Rediscovery of *Toribolium freemani* Hinton: a Stored Product Insect Unexposed to Entomologists for the Past 100 Years

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Several hundred species of insect pests have been found associated with stored products such as grains, seeds, etc. Among those insects, both flour beetles of *Tribolium castaneum* and *T. confusum* are well known to economic entomologists or persons who concern with insect control in every part of the world; especially these species are familiar to those people in tropical and semi-tropical regions because the insects can easily be found in stock cereal products in households. On the other hand, apart from pest insects, both species as well as *Drosophila* spp. are also familiar to researchers in the field of ecology, physiology, and genetics as the experimental insects; recently, Sokoloff compiled the massive information on *Tribolium* spp. into three voluminous books[7,8,9].

In genus *Tribolium*, to which both species of *T. castaneum* and *T. confusum* belong, there are at least 33 species[7]. Among the species, *T. freemani* has been considered to be a very close species to *T. castaneum*. However, except Hinton's morphological description[2], no information on the insect including whether or not the insect can attack stored products has been available. Because, *T. freemani* has not been exposed to entomologists for nearly a century since a single female adult was captured at Hispar, Kashimir in India, at the end of last century, 189(3?), and was thereafter named by Hinton in 1948.

Recently, few adults of *T. freemani* (identified by Dr. D. G. H. Halstead, Slough laboratory, Ministry of Agriculture, Fisheries and Food, England) were found in Japan in a shipment of maize imported from Brazil. It was not possible, however, to determine whether the infestation originated in Brazil or was acquired during shipment from residues of a previous cargo. These adults were taken into culture and successfully reared.

In this paper, an attempt is made to bring a brief review on characteristics of *T. freemani* based on our recent investigations[4,5,6].

Morphological differences between *T. freemani* and *T. castaneum*

A dorsal view of adults of *T. freemani* and *T. castaneum* is shown in Plate 1. As Hinton described, *T. freemani* is much larger than *T. castaneum*, and other external characters including shape of antenna (forming enlarged three tips; a key point for distinguishing *T. castaneum* from *T. confusum*) and color (dark reddish-brown) of *T. freemani* are very similar to those of *T. castaneum*.

On the other hand, as described later, both *T. madens* and *T. audax* are another close species to *T. castaneum*. They also have similar antennas to that of *T. castaneum*, but easily distinguished from it by their black body in the adult stage.

The details of the size difference between *T. freemani* and *T. castaneum* are shown in Table 1. The weight of *T. freemani* female pupae averaged 2.3 times heavier than that of female pupae of *T. castaneum*. The corresponding factor between males was 2.4. The body length and pronotum width of *T. freemani* pupae were from 1.3 to 1.39 times

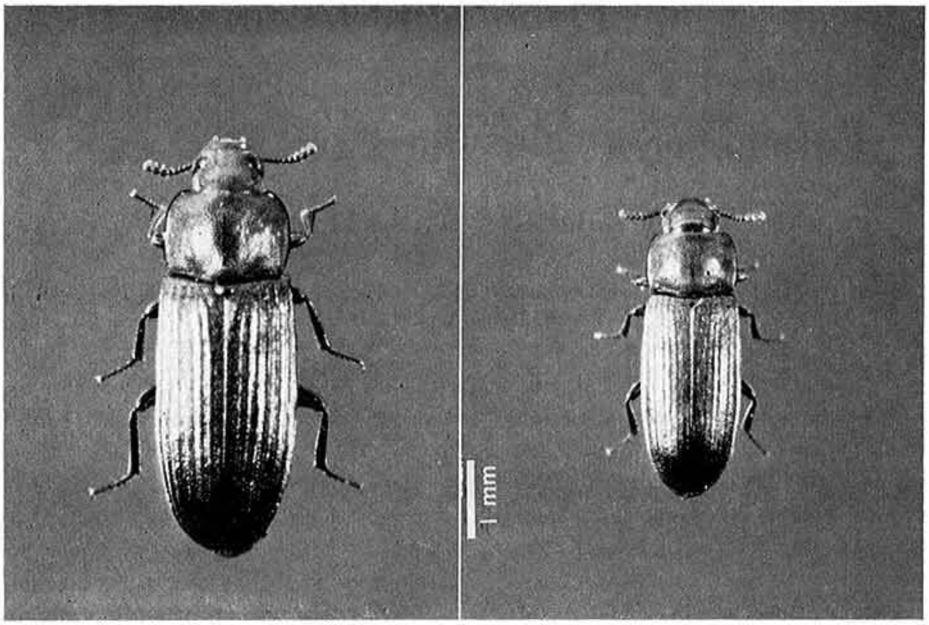

Plate 1. Dorsal view of adult of *Tribolium freemani* (left) and *Tribolium castaneum* (right)

Table 1. Comparison of body measurements of pupae of *T. freemani* and *T. castaneum*

		Mean ± S.E.*		
		Body weight (mg)	Body length (mm)	Pronotum width (mm)
T. freemani	♀	5.655±0.05 (144)	5.299±0.04 (32)	1.519±0.02 (32)
	♂	5.377±0.05 (123)	5.215±0.04 (26)	1.570±0.05 (26)
T. castaneum	♀	2.449±0.03 (32)	3.940±0.04 (22)	1.133±0.01 (22)
	♂	2.250±0.03 (30)	3.811±0.02 (23)	1.126±0.01 (23)

* Figures in parenthesis are the number of pupae used in measurements.

greater than those of *T. castaneum*.

Although the size differences between both species would be one of useful way to distinguish *T. freemani* from *T. castaneum*, the environmental conditions such as diet, population density, temperature, humidity, etc. are likely to change the body size of both insects. Moreover, a laboratory selected strain of *T. castaneum* was reported to weight twice as much as the usual one[9]. Thus it needs more stable and precise methods to determine *T. freemani*. According to Hinton, the arrangement of facets in compound eye of the adult is an important key for identification of *T. freemani*; "eye with narrowest part, where divided by side of front, only as broad as two facets". In fact, from our investigations, the observation of the eyes would be a useful way to distinguish *T. freemani* from *T. castaneum*, although there were minor variations depending on individuals; number of facets in *T. freemani* varied from 2 to 3 whereas those of *T. castaneum* 4–5. Plate 2 shows the compound eye of both species.

Further taxonomic information of this species, including details of male genitalia, will be reported by Halstead (personal communication).

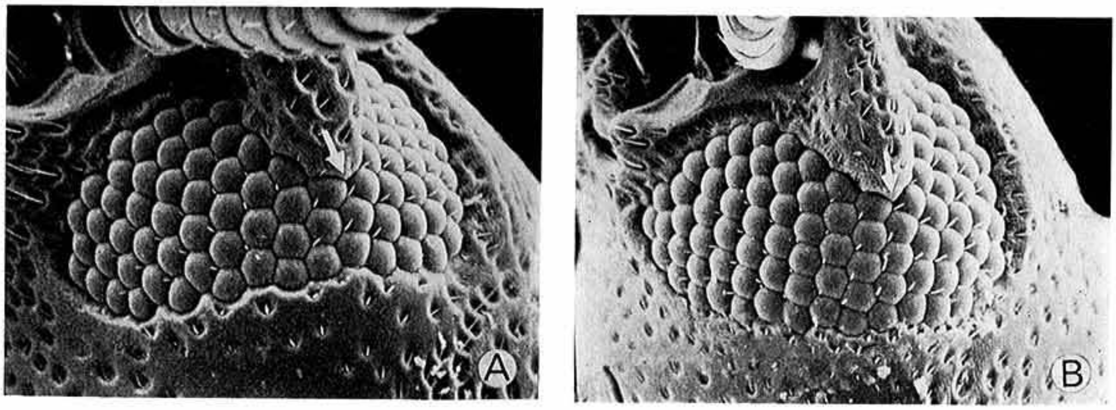

Plate 2. Lateral view of the facets in the compound eye of adult *T. freemani* (A) and *T. castaneum* (B)

Hybridization between *T. freemani* and *T. castaneum*

As mentioned above, *T. freemani* closely resembles *T. castaneum* in appearance. Moreover, we found a very interesting evidence that many F_1 hybrids were obtained by interspecific cross between both species[5].

In the interspecific hybridization, newly formed pupae of each species of *T. freemani* and *T. castaneum* were sexed, weighed and segregated individually in small vials (55 mm deep, 25 mm dia.) until the adults emerged. Both combinations of single-pair crosses of one-week-old adults of *T. freemani* and *T. castaneum* were established in vials containing 5 g of wheat-feed. Five replicas of each pair were placed in an incubator maintained at 30°C and 70% RH. After 2 weeks, all parental adults were removed from each vials.

As shown in Table 2, many hybrid progenies were produced from the interspecific crossing between *T. freemani* and *T. castaneum*.

We also found that no F_2 progeny was produced from all matings of F_1 progeny; both filial crosses and crosses with the parent strains. These results indicate that both the male and female hybrids were sterile.

From the interspecific crossing, it was concluded that *T. freemani* was a sibling species (genetically extremely close species) of *T. castaneum*.

Table 2. Total number of hybrid adults obtained from crosses between *T. freemani* and *T. castaneum*

Cross	No. of progeny[a] ♂	No. of progeny[a] ♀	Total	Sex ratio ♀ / ♂
♀ *T. freemani* × ♂ *T. castaneum*	37 (7.4±3.9)[b]	118 (23.6±5.9)	155	3.2:1
♂ *T. freemani* × ♀ *T. castaneum*	179 (35.8±4.4)	96 (19.2±3.0)	275	0.5:1

a: Total adult progeny from the five pairs of parents
b: Figures in parenthesis are the average number of progeny per female ± S.D.

Table 3. Median duration of eggs, larvae and pupae of *T. freemani* at different temperatures and relative humidities

°C	RH%	Duration in days and mortality (%)			Total period
		Egg	Larva	Pupa	
25	22	4.7 (96)[a]	71.4 (20.0)[b]	11.8	87.9
	75	4.5 (94)	53.2 (16.7)	9.0	66.7
30	22	3.4 (92)	33.8 (10.0)	7.3	44.5
	75	3.1 (96)	28.9 (3.4)	6.3	38.3
33	22	2.8 (90)	29.5 (33.4)	5.7	38.0
	75	2.6 (94)	23.1 (5.0)	5.2	30.9

a: Hatchability (%) b: Mortality (%)

Food habit and life cycle of *T. freemani*

Since *T. freemani* rediscovered was found from the imported corn, it would be fully expected that the food habit of the insect will be similar to *T. castaneum*. In fact, from laboratory observations, it can be said that *T. freemani* is an omnivorous insect like *T. casteneum*. They can grow up on various kinds of grain, flour, meal and other cereal products. In addition, both stages of adult and larva are cannibalistic on inactive stages of egg and pupa. This indicates strongly that the insect must have zoophagous character in its food habit. As *T. castaneum*, *T. freemani* preferred powdery foods to whole grain because its mandibles seem to be not strong enough to chew through tough outer coating.

To know life history of *T. freemani*, we observed the developmental periods of eggs, larvae, and pupae of the insect, together with the fertility of egg and natural mortality that occurred during larval period, on wheat-feed (standard medium for *T. castaneum* and other stored product insects) under different conditions of temperature and humidity[5]. (Table 3). The duration of the larval periods was affected by both temperature and humidity while that of egg and pupal stage was influenced mostly by temperature. Although higher temperature caused rapid development of larvae, there was a tendency that survival rate of eggs and larvae gradually decreased with rising temperature from 30° to 33°C. Thus optimal temperature for *T. freemani* is likely between 30°–33°C. This indicates that *T. freemani* is almost similar to *T. castaneum* in the optimum conditions but has a slightly longer larval period than that of *T. castaneum*; according to Howe the time required for the development of *T. castaneum* at 32.5°C and 70% RH was totally 22.1 days (2.9 for egg, 14.6 for larva and 4.6 for pupa)[3].

On the other hand it was assumed that the number of larval instars in *T. freemani* was usually 6 as same as that in *T. castaneum*[4].

Prevention of pupation due to crowding in *T. freemani*

Since both species of *T. freemani* and *T. castaneum* were found to be the sibling species, it is reasonable that many characteristics of *T. freemani* observed are very similar to those of *T. castaneum*. However, a typical characteristic of *T. freemani* was observed that the rate of pupation of the larvae

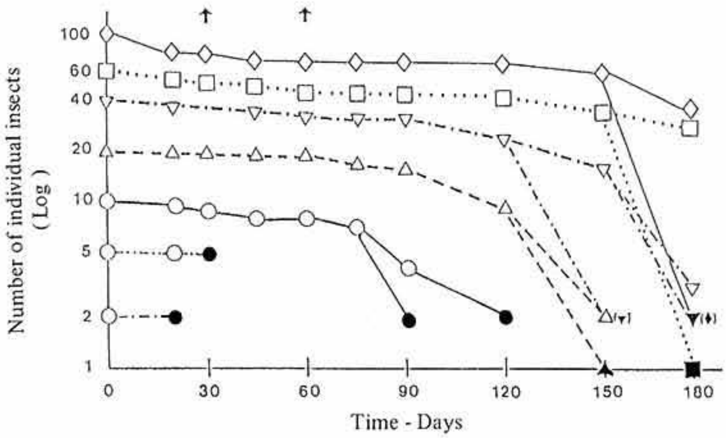

Fig. 1. Effect of larval population density on pupation and survival of larvae in *T. freemani*
Number of pupae is indicated by solid symbols and number of surviving larvae is indicated by open symbols. Initial larval densities; 2(○-·-·●), 5(○···●), 10(○——●), 20 (△---▲), 40(▽-·-·▼), 60(□···■) and 100(◇——◆). Arrows indicate the day on which isolation tests were carried out.

was greatly influenced by population density as shown in Fig. 1[6]. At low densities of less than 5 larvae per vial (2g diet), the larvae could pupate within one month. In contrast, at higher densities of more than 10 larvae, pupation was greatly delayed. A very few larvae had pupated sporadically with densities higher than 20 larvae by the 180th day when the observation was ended. However, all larvae that had failed to pupate by the 30th day or the 60th day due to the crowding effect shortly pupated when the larvae were isolated to reduce the density to either two larvae on 2g diet in a vial or one larva in an empty vial. The phenomenon observed would be the typical characteristic of *T. freemani* because no such distinct crowding effect has been observed in *T. castaneum* or other insects in the genus *Tribolium*.

Position of *T. freemani* in the genus *Tribolium*

According to Hinton's theory on the evolution of the genus *Tribolium*[2], which included at least 33 species, the genus was subdivided into 5 species-groups; *brebicornis, confusum, alcine, castaneum* and *myrmecophilum*, which were considered to have separately evolved in different regions after South-American and the Indo-African continent had drifted apart (Fig. 2). The theory was based principally on the taxonomic characters and geographical distributions of the insect species.

Hinton placed *T. freemani* in the *castaneum*-group. In addition, on the basis of close resemblance in the group, he gathered together three species, *T. castaneum, T. freemani* and *T. madens* into a small group, the *castaneum*-section, although lately North American *T. madens* has been referred to as *T. audax*[1]. Hinton speculated that India had to be the place of origin for the insect species in the section, because the wild state of *T. castaneum* was often found under barks or in decaying trees in India. This idea was strongly supported by the capture of *T. freemani* in Kashimir. However, a question has been raised that, upto now, there is no capture record of both species, *T. madens* (distributed

Species-group	*Brevicornis-*	*Confusum-*	*Alcine-*	*Castaneum-*	*Myrmecophilum-*
Species	• *T. brevicornis*	• *T. anaphe*	*T. alcine*	• *T. castaneum*	*T. mymecophilum*
	T. linsleyi	• *T. confusum*	*T. quadricollis*	• *T. freemani*	*T. antennatum*
	• *T. parallelus*	• *T. destructor*	*T. ceto*	• *T. madens*	
	T. gebieni	*T. semicostata*		• *T. audax*	
	T. carinatum	*T. dawnesi*		*T. apiculum*	
	T. carinatum dubium	*T. beccarii*		*T. cylindricum*	
		T. semele		*T. politum*	
	T. uezumii	*T. sulmo*		*T. waterhousei*	
		T. indicum		*T. parki*	
		T. indicum f. seres			
		T. indicum f. ares			
		• *T. thusa*			

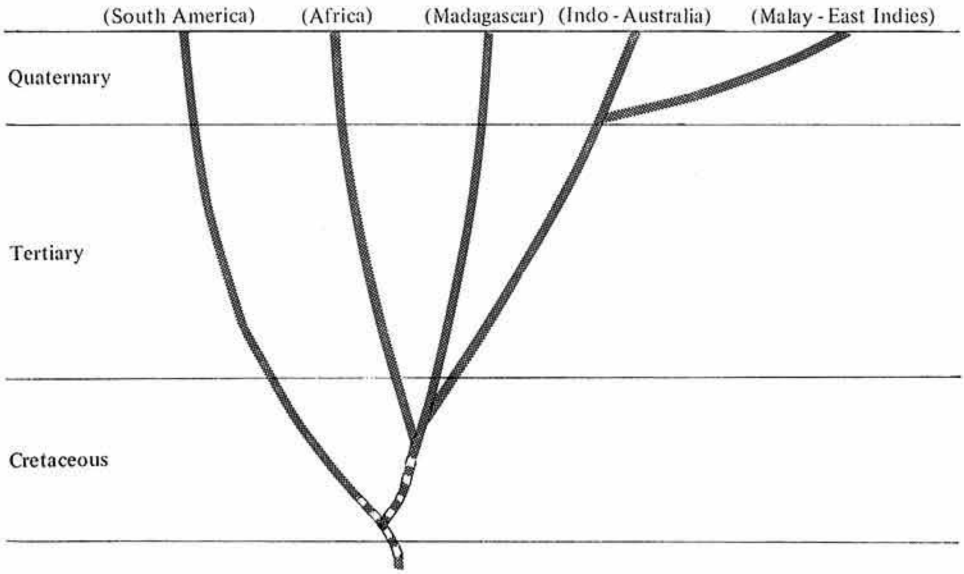

Fig. 2. The five species-groups in the genus *Tribolium* and their evolutionary lines. After Hinton. Solid circles prefixed to species names indicate the species of stored product insect.

in Europe and *T. audax* (distributed in North America) in India.

On the other hand, there was an interesting fact that the cross between *T. madens* and *T. audax* produced infertile F_1 hybrids in the laboratory[1]. In the study of the rediscovered *T. freemani*, as mentioned above we obtained many infertile F_1 hybrids between *T. freemani* and *T. castaneum*. To know the relationship among the insects in the *castaneum*-section, the interspecific crossing between *T. freemani* and *T. madens* and between *T. freemani* and *T. audax* was tried. However, there was no F_1 progeny produced (unpublished). These result indicated that *T. freemani* might be a closer specie to *T. castaneum* than *T. madens* or *T. audax*.

Summary and conclusion

T. freemani, which had not been captured for nearly a century, was rediscovered, in 1981, from imported corn in Japan. Before the rediscovering, there were no available information on the characteristics of *T. freemani* except Hinton's morphological description.

Through the investigations of the rediscovered population of *T. freemani*, several distinct facts were obtained as follows.

1) A sibling species of T. castaneum

The fact of infertile hybrid progeny produced by crossing between *T. freemani* and *T. castaneum* indicates that *T. freemani* is a sibling species of *T. castaneum*. This is the first observation of a hybrid produced from *T. castaneum*.

2) A potential stored product insect

T. freemani was easily developed on the standard wheat-feed medium used for many stored product insects and successfully reared on other stored products. This fact strongly suggests that *T. freemani* can be a stored product insect.

3) The prevention of pupation by crowding

The pupation of *T. freemani* larvae was greatly prevented by increasing larval density. This distinct phenomenon is the first observation in the genus *Tribolium*.

4) The position of T. freemani in the genus Tribolium

In the *castaneum*-section, *T. freemani* might be a closer species to *T. castaneum* than to both species of *T. madens* and *T. audax*, because, beside a sibling species of *T. castaneus*, *T. freemani* did not produce any F_1 progeny in the interspecific crossing of *T. freemani-T. madens and T. freemani-T. audax*.

From the characteristics summarized above, it can be concluded that: (1) *T. freemani* must be distributed into stored product environments; especially in the tropical or semitropical zones, although it seems, at present, of negligible economic importance or extremely localized. (2) As *T. castaneum*, *T. freemani* would be a useful insect for ecological, physiological and genetic studies as an experimental insect.

Acknowledgments

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