar phenotypic effects.

\* \* \* \*

The editor is concerned about the fact that there has been a sudden increase in the number of notes pertaining to the effect of insecticides on various Coleoptera. If this were the only outlet for such notes, it would seem proper to continue publishing them in TIB. However, since 1958 Dr. D. Dresden, Prinses Marijkeweg 22, Wageningen, Holland, has been publishing ITIS (Insect Toxicologists Information Service). In view of the existence of ITIS (and the anticipated further growth of TIB) it would seem to the writer that notes dealing with effects of insecticides on Coleoptera (except, perhaps, those dealing with genetic aspects of insecticide resistance in this order) should be submitted to ITIS instead of TIB. I would welcome any comments on this point.

\* \* \* \*

The illustration on the cover, prepared by Mrs. Barbara Daly, shows various mutants in *T. confusum* having the prothorax affected. A and B are the pupal and adult phenotypes of "knobby prothorax." While these processes are not exactly wing-like, they are suggestive of an extra set of appendages. (Two homeotic mutants producing a real elytra-like wing or a membranous-wing-like appendage arising from the prothorax, described in the New Mutant section under the names "alate prothorax" and "megalothorax," have been found in *T. castaneum*). C is a ventral view of the normal prothorax; D illustrates "deflected epimera." Of greater importance to the taxonomist should be figures E, F illustrating "separated epimera" (sep). In F the epimera are short and the coxal cavities become open. Specimens of sep with shorter and practically non-existent epimera can be found. It may be noted also that the mutant "sleek" described elsewhere, among the various parts of the body deformed, also had coxal cavities of the first pair of legs open.

\* \* \* \*

On September 1, 1965, the editor will begin teaching at the California State College at San Bernardino, but will continue as Associate Research Geneticist at Berkeley. In order to assure prompt delivery, correspondence should be addressed to the writer directly at California State College at San Bernardino, San Bernardino, California.

ANNOUNCEMENTS

Grosch, D. S.  
Genetics Department, North Carolina State Campus  
Raleigh, North Carolina

As a result of our interest in collecting new wild strains of wasps which parasitize lepidopteran grain pests we are setting traps in rural grain bins. Often we find live *Tribolium* in these traps which we would be willing to mail to investigators in the United States.

Sokoloff, A.  
Genetics Department, University of California  
Berkeley, California

Investigators of *Tribolium* and other pests are herewith informed of the existence of the new *Journal of Stored Products Research*. Four issues of this journal will be published by the Pergamon Press Ltd. starting January, 1965. The expected subscription rates are 10 pounds per annum for libraries and institutions or 5 pounds per annum for individuals.

Papers offered for publication should be original contributions dealing with the biology, ecology, physiology, behavior, taxonomy, genetics and control of the insects, mites, fungi and other organisms associated with stored products, together with studies on the physical and chemical nature of the stored product environment which have relevance to these organisms and their control. Short communications that the author does not intend to publish in more detail at a later date will also be acceptable. Occasional review articles will be accepted by arrangement with the editor.

Papers should be written in English, French or German. Those in French or German should have an English abstract.

Interested TIB readers should submit their manuscripts in standard form to:

G. V. B. Herford, Editor, or  
C. E. Dyte and  
L. P. Lefkovitch, Associate Editors

Pest Infestation Laboratory  
Slough, Bucks, England

Stanley, J.  
Department of Zoology, McGill University  
Montreal, P. Q., Canada

Work is proceeding with the design of an air-stream cleaner for eggs, based on putting the mass of mixed eggs and frass in a tall glass tube with a bottom made of fine mesh stainless steel. A gentle stream of air lifts the eggs and frass, and blows the frass out of the top of the tube, but cannot lift the eggs. Several prototypes have been built, but the design is not yet such as to give perfect separation (occasional eggs are lost). However, the results are good enough to warrant further work. If others are working on a similar device, the author would like to hear from them.

QUOTABILITY OF NOTES

DAWSON, P. S., has given authorization to quote from his descriptions of new mutants.

DYTE and BLACKMAN authorize anyone who wishes to quote from any past contributions on new mutants described in TIB.

HO, FRANK. The descriptions appearing in the section on New Mutants prior to 1964 may be quoted.

KRAUSE, E. Articles appearing in TIB 6, pp. 44-45, may be quoted.

SOKOLOFF, A. All descriptions of New Mutants in issues of TIB prior to 1964 may be quoted.

## NEW MUTANTS

\*REPORT OF A. C. BARTLETTAnthonomus grandis

1. apricot ( $p^a$ ): Recessive autosomal gene controlling eye color. Allelic and dominant to pearl. Isolated in the  $F_2$  of a cross between yellow and pearl. Eyes of the mutant show the dark ocular ring of pearl with the apricot-colored ommatidia.
2. ebony ( $e$ ): Semi-dominant autosomal gene controlling body color. Identical in color and gene action to slate; however, crossing results show that these are two different loci. The strain was started by a single virgin female picked up in the laboratory on a bench top. The female exhibited the black color characteristic of the homozygous form. The heterozygote has a dark bronze color. The heterozygous state of ebony is distinguishable from the heterozygote of slate even though the homozygotes are indistinguishable.
3. gnarled ( $g$ ): A recessive lethal mutation, presumably autosomal but this has not been tested adequately. So far no obvious phenotype is observed in the heterozygotes carrying a gnarled gene but the expression of the homozygote is very striking. Expression of  $g/g$  is variable but the normal appearance shows the legs and elytra twisted and shortened. The tibia is shortened and the tarsi are folded away from the body. The beak is shortened and the antenna shortened and twisted. The homozygotes sometimes eclose but are always too crippled to eat or walk and soon die. A majority of homozygous pupae darken but do not eclose. We are trying to find a way to identify heterozygotes so selection can be practiced on each generation to perpetuate the stock. This mutant was found during the third generation of inbreeding of a pair of weevils from the Florence strain. Goodness-of-fit tests have been run on the proportions of gnarled in the line and show a good fit to the expected 3 to 1 ratio for a recessive gene.
4. pearl ( $p$ ): Recessive autosomal gene controlling eye color. Color of eyes translucent white in adults of all ages. Expressed in pupae at the time when darkening of eyes occurs in wild-type stocks. Complete penetrance and good expressivity. Never overlaps wild-type. In this stock the center of the eyes are pearl colored but the outer margin is dark giving the weevil a spectacled appearance when viewed from the side. Obtained in  $F_2$  of an irradiation test. Probably radiation induced. Not linked to yellow, slate or ebony. Allelic to apricot.
5. slate ( $s$ ): Semi-dominant autosomal gene controlling body color. Homozygote deep black color, heterozygote is light bronze and easily classified when compared to wild-type or slate. This mutant was

found as heterozygotes in a culture from Acala, Mexico. Preliminary observations on viability and fertility indicate that the heterozygote is more fertile than either homozygote and may be somewhat faster in development.

\*REPORT OF A. E. BELL

T. castaneum

1. bead (bd). Shideler. Autosomal recessive appearing spontaneously in our Chicago Inbred Line at generation 51. Antennal segments are elongated and reduced in size giving a "beaded" appearance. Frequently, the antennae are lighter in color (blond) than the wild type. Expression is variable with about 75% penetrance.
2. deformed antenna (da). Shideler. Autosomal recessive found in a mc m j marker stock. The three terminal segments are fused as in the paddle mutation. Variable expression with about 90% penetrance.
3. pearl (p<sup>S</sup>). Shideler. Spontaneous in our Fla Inbred Line after four generations of full sibbing. Allelic to pearl (p) and similar in expression.
4. red (r<sup>S</sup>). Shideler. Spontaneous in a body weight selection line. Allelic to red (r) and similar in expression.

\*REPORT OF C. E. DYTE, D. D. SHAW, AND MISS D. G. BLACKMAN

Tribolium castaneum

tawny (b<sup>t</sup>). This name is proposed for the autosomal recessive previously called "bronze" in TIB-6, which has proved to be allelic to black. B/b and b<sup>t</sup>/b<sup>t</sup> are a similar shade of bronze; b/b<sup>t</sup> is a darker bronze. B/B;s/s beetles appear intermediate between b<sup>t</sup>/b<sup>t</sup>;S/S and b<sup>t</sup>/b;S/S when compared en masse, but it would be very difficult to distinguish sooty homozygotes from these two tawny genotypes in mixed populations.

Tenebrio molitor (Tenebrionidae)

pearl (p). Similar to other pearl mutants. Probably similar to fleischfarbenen Augen of Ferwerda but genetics not yet studied.

Rhizopertha dominica (Bostrichidae)

black (b). Spontaneous in laboratory culture of unrecorded origin. Body colour is blackish instead of brown. True-breeding culture established but genetics not yet studied.



Oryzaephilus surinamensis (Silvanidae)

pearl (p). Similar to other pearl mutants, and noted as unstudied genetically in TIB-6. Apparently an autosomal recessive yielding normal  $F_1$  and an  $F_2$  of 87 pearl and 273 normal when mated with wild type.

Cryptolestes turcicus (Cucujidae)

red (r). Eye-colour mutation similar to red in some strains of T. castaneum. Undoubtedly a sex-linked recessive producing a pale pink eye colour but extrinsic factors have disturbed ratios in some experiments. We have previously called this mutant "pearl" but Sokoloff has suggested red is more appropriate, and having seen red T. castaneum we agree.

Dermestes maculatus (Dermestidae)

1. fuscous (fu). Spontaneous in a culture originating from Australia. Elytra deep brown instead of black. Preliminary crosses suggest autosomal semi-dominance.
2. light wing (l). Spontaneous in culture originating from Australia. Costa, subcosta, radius and sector and enclosed cells unpigmented. Genetics not yet studied but Philip (1940) mentions similar autosomal recessive.
3. pearl (p). Spontaneous in culture of unrecorded origin. Appears similar to other pearl mutants but genetics not yet studied. Possibly a re-occurrence of "white-eye" reported by Philip (1940) but her cultures are known to have been destroyed.
4. rufous (ru). Spontaneous. Eye colour red-brown. Genetics not yet studied.
5. second sex pit (ssp). Spontaneous in culture originating from Australia. Males with sex pit on 3rd abdominal sternite besides the one normally present on sternite 4. Genetics not yet studied. Philip (1940) reported limited tests with a similar mutant which suggested it was an autosomal recessive with sex-limited expression.
6. short elytra (sh). Spontaneous in culture originating from Australia. Elytra shortened exposing last abdominal segment. Genetics not yet studied.

\*REPORT OF E. R. RICHTribolium castaneum

pearl-like. In general appearance this mutant looks like pearl but has not yet been checked for allelism. Autosomal recessive inheritance, no indication of decreased viability.

\*REPORT OF A. SOKOLOFFCryptolestes turcicus

The following two abnormalities were found in some material derived from stocks maintained at the Pest Infestation Laboratory, Slough, Bucks, England.

1. crooked antennal (cka). Hoy and Sokoloff, 1964. Autosomal recessive of variable expression and incomplete penetrance. Usually segments 4 and 5 of one or both antennae become fused into a sausage-shaped segment of about the same length as the two separate segments. Sometimes more distal segments may be affected in the same individual; occasional individuals may exhibit a bifurcated antenna beyond the fused segments but these may be teratologies.
2. runty (rtty). Sokoloff and Hoy, 1964. Normally males are smaller than females. The abnormality cited herein is restricted to the females, which are reduced to about half the size of normal females. No males have been observed to be reduced in size to that extent. The fact that many females exhibit this phenotype indicates the condition is heritable, but the mode of inheritance has not been worked out.

Latheticus oryzae

1. droopy elytra (dre). Sokoloff, 1960. As in T. castaneum and in T. confusum this abnormality is characterized by a divergence of the elytra, often starting at the scutellum. The sclerotized wings may droop at the sides, or they may be only slightly "split" at the posterior end. Probably a phenodeviant, since dre × dre crosses produce beetles predominantly with normal elytra.
2. elongated elytra (ele). Hoy and Sokoloff, 1964. A recessive of incomplete penetrance. The elytra extend beyond the tip of the last abdominal segment, but they are not elongated to the extent as in a similarly named mutant in T. confusum, the elongation being generally much less than the length of one abdominal segment. A very large number of larvae in the ele stock exhibit prothetely. Sometimes the elytra are expanded becoming as long as the combined length of the two wing-bearing segments, plus the first two abdominal segments. In other cases the buds are brief lateral bud-like structures. If so, the elytral buds or the membranous wing buds or both may be everted. It is not clear whether this prothetelous condition is associated with the ele gene, or whether it is due to the release of quinone by the contemporary imagoes confined in the same creamer. Whatever the reason, it is clear that the incidence of prothetelous larvae in this stock is far greater than any so far observed in handling other stocks or in various crosses.

3. fused antennal segments-1 (fas-1). Sokoloff, 1960. Spontaneous recessive found while attempting to establish the mode of inheritance of pearl. The fas-1 gene has incomplete penetrance: the stock has a very large number of beetles with both antennae normal. Even in one individual the antennal segments on one side are normal and those on the other are variously fused. Most frequently encountered are fusions in segments 8-9 (in the club). However, fusions of these segments together with fusions in segments 4-5, and 6-7 (in the funicle) or fusions of only these segments in the funicle are not rare, as can be seen in Table 1.
4. tucked elytra (tke). Sokoloff, 1963. Spontaneous in brown body crosses. One male and two females appeared in a single-pair mating whose elytra were folded under as in the sex-linked te. This proved to be but one expression of the recessive tke. In other pupae the elytra may be widely separated and/or short exposing the tarsi of the hind legs. In the adult the phenotype is also quite variable ranging from beetles with elytra short as in T. castaneum she, to elytra slightly split, to elytra split starting at the scutellum, to elytra split and tips reduced in width; to elytra with tips tucked under in te-like fashion. Any combination of two of these phenotypes may occur, and the elytra may bear a blister. Viability may be reduced, but so far tke has not been freed of bwb which by itself reduces viability, so that the reduction in viability of tke may be due to the bwb gene.

#### T. castaneum

1. akimbo (akb). Hoy and Sokoloff, 1964. Derived from a population traceable back to an irradiated (6000 Kr) male mated to an unirradiated female. Several (more than three) generations later two females and one male were found with rt (reduced tibia, described below. Their descendants produced a number of mutations including sta-like, jagged antecoxal piece (jac), and akb. This mutant resembles thu in T. confusum: the elytra are variously raised above the abdomen, exposing the posterior abdominal segment to a varying degree. At a point one fifth to one sixth of the elytral length behind the antero-lateral margin of the elytra and the scutellum there is a notable crease or depression as if the elytra had been pushed down at this point. The elytra in akb usually meet at the midline, but in a small number of mutants they may be divergent, starting at the scutellum. Examination of the pupa reveals that the primary cause of this abnormality is the development of a blister in the membranous wings which displace the elytra. Apparently the fluid in these blisters is not withdrawn into the body cavity before the beetle sclerotizes, producing the misshapen elytra. Preliminary crosses suggest an autosomal recessive mode of inheritance.
2. alate prothorax (apt). Sokoloff and Hoy, 1964. A case of hereditary homoeosis. It was first found by the writer as a female pupa in crosses involving ca and ble. The prothorax in this pupa was

Table 1. Fusions observed in the antennae of fas-1 in L. oryzae.

Males		Females	
Right	Left	Right	Left
6-7	0	8-9	8-9
8-9	0	8-9	0
8-9	0	0	4-5
0	6-7	8-9	8-9
6-7, 8-9, 10-11	0	0	8-9
6-7	0	8-9, 10-11	6-7, 8-9, 10-11
4-5	0	4-5	0
4-5, 8-9	0	0	4-5, 8-9
5-6, 8-9	8-9	8-9	8-9
0	8-9	8-9	7-9
4-5	0	4-5	0
8-9	6-7, 8-9	4-5	4-5
5-6	0	8-9	8-9
4-5, 8-9	8-9	4-5	8-9
8-9	8-9	0	8-9
4-5	0	0	9-10
0	7-8	8-9	0
0	7-9	0	4-5
0	7-8	0	8-9
0	8-9	8-9	8-9
8-9	8-9	0	7-9
4-5, 6-8	4-5, 8-9	0	7-9
0	6-7	4-5	0
0	8-9	5-7, 8-11	0
4-5, 8-9	8-9	8-9	8-9
4-5	0	8-9	8-9
8-9	4-5, 8-9	4-5	8-9
0	8-9	0	6-7
0	8-9		
8-9	0		
0	5-8		
0	8-9		
0	8-9		
0	4-5		
4-5	0		
8-9	8-9		
8-9	8-9		
5-6	0		
8-9	4-5, 8-9		
8-9	8-9		
8-9	8-9		

greatly enlarged and the head directed away from the body at a 45° angle. The imago emerging from it had a similarly enlarged prothorax. This proved to be but one expression of the gene. A more frequent expression was the production of elytra- or membranous wingbud-like appendages which arise from the lateral edges of the prothorax about midway between the anterior and the posterior edges of this body segment. These growths are evident in the pupa, but they may break off upon eclosion of the imago, leaving a roughly circular, unsclerotized area. Often, in the imago, the anterior dorsal margin of the prothorax is incomplete, irregularly V-shaped, and the dorsal surface of the pronotum is variously indented. With selection, the wing-bud like processes in the pupa have been observed to form an appendage which, except for the reduction in size, resembled the elytra in shape. Furthermore, its wing venation closely resembled that of the elytra, and tracheae were visible. Thus, the presence of these two characters leave little doubt that we are here dealing with a homoeotic mutant in which a pair of prothoracic wings is formed. The mutant can be recognized in the larva only if the prothorax is enlarged, since (if prothelous cases are excluded) wing and elytral buds develop in the pupa, or if the prothorax is irregular in shape. If so, the pigmented prothoracic tergites may become asymmetrical. Preliminary crosses suggest a semidominant mode of inheritance, but penetrance is poor and viability of "alate" individuals very low, most dying in the pupa. A mutation producing pupae with similar swollen prothoraces has recently been found in a stock of Fta c/+c.

3. antennae and tarsi fused (atf). Sokoloff, 1961. Spontaneous autosomal recessive of variable expression found in the course of determining linkage relationships between aa and c<sup>S</sup>. The atf gene causes a fusion of variable segments of the tarsi and sometimes the effect extends to the funicular segments of the antennae, but these appendages may be free of fusions while the tarsal segments are nearly always fused. The data given in Table 2 are confined to the distal segments of the tarsus. After mounting the legs it became evident that when atf is strongly expressed there is also a partial fusion of the first tarsomeres which is not very obvious when the tarsi are examined in situ.
4. banjo (bj). Lasley and Sokoloff, 1960. Autosomal recessive. Spontaneous in Chicago wild type. The elytra in the adult may be widely divergent and drooping at the sides, or they may meet at the midline but they are short, not reaching the tip of the abdomen. Tests of allelism are under way.
5. bent elytral tips (bet). Sokoloff and Hoy, 1964. Found in a stock of ap bf. A recessive of variable expression and incomplete penetrance. In the pupa the elytra are variously separated from the membranous wings (which remain in their normal position over the legs) and in a few cases the tips may be folded under resembling te.

Table 2. Tarsal fusions found in atf in T. castaneum.

No.	Males						Females					
	Leg 1		Leg 2		Leg 3		Leg 1		Leg 2		Leg 3	
	L	R	L	R	L	R	R	L	R	L	R	L
1	4-5	4-5	4-5	4-5	3-4	3-4	4-5	4-5	4-5	4-5	0	0
2	4-5	4-5	4-5	4-5	2-4	2-4	4-5	0	0	4-5	3-4	3-4
3	4-5	4-5	4-5	4-5	3-4	3-4	4-5	4-5	3-5	3-5	1-3	1-3
4	4-5	4-5	4-5	4-5	3-4	3-4	4-5	4-5	0	4-5	2-4	2-4
5	4-5	4-5	4-5	4-5	3-4	3-4	4-5	4-5	3-5	3-5	3-4	3-4
6	4-5	4-5	4-5	4-5	2-4	3-4	4-5	4-5	0	4-5	3-4	3-4
7	4-5	4-5	4-5	4-5	2-3	2-3	4-5	4-5	4-5	4-5	3-4	3-4
8	4-5	4-5	4-5	4-5	2-4	3-4	4-5	4-5	3-5	3-5	2-4	2-4
9	4-5	4-5	4-5	0	1-4	2-4	4-5	4-5	3-5	3-5	1-3	1-4
10	4-5	4-5	4-5	4-5	2-4	2-4	4-5	4-5	4-5	4-5	3-4	1-3
11	3-5	4-5	-	3-5	1-4	1-4	3-5	3-5	3-5	3-5	1-4	1-3
12	4-5	4-5	4-5	4-5	3-4	3-4	3-5	3-5	3-5	3-5	2-4	2-4
13	4-5	4-5	3-5	3-5	1-4	1-4	4-5	4-5	3-5	3-5	2-4	2-4
14	0	4-5	4-5	0	0	3-4	4-5	4-5	4-5	4-5	2-4	2-4
15	4-5	4-5	4-5	4-5	2-4	3-4	4-5	4-5	4-5	4-5	2-4	2-4
16	4-5	4-5	4-5	4-5	2-4	3-4	4-5	4-5	4-5	4-5	2-4	3-4
17	3-5	4-5	3-5	3-5	1-4	1-4	4-5	4-5	2-5	2-5	2-4	2-4
18	3-5	3-5	3-5	3-5	2-4	2-4	4-5	4-5	3-5	3-5	2-4	2-4
19	3-5	3-5	3-5	3-5	2-4	2-4	4-5	4-5	4-5	4-5	3-4	3-4
20	4-5	4-5	3-5	3-5	2-4	2-4	4-5	4-5	0	0	2-4	3-4

In the imago the elytra are variously divergent, sometimes starting at the scutellum and the tips of one or both elytra may be bent downward (but usually not folded under, as in te imagoes) and they may bear a blister of varying size.

6. concave split (cspl). Sokoloff and Lasley, 1960. Autosomal recessive. Resembles spl but is not allelic with this gene. In the pupa the elytra may be widely separated, and the hind tarsi extend beyond the elytral tips. In some pupae the elytra and membranous wings curve away from the body. In the adult the elytra may be split and short, or they may not exhibit any divergence, but they may not reach

the end of the abdomen to cover it completely. In this sense the phenotype resembles she. Tests of allelism just completed indicate cspl is allelic with aa and it is renamed aa-1.

7. deflected epimera (dep). Hoy and Sokoloff, 1964. In the normal beetle the epimera extend medially behind the coxae of the first pair of legs and their tips lie under the sternellum. In dep the tip of one or both epimera may be deflected, ending somewhat posteriorly from their normal position, some showing only the posterior part of the epimeral tip behind the sternellum, others with a more pronounced deflection, lying completely behind the sternellum. In a few cases the sternellum lies under one or both epimeral ends. A shortening of the epimeron as that observed in sep in T. confusum has not been observed so far. Autosomal recessive with incomplete penetrance.
8. deformed femur (dff). Hoy and Sokoloff, 1964. Possibly a phenodeviant found in the descendants (more than three generations) of an irradiated (12 Kr) male × unirradiated female. The defect can be identified more often in the first pair of legs: the femur is bent toward the head at or near the femoro-trochanteral joint, and somewhat reduced in size. The femora of the middle pair of legs may also be considerably reduced in size, and in some cases the femur is bent cephalad.
9. deformed podomeres (dpm). Sokoloff, 1964. Sex-linked recessive with incomplete penetrance and variable expression found in linkage studies between ser, py and pd.

In strongly expressed phenotypes the femur is nearly globose, the trochanter is missing and the proximal end of the femur is fused to the coxa, but the tibia and tarsi appear not to be affected to any large extent. In mildly deformed beetles the femur of only one leg, most often the mesothoracic one (less often the femur of the first pair of legs) is short and thick but the remaining legs have normal femora. Occasionally the tibiae are bent as in btt, and they may, in fact be deformed because of this autosomal gene. Preliminary counts suggest the position of dpm to the right of pd. The exact location of dpm will be difficult to establish since penetrance is very low, at least at 37°C and 70% R.H.

10. deformed tibia (dft). Hoy and Sokoloff, 1964. Spontaneous. Found in descendants of a strain reconstituted from four highly inbred strains marked with sooty (over 40 generations of brother-sister mating) which did not exhibit this character. Resembles dfl but tests of allelism have not been performed. Autosomal recessive of variable expression and incomplete penetrance.
11. elbowed antenna-1 (elb-1). Hoy and Sokoloff, 1964. Spontaneous in a stock of Ds/+; aa/aa. An autosomal recessive of incomplete penetrance and fairly uniform expression. The antennae exhibit a

- retroflexion, with the club directed toward the head, the point of retroflexion in the limited sample so far examined being located at the seventh antennomere, which is smaller than the preceding segment. Probably allelic to the now extinct mutant discovered by Dawson and Ho (see TIB 5:15, 1962), and found to be linked with she in linkage group VIII. (Sokoloff and Dawson, 1963)
12. elongated elytra (ele). Sokoloff and Hoy, 1964. This autosomal recessive mutant was found in two unrelated stocks. It resembles in every way the ele mutant in T. confusum (see TIB 7:40). Females with extremely long elytra (extending beyond the posterior end of the abdomen by the equivalent of the length of the posterior segment) often remain unfertilized, probably owing to the fact that the elytra are too long to permit successful copulation.
  13. emasculated (em). Hoy and Sokoloff, 1964. A male was found in the Fta c/+c stock and another male in some crosses between ble+/-ca (in attempts to isolate a ble ca stock), which, upon squeezing, had no apparent aedeagus. After dissection these beetles proved to have normal testes and accessory glands, but the aedeagus had failed to evert, forming a ball-like sclerotized structure. So far no attempts have been made to determine the mode of inheritance of em, but by analogy with a similar mutation found in T. confusum (see below), it must be due to a sex-limited autosomal recessive gene.
  14. fused antennal segments-3a (fas-3a). This appears to be a more strongly expressed allele of fas-3. When first found the fas-3 mutant had only slight abnormalities of the funicle and a diffuse fusion of the club segments (see table in TIB 6:24). The stock established from the original mutants has retained the original range of expression and the tarsi do not exhibit any fusions. The expression of the new allele as can be seen from the table below (Table 3) has segments 3-5, and 6-7 of the funicle fused, and in addition segment 8 of the funicle may be fused with all of the club segments, or may remain intact, separating fused blocks from the funicle and the club, the latter consisting of fusions of segments 9-10, 10-11 or 8-11. The tarsus is affected by the fas-3a gene, adjacent tarsomeres becoming fused partially or completely resulting in a podomere consisting of 4, 3 or even 2 tarsomeres, but the total length of the tarsus from casual observations, seems to be as long as the tarsi of corresponding legs in normal beetles. The fas-3a allele overlaps wild type in dominance.
  15. Fused antennal segments-4 (Fas-4). Sokoloff, 1963. This mutant resembles fas-1 and fas-2 in having segments 4-5, and/or 5-6 and 9-10 affected. Indeed, if single individuals are compared, it would be difficult to decide whether they belong to fas-1, fas-2, or Fas-4, since there is much overlap in expression. (Compare tables given in TIB 5, p. 16 and 17 with Table 4.) However, in Fas-4 funicular segments 3-4 and 5-6 are often fused in the same individual, something which rarely happens in fas-1 and fas-2. Penetrance of Fas-4 is



Table 3. Fusions found in the antennae of fas-3a in T. castaneum

No.	Males		Females	
	Right	Left	Right	Left
1	3-5, 6-7	3-5, 6-7	3-5, 6-7	3-5, 6-7
2	3-5, 6-7, 10-11	3-5, 6-7, 8-9	3-5, 6-7	3-5, 6-7
3	3-5, 6-7, 9-11	3-5, 6-7, 8-11	3-5, 6-7, 8-9	3-5, 6-7, 8-11
4	3-5, 6-7, 10-11	3-5, 6-7, 10-11	3-5, 6-7, 8-9	3-5, 6-7
5	3-5, 6-7, 8-9	3-5, 6-7, 8-9	3-5, 6-7, 8-11	3-5, 6-7, 8-11
6	4-5, 6-7, 8-9	4-5, 6-7	3-5, 6-7, 8-11	3-5, 6-7, 8-11
7	4-5, 6-7	4-5, 6-7	3-5, 6-7	3-5, 6-7
8	3-5, 6-7, 9-11	3-7, 8-11	3-5, 6-7	3-5, 6-7
9	3-4, 6-7, 9-11	3-5, 6-7, 8-11	3-5, 6-7, 8-9, 10-11	3-5, 6-7, 8-11
10	3-5, 6-7, 8-11	3-5, 6-7, 8-11	3-5, 6-7	3-5, 6-7
11	3-5	0	3-5, 6-7, 8-11	3-5, 6-7, 8-11
12	---	3-5, 6-7, 8-11	3-5, 6-7, 8-9	3-5, 6-7, 8-9
13	3-5, 6-7	3-5, 6-7	3-5, 6-7, 8-11	3-7, 8-11
14	3-5	3-5	3-5, 6-7, 8-9, 10-11	3-5, 6-7, 8-9
15	3-5, 6-7, 8-11	3-5, 6-7, 8-11	3-7, 8-11	3-7, 9-11
16	3-5, 6-7, 8-11	3-5, 6-7, 8-11	3-5, 6-7, 8-9, 10-11	3-5, 6-7
17	3-5, 6-7, 8-9, 10-11	3-5, 6-7, 8-9, 10-11	3-7, 8-11	3-7, 8-11
18	3-5, 6-7, 8-11	3-7, 8-11	3-5, 6-7, 8-9	3-5, 6-7
19	3-5, 6-7, 9-10	3-5, 6-7, 8-9, 10-11	3-5, 6-7, 8-11	3-5, 6-7, 8-11
20	3-5, 6-7, 8-11	3-5, 6-7, 8-11	3-5, 6-7	3-5, 6-7, 8-9

Table 4. Antennal fusions found in a sample of Fas-4 in T. castaneum

Males		Females	
Right	Left	Right	Left
3-4, 5-6	3-4, 5-6	4-5	4-5
4-5	4-6	4-5	4-5
4-6	4-6	4-5	4-5
3-4, 5-6, 9-10	3-4, 5-6	4-5	4-5
3-4	3-4, 5-6	4-5	5-6
3-4, 9-10	3-4, 9-10	4-5	5-6
3-4, 9-10	3-4	5-6	5-6, 9-10
3-4	3-4	4-6, 9-10	5-6, 9-10
3-4, 9-10	3-4, 5-6	5-6, 9-10	5-6, 9-10
3-4, 5-6	3-4, 5-6	5-6	5-6
4-5	4-5	4-5, 9-10	5-6, 9-10
3-4, 9-10	3-4, 9-10	4-6, 9-10	4-6
3-4, 5-6, 9-10	3-4, 5-6, 9-10	5-6, 9-10	5-6
3-4, 9-10	3-4, 9-10	4-6	5-6, 9-10
3-4, 5-6	3-4, 5-6	4-6, 9-10	4-6
3-4	3-4, 5-6	4-6, 9-10	4-6
5-6, 9-10	5-6, 9-10	4-6	4-6
3-4, 5-6	3-4, 5-6	4-5, 9-10	4-6, 9-10
3-4, 5-6, 9-10	3-4, 5-6, 9-10	4-6	4-6
3-4, 9-10	4-6	4-6, 9-10	4-5
3-4, 5-6	3-4, 5-6	4-6	4-6
3-4, 9-10	3-4, 9-10	3-4, 9-10	3-4, 9-10
3-4, 5-6, 9-10	3-4, 5-6, 9-10	3-4, 5-6, 9-10	3-4, 5-6, 9-10
3-4, 5-6, 9-10	3-4, 5-6, 9-10	5-6	5-6
3-4, 5-6, 9-10	3-4, 5-6, 9-10	4-6, 9-10	4-5

- more complete than that of other fas mutants. Genetically Fas-4 behaves mostly as a dominant, but it overlaps wild type in expression in some crosses.
16. Fused antennal segments-5 (Fas-5). Sokoloff, 1963. Autosomal dominant with some overlap with wild type. This mutant resembles fas-1 and fas-2 and fas-3 in that segments 4-5, 5-6, 6-7 may be affected. It differs, as shown in the accompanying table (Table 5) in that several consecutive segments (3-8 or 6-8, for example) may be fused. In addition, pleiotropic effects of this gene can be observed in the tarsi: adjacent segments become fused, and the distal tarsus is greatly swollen. Fas-5 is not allelic with fas-1, fas-2, fas-3, Fas-4 or fas-6.
  17. fused antennal segments-6 (fas-6). Sokoloff, 1963. This autosomal recessive mutant was found in the course of testing linkage relationships of antennapedia (ap<sup>D</sup>). It is unusual in that the number of antennameres exceeds the normal number of 11 in some individuals as can be seen in Table 6. The antennae of these individuals are greatly modified, forming a club-like structure which results from the fusion of segments 8-11 or 9-12. In many of these individuals there is evidence of claw-like structures at the tip of the antennae which are evidently produced by the ap<sup>D</sup> gene. This mutant differs from ap<sup>D</sup> in that the antennae are not leg-like, the metathorax is not shortened, and the distal segments of the tarsus are completely separated, which is not true for the ap<sup>D</sup> mutant. The fas-6 gene is not allelic with fas-1, fas-2, fas-3, Fas-4, Fas-5, but it has been found to be allelic with ap<sup>D</sup>; hence it is renamed ap<sup>S</sup>.
  18. incomplete metathoracic projections (imp). Sokoloff, 1963. Spontaneous in crosses attempting to establish the position of the sex-linked M<sup>r</sup>. An autosomal recessive of poor penetrance and variable expression characterized by the elimination or displacement of the posterior processes of the metasternum, which normally form an inverted V to accommodate the median sternal projection of the first apparent abdominal segment. In addition, the median groove is deflected to one side, and the metasternum acquires a protuberant appearance.
  19. jagged antecoxal piece (jac). Hoy and Sokoloff, 1964. Derived from a population traceable to an irradiated (6000 Kr) male mated with an unirradiated female (but more than three generations had elapsed before it was detected). In normal beetles the antecoxal piece is a band-like area delineated by the anterior transverse grooves (which extend from the median groove laterally almost to the junction between the metasternum and the pleural sclerite), and the rear metasternal margins which assume a smooth curvilinear appearance. In jac either the portion including only the transverse groove, or this portion and the antecoxal piece are drawn anteriorly, forming a triangle with the anterior edge of the hind coxae. This mutation is not the same as scar (sc) since, in the latter, part of the

Table 5. Antennal fusions found in a sample of Fas-5 in T. castaneum

Males		Females	
Right	Left	Right	Left
6-8	4-5, 6-7	4-5, 6-8	4-5, 6-8, 10-11
4-5, 6-8	4-5, 6-7	6-8	4-5, 7-8
4-5, 6-7	4-5, 7-8	4-5, 6-8	4-5, 7-8
4-5	4-5	4-5	4-5
5-6, 7-8	4-5, 7-8	3-4, 5-6, 7-8	3-4, 5-6, 7-8
4-5, 7-8	4-5, 7-8	4-5	4-5
6-8	5-8	4-5, 6-8	4-5, 7-8
4-5	4-5, 7-8	4-5	0
4-5, 7-8, 9-10	4-5, 6-8	4-6	4-5
4-5, 7-8	4-5, 7-8	4-5, 6-7	4-5, 7-8
4-5, 7-8	4-5, 6-8	4-5, 6-8	4-5, 7-8
4-5	4-5	4-5	4-5
4-5, 7-8, 10-11	4-5, 7-8	4-5	4-5
5-6	4-5	4-5, 6-8	4-5, 6-8, 9-10
3-8	3-6, 7-8	4-5, 6-8	4-5, 6-8
4-5, 6-7	4-5, 6-7	4-7, 7-8	4-5, 6-8
4-5, 6-8	4-5, 6-8	4-5	4-5
3-8	4-5, 6-8	4-5, 6-8	4-5, 6-8
4-5	4-5	3-8	4-8
0	4-5	4-5, 6-8	4-5, 6-8
4-5	4-5	4-5, 6-8	4-5, 6-8
4-5, 6-8	4-5, 6-8	4-5, 6-8	4-5, 6-8
4-5, 7-8	4-5, 6-7	4-5, 7-8	4-5
4-5, 6-7	4-5, 6-8	4-5, 6-8	4-5, 6-8
4-5, 6-7	4-5, 6-7	5-6	5-6

Table 6. Antennal fusions and numbers of segments found in a sample of fas-6 (ap<sup>S</sup>) in T. castaneum

("c" denotes that the distal segments had claw-like bristles)

Males		Females	
Right	Left	Right	Left
4-5, 6-11c	7-8, 9-11c	8-11c	8-11c
6-8, 9-11	9-11	4-5, 8-11c	8-11c
6-8, 9-12	4-5, 9-11	6-7, 8-11c	8-11c
4-5, 6-8, 9-12	4-5, 7-11c	4-5, 8-11c	7-8, 9-11c
4-5, 8-10c	6-7, 8-11c	7-8	0
9-10	9-11	9-10	9-10
7-8, 9-11c	4-5, 7-8, 9-11c	4-5, 8-11	7-8, 9-11
9-10	10-11	5-6, 8-11c	5-6, 8-11c
9-11c	9-11	7-8, 9-11c	7-8, 9-11c
7-8, 9-12	7-8, 9-12	7-8, 9-12c	9-11
7-8, 10-11c	7-8, 9-11	7-8, 9-11	6-8, 9-11c
7-8, 9-11	7-8, 9-11	4-5, 7-8, 9-10	4-5, 6-7, 8-11
7-8, 9-12	7-8, 9-12	0	9-10
0	7-8	7-8, 9-12	4-5, 7-8, 9-13
0	10-11	0	7-8
4-5, 7-8, 9-10	7-8, 9-11	7-8, 10-11	7-8, 9-12
7-8, 9-10, 11-12, 13	4-5	7-8, 9-11	4-5, 7-8, 9-13
5-6, 9-10	7-8	4-5, 7-8c	7-8, 9-10
9-10c	4-5, 9-10c	7-8, 9-10	7-8, 9-11
4-5, 6-11c	4-5, 7-11c	7-8, 9-11c	7-8, 9-11c
4-5, 7-8, 9-11c	4-5, 7-8, 9-11c	7-8, 9-10	8-9, 10-11c
4-5, 7-8, 9-12c	4-7, 8-10c	3-4, 9-11	3-4, 6-7, 8-10 11-12
4-5, 8-11, 12	6-7, 8-10, 11c	7-8	0
4-5, 7-8, 9-11c	4-5, 8-11	4-5, 6-8, 9-11	4-5, 6-8, 9-11
4-5, 8-11c	4-5, 7-8, 9-10c	7-8, 10-12c	7-8, 11-12
0	9-11	4-5, 7-8, 9-11c	4-5, 9-11c
7-8, 9-11	0	9-10	7-8, 10-11
4-5, 6-8, 9-10c	4-5, 6-8, 9-10c		
6-7, 8-11c	6-7, 8-11		
4-5, 7-8, 9-10c	4-5, 7-8, 9-11c		

exoskeleton anterior to the transverse groove is scar-like and triangular in shape. Some jac beetles exhibit a hole between the ante-coxal piece and the transverse groove. Preliminary crosses suggest a recessive mode of inheritance.

20. looped median groove (lmg). Hoy and Sokoloff, 1964. Spontaneous in derivatives of a sample of scar provided by A. E. Bell. The median groove in normal beetles is a shallow line extending anteriorly from the posterior end of the metasternum and terminating approximately three-fifths of the way between the third and second pair of legs. The remaining two-fifths, representing the basisternum, are not grooved. Anteriorly, the single medial metasternal process is fused with, and covers the mesospinasternum, a posteriorly bifurcated structure which is normally not observable because of this fusion. In weakly expressed lmg beetles, the median groove forms a tiny oval-shaped loop (antero-posteriorly oriented) at about the same position where umb forms its hemispherical depression. This loop is larger in strong expression of the character; it may be located more anteriorly and is very shiny, suggesting a delayed sclerotization of this part. Midway along the loop there may arise some secondary, short, transverse branches perpendicular to the long axis of the median groove. Furthermore, the median groove may extend to the anterior border of the metasternum splitting the medial process into two components and uncovering the two prongs of the mesospinasternum.
21. megalothorax (mgt). Sokoloff and Hoy, 1964. Found in a stock of Be s/+s. Characterized by having a prothorax greatly expanded and tumor-like, usually on one side of the body. In a few cases the prothorax may exhibit a variable reduction of some of its parts resembling ptl. The forelegs, however, have never been observed to be affected as in ptl. Another difference lies in the fact that mgt sometimes produces a wing-bud-like appendage on the affected (enlarged) side, in a manner similar to that produced by apt. Since viability of mgt is low and penetrance incomplete, tests of allelism between mgt and ptl or apt have not been attempted.
22. melanotic stink glands (msg). Sokoloff and Hoy, 1964. In normal Tribolium there are two pairs of odoriferous or stink glands, one pair in the prothorax and the other in the abdomen. These glands are connected with reservoirs which are filled with a volatile liquid which is yellowish in young beetles but dark reddish brown in old beetles. In msg the reservoirs in beetles one or two weeks old become visible through the exoskeleton owing to a change in the composition of the substances contained in the reservoirs. These substances form a solid black mass which may assume the shape of the reservoir or may break up into several components, some appearing dot-like. As in T. confusum the contents in the prothoracic reservoirs undergo the chemical changes earlier than the abdominal reservoirs. Hence, the phenotype of the prothorax is more reliable for identification of msg than the phenotype of the abdomen.

- Autosomal recessive with incomplete penetrance. Preliminary tests suggest this gene is located in linkage group III.
23. missing abdominal sternites (mas). Hoy and Sokoloff, 1964. A recessive of good penetrance, expressivity and viability. cursory examination of the mutant reveals only four instead of five apparent abdominal segments, with a considerable, unsclerotized area in front of the apparent second abdominal segment, and only a slight displacement forward of the whole abdomen leaving but a tiny gap between the elytral edges and the lateral margins of the abdomen. Dissection of the beetles reveals that abdominal segments I and II, normally feebly sclerotized structures located dorsal to the coxae, are completely gone. The third abdominal segment is present but greatly reduced and only feebly sclerotized. The median anterior process of this segment is practically the only thing that identifies it from the apparent second segment at the midline. Lateral to the median process the segment forms some pocket-like recesses which resemble the recesses into which the hind coxae fit, but they are only about one-fourth as wide as the second apparent abdominal segment. The character is not recognizable in the pupa because the elytra cover this area. It is not known at this writing whether the mutant can be recognized in the larval stage.
  24. pectinate antenna (pec). Hoy and Sokoloff, 1964. Spontaneous in selection vials involving ptl, ap and sq. Fusions of this incompletely recessive mutant are primarily confined to the funicle and club, although rarely the scape may also be fused to other distal segments. One of the expressions of pec is complete fusion of several antennomeres on one side, but partial segmentation on the other side of the antenna, producing a structure remotely resembling the teeth of a comb. The antennomeres of the funicle and club may be greatly swollen. The distribution of fusions in the original sample of beetles is as shown in Table 7 below. Since this mutant was just discovered, tests of allelism between pec and the various mutants described under the general name of fused antennal segments (fas-1 to fas-6) have not been carried out, but the phenotype of these beetles is so different that it is probably a distinct gene.
  25. reduced tibia (rt). Sokoloff and Hofer, 1964. Found in same population as akimbo. The tibia may be completely missing with the tarsi originating from the femur, or it may be present in reduced form: sometimes it is a short, curved tibia, in other cases it is hemispherical in shape; in still others the tibia is drawn into a very slender, almost filamentous shape connecting the tarsus and femur. If so, the legs may break off shortly after eclosion. The tarsus is generally complete, but sometimes the first segment is firmly fused with the tibia. Sometimes the lateral surface of the tibia is extended posteriorly into a hook-like structure more or less paralleling the femur, and in some individuals the tarsal spurs develop more proximally on the tibia than normal. Preliminary crosses suggest a recessive mode of inheritance. Tests of allelism

Table 7. Fusions found in the antennae of pec in T. castaneum

No.	Males		Females	
	Right	Left	Right	Left
1	4-5	4-5	4-5	4-5
2	9-10	7-10	5-6, 7-8	4-7, 8-9
3	5-6	5-6, 7-8	4-5	3-5, 7-8
4	2-7	2-8	3-4	4-5, 6-7
5	0	4-5	4-6	4-6, 7-8
6	4-7, 6-7	4-5	3-5, 6-7	3-8
7	0	4-5	4-6	4-6
8	3-7	3-6	4-5, 7-8	4-5, 7-8
9	4-5, 6-7	5-6	3-4, 5-6, 7-8, 9-10	3-6, 7-8
10	0	9-10	3-6, 7-8, 9-10	4-5, 7-8, 9-10
11	4-5, 6-10	5-6, 8-10	4-5	4-5
12	4-5	0	2-5	2-5
13	3-4, 5-6	5-6	4-7	4-8
14	7-8	7-8		
15	7-8, 10-11	9-10		

just completed suggest this mutant is allelic with dfl, but since it has stronger expression it is renamed dfl-1.

26. rough (ro). Hoy and Sokoloff, 1964. This recessive mutant was found in a vial selecting for an abnormal condition affecting the spinasterna (which proved not to have any genetic basis). It is characterized by the appearance of a sizable uni- or bilateral blister in the elytral buds of the pupa, which interferes with normal eclosion of a large number of imagoes resulting in their death. Individuals not exhibiting a blister in the pupa may develop one in the adult, or the elytra may have a roughened appearance. The phenotype of ro in this species resembles in every way the ro mutant in T. confusum.
27. sleek (slk). Sokoloff and Hofer, 1964. This mutant appeared spontaneously in crosses attempting to establish linkage between bal, lod and p. Two female imagoes were produced from a single pair mating and they died without leaving progeny. Hence, the mode of inheritance has not been established. However, the two females had



identical appearance so that there is no doubt that the following abnormalities, modifying some major taxonomic characters, had genetic basis:

- a. Antennae: first and second basal segments not fused but somewhat reduced in size; segments 3-8 of the funicle and 9-11 of the club fused into a continuous paddle-like structure exhibiting no segmentation.
  - b. Head rounded and somewhat reduced in size.
  - c. Prothorax also rounded, with the antero-lateral extensions missing, and more convex dorsally. Ventrally the epimeron (E), trochantin (T), and the medial extension of the episternum between E and T were missing so that the coxae of the first pair of legs were exposed, i.e., they were "open behind" in taxonomic terms. The sternellum was reduced in size.
  - d. Mesosternum reduced in size and the sternellum short and pointed, failing to separate the middle coxae.
  - e. Metasternum without median anterior projections and with the median groove missing. The hind coxae incomplete, with a circular opening showing the proximal end of the femur lying within.
  - f. Elytra and membranous wings abbreviated, reaching only the posterior edge of the first abdominal segment.
  - g. Medial anterior projection of the first apparent abdominal segment missing or vestigial. The remaining abdominal segments were separated by a wide membranous (unsclerotized) area.
  - h. The last apparent abdominal segment was considerably reduced in size and less rounded.
  - i. Proximal podomeres normal, but the tarsus conforms to the formula 4-4-3, with partial or complete segmentation visible between all adjacent remaining tarsomeres.
28. Spatulate antenna (Spa). Sokoloff and Hoy, 1964. Spontaneous in attempts to select a ju ct; c ca stock. Preliminary crosses suggest it is an autosomal dominant with recessive lethal effects. The phenotype of this mutant is different from that produced by Df, Fta, and Sa (including its dominant, semidominant or incompletely recessive alleles). As shown in Table 8, the 10 males and 10 females scored exhibit fusions in the funicle and/or the club. In addition, the fused club may resemble a small scoop or spatula. Both antennae must be examined since penetrance appears to be unequal in the two

sides of the body. Badly deformed Spa may be identified in the pupa. Crosses between Spa and Be result in the manifestation of a dominant lethal of the type produced by Fta and Sa (i.e., Spa Be fail to show up in the  $F_1$  of Spa × Be crosses), suggesting Spa is on the Be linkage group.

Table 8. Antennal fusions found in a sample of Spa in T. castaneum

No.	Males		Females	
	Right	Left	Right	Left
1	5-6, 10-11	6-8, 9-10	4-5, 6-8, 9-11	4-11
2	7-8, 9-11	9-11	7-8, 9-11	10-11
3	3-8, 9-11	5-8, 9-10	9-11	5-8, 9-11
4	10-11	6-8, 9-11	5-6, 9-11	4-8, 9-11
5	6-8, 9-11	9-11	7-8, 9-11	5-6, 7-8, 9-11
6	10-11	0	5-6, 10-11	5-6, 10-11
7	6-7, 10-11	10-11	7-11	6-9
8	6-8, 9-11	9-11	3-4, 6-8, 9-11	7-8, 10-11
9	10-11	10-11	5-8, 9-11	5-6, 9-11
10	4-8, 9-11	5-8, 9-11	0	4-8, 10-11

29. split, curved elytra (spce). Sokoloff and Rodriguez, 1963. Resembles cye, or cspl, in having the elytra and membranous wings drawn away from the tarsi in the pupa. In the adult the elytra are split and/or short. Tests of allelism have been set up, but there are too many gaps to be sure whether this mutant is new or allelic to others.
30. tiny (originally symbolized ti by Sokoloff and Shrode, 1962, is herewith changed to ty since Shideler, unaware of the fact that this symbol had been preempted has used it to symbolize tarsal incomplete). Apart from the sex-linked py gene which reduces the size of the beetle without deforming it, often, in single-pair matings of sibs, there appear beetles strikingly reduced in size and almost as small as py. The number of these individuals varies. When these small beetles are mated inter-se, tiny individuals, if they appear at all, are produced only in very small numbers, the size of the remaining individuals appearing to be distributed over a wide range,

indicating a very large number of factors controlling body size. Since the determination of the number of genes involved would require weighing carefully pedigreed beetles for several generations this study has not been attempted. It may be noted, however, that Bray, *et al* (1961), in their selection experiments for pupal weight obtained very good symmetrical response in increase and decrease in body weight for eight generations. The shape of the curves they obtained indicate the presence of a very large number of genes controlling body size, but their estimate of the numbers involved, to the writers' knowledge, has not been published.

31. troll (tro). Hoy and Sokoloff, 1964. Eight pupae of both sexes of tro have been isolated, suggesting an autosomal mode of inheritance. The adults emerging from the pupae resemble the sex-linked ma in every respect except that the tarsi of all the legs are reduced in number by one or two tarsomeres. Viability is greatly reduced. It is not possible to state at present whether the gene is lethal or semilethal.
32. umbilicus (umb). Hoy and Sokoloff, 1964. A spontaneous autosomal recessive found in a stock of scar (sc-1), characterized by a roughly hemispherical depression on the median groove of the metathorax, about one-third of the distance between the third and second pair of legs. The depression may vary in size from barely wider than the groove to one of considerable size. It may be absent altogether in beetles known to be umb/umb indicating incomplete penetrance. Tests of allelism between umb and dent (dt, Eddleman and Hudson, 1962) or dented (d, Ganguly, 1964), which from the descriptions in TIB appear to be similar in phenotype, have not been performed, since the latter two mutants have not been released.

#### T. confusum

1. bent femur (btf) Hoy and Sokoloff, 1964. Found while selecting for a pure stock of es tet. About 30 individuals of both sexes were found with very strong expression of bent tibia (btt). The btf differs from btt in having, in addition, a deformed femur. The deformed femur can occur in any pair of legs, but it is abnormal only in those legs exhibiting a strong expression of the bent tibia phenotype. The deformity consists in having the proximal third of the femur somewhat narrower than the rest, and at this point the femur is sharply bent, producing an angle of approximately 135° between the two parts of the femur. Tests of allelism with btt have not been performed.
2. black-3 (b-3). Sokoloff and Slater, 1964. Spontaneous in a stock originally derived from Park's Chicago wild type strain. Autosomal recessive. Tests of allelism with McGill black indicate McGb and b-3 are allelic. An interesting feature is that b-3 × McGb give black. Another point of interest is that the b-3 allele is considerably smaller than either the McGb or the wild type laboratory strains.

3. blade elytra (bld). Sokoloff and Hofer, 1964. In a single pair mating possibly involving em (q.v.) 11 males and 8 female pupae were isolated because they appeared to be similar to pointed elytra in T. castaneum. Seven pupae became imagoes but died without leaving progeny. They had the following defects:
  - a. Elytra divergent, sometimes starting at the scutellum, sometimes farther back, and somewhat narrower but as long as the normal elytra.
  - b. The distal fourth of the elytra are gradually reduced in width terminating in a sharp point, or the tips may be narrow but not pointed and slightly curving toward the midline, or distal fourth may be almost normal but depressed toward the abdomen; or the tips of the elytra may be blistered and pointed away from the abdomen.
  - c. The legs beyond the tibia-femoral joint may be missing, but this may have been due to a quinone effect. Other deformities not attributable to quinones were present: the epimera were shorter than normal, failing to extend under, and to fuse with, the prosternum, or could be altogether wanting. In extreme form the abnormality is increased to the point that the epimeron (E), and the trochantin (T) and that part of the episternum separating E and T are missing, so that the front coxae are open behind and may be completely uncovered. The sternellum of the mesosternum may be narrowly or widely separated from the anterior medial projection of the metasternum in a manner similar to the condition produced by ims in T. castaneum.
4. crumpled (cru). Hoy and Sokoloff, 1964. A sex-linked recessive, characterized by the possession of split, drooping elytra, somewhat reduced in size in the adult so that the posterior tips cover only part of the posterior abdominal segment. The dorsal surface of one or both elytra may present a roughened, sometimes wavy appearance. In addition many of the beetles exhibit a huge blister in the proximal portions of the elytra. Detectable in the pupa either by the fact that the elytra do not reach the tips of the hind tarsi, or by the presence of a blister. The latter pupae resemble akimbo in T. castaneum or thu, and thu<sup>S</sup> in T. confusum. Since the mutant was just discovered, information on penetrance or viability is not available.
5. deflected epimera (dep). Hoy and Sokoloff, 1964. In the normal beetle the epimera extend medially behind the coxae of the first pair of legs and the tips lie under the sternellum. In dep the tip of one or both epimera may be deflected, ending somewhat posteriorly from their normal position, some with only part of the epimeral tip showing behind the sternellum, others with a more pronounced deflection so the end of epimeron lies completely behind the sternellum. In other cases the sternellum lies under one or both of the epimeral ends.

6. emasculated (em). Sokoloff and Hoy, 1964. Was found in several linkage test-crosses: In the F<sub>2</sub> of +/e; +/umb; +/p mated inter-se, five males were found which, on squeezing, appeared to have no aedeagi. A number of males with no apparent aedeagi was found in some backcrosses of F<sub>1</sub> of the cross p/p; umb/umb; ems/ems; cas/cas; sti/sti (imp?) males which also had short epimera (sep, q. v.) × +/+ ♂♂ back to the P<sub>1</sub>; and finally one male was found in the F<sub>2</sub> of crosses between e and b. The em males, superficially examined, resemble normal males in the possession of normal basal pits with associated hairs on the femura of the first and second pairs of legs (the latter being less pronounced), but no aedeagi are extrudable when gentle pressure is applied to the abdomen. Dissection of these beetles reveals normal internal reproductive organs (testes and associated glands and structures) connected to a ball-like sclerotized structure, sometimes connected to a small projection which may be an incipient aedeagus, located entirely within apparent abdominal segment III, or over the suture separating apparent segments III and IV. Matings of these beetles, which survive for a long time, are apparently sterile because they are incapable of transferring their sperm. It is possible that em/em males may form short aedeagi, but more work is needed to clarify this point. The results of various crosses seem to indicate that em is an autosomal recessive sex-limited gene of variable expression. Preliminary crosses fail to establish linkage between em, p and rus.
7. frosted (fro). Hoy and Sokoloff, 1964. An autosomal recessive mutation not allelic to pearl but which nevertheless resembles the phenotype of this mutation.
8. incomplete metathoracic projections (imp). Sokoloff and Hoy, 1964. Spontaneous in a stock bearing p and possibly umb and sc. The posterior metathoracic processes, which normally produce an inverted V to accommodate the median anterior process of the first apparent abdominal segment, is missing. In some individuals the median groove is deflected, usually to the right and the metasternum may appear protuberant. Penetrance poor.
9. knobby prothorax (knp). Sokoloff and Hoy, 1964. An autosomal recessive homeotic mutation found in a b rus (sp) selection creamer. In the pupa the posterior lateral corners of the prothorax are extended into a growth resembling the elytral and membranous buds of certain vestigial mutations. As the pupa ages, this bud may become filled with fluid and in certain cases the bud may subsequently necrotize, falling off at metamorphosis. If the tissue does not necrotize, the posterior angles of the prothorax are drawn into knob-like structures, sclerotizing normally. No linkage information. Preliminary crosses suggest viability of knp is low.
10. medial abdominal groove (mag). Sokoloff and Hoy, 1964. Two mag males and one female were found in the F<sub>2</sub> males derived from the St stock being tested to see whether a bleached condition of the

elytral tips of a male was heritable. (It was not.) Autosomal recessive of variable expression and incomplete penetrance (only about 20 per cent of the beetles will exhibit the character in the progeny of mag × mag matings). The mutant is characterized by the presence of a shallow medial depression in the last two abdominal segments, visible when the light reflects at a certain angle from the sternites. In weakly expressed mutants only the penultimate segment will show a shallow depression. So far as is known this character cannot be observed in the pupa.

11. nude (nd). Hoy and Sokoloff, 1964. Spontaneous in crosses attempting to establish the mode of inheritance of em. One male and two female pupae were found with distal ends of the elytra folded under as in the T. castaneum te. The male imago had one elytron bent, and the other appeared folded under, but it had a huge blister. The  $F_1$  were normal; the  $F_2$  exhibited a wide range of elytral abnormalities: in some pupae the elytral and membranous wing buds were greatly reduced, and the elytra tucked between the prothorax and the first two pairs of legs. The third pair of legs was exposed. These extremely deformed pupae failed to eclose. Among the  $F_2$  imagoes were large numbers of beetles bearing fairly normal-sized elytra and membranous wings but variously split. At this writing it is known that the character is heritable, but the mode of inheritance is to be determined.
12. prothoraxless-like (ptll). Sokoloff and Daly, 1964. 20 ptll male specimens, progeny of a single female, were recently found. Their phenotype is similar to ptl in T. castaneum in the following ways:

In the most weakly expressed beetles the prothorax is symmetrical and reduced by about one-fifth (along the longitudinal axis of the body), the reduction appearing to take place in the posterior part of the prothorax. In more strongly affected beetles the pronotum from the left or right side of the body is missing, the remaining portion acquiring a triangular shape. In an attempt to cover both halves of the prothorax, this triangular piece may be slightly modified in direction. On the ventral portion of the prothorax the pro- and basisternum may be considerably reduced in size and deformed, but the posterior portion of the basisternum and the sternellum generally are unaffected. The legs may be deformed, the deformity resembling that in the T. castaneum ptl heterozygotes, but so far a reduction of the forelegs to the extent that they become vestigial has not been observed, perhaps because ptll/ptll beetles are not yet available.

The ptll mutant differs from ptl in that the labium in the latter is not affected, but in ptll the labium appears considerably reduced in size, and oriented ventrally. The labial palps are three segmented but likewise reduced in size. In one specimen the gular region was found fused with the prothorax. In mildly deformed beetles the head retains the normal orientation of the head characteristic of

prognathous beetles, although the head may appear broader than normal, and the head may be twisted at an angle. In strongly expressed ptll, where the prothorax is badly deformed, the prothorax is oriented dorsally at an angle of about  $45^\circ$  from the body and the head appears at a higher level than, but parallel to, the long axis of the body.

The mutant is readily recognizable in the larva or the pupa by deformities in the prothorax. Imagoes have no trouble eclosing from the pupa, but the majority survive only briefly after becoming imagoes, probably because they are unable to feed.

13. separated epimera (sep). Sokoloff and Hoy, 1964. Spontaneous preliminary crosses suggest the gene is an autosomal semidominant with variable expression and probably incomplete penetrance. In the normal beetle the basisternum continues posteriorly between the coxae of the first pair of legs as the sternellum of the prothorax, to cover the tips of the epimera, thus the coxal cavities become closed. In sep the epimera are variously short: in the extreme case they fail to reach the sternellum by almost the equivalent of the width of this structure, the coxal cavities becoming open. The shortening of the epimera may not be symmetrical, more unsclerotized tissue showing to the left (or right) of the sternellum than on the other side. In the mildly expressed classifiable beetles the tips of both epimera almost reach the sternellum. Selection for stronger expression of this gene is being attempted. No linkage information.
14. tiny (ty). Sokoloff, 1961. Small-sized beetles have often appeared in small numbers in various crosses in T. confusum, some approaching the size of pygmy (py) in T. castaneum. Because such a mutation would be very useful in mapping sex-linked genes, considerable time and effort has been spent in determining whether these small beetles result from the action of a single sex-linked recessive or semidominant gene. The efforts have proved fruitless, and the reduction in size has been attributed to the action of a large number of multiple factors controlling body size, grouped under the same designation as ty in T. castaneum (see above).

\*REPORT OF M. T. M. STANLEY

Tribolium confusum

1. creased abdominal sternites (cas-1). Stanley, 1963. Found in Park wild type stock. Identical in appearance to cas Sokoloff, 1963 (Sokoloff, personal communication). It shows good viability and variable expressivity. It apparently is incompletely penetrant since with rigorous selection the trait appeared in no more than 70% of the offspring. Attempts to derive stocks free from this gene from the wild type were unsuccessful.

TESTS OF ALLELISM

Tribolium confusum

1. The thu and rsp mutants described in TIB 7 are allelic, and have been redesignated thu and thu<sup>S</sup>.

P. S. Dawson

Some mutants described in the New Mutant section have proved to be allelic to others previously described. This information has been included in the description of these mutants (see for example fas-3a, and dt in T. castaneum, and b-3 in T. confusum. (Ed.)