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Sexual Isolation in Parthenogenetic *Pycnoscelus surinamensis* and Application of the Name *Pycnoscelus indicus* to Its Bisexual Relative (Dictyoptera: Blattaria: Blaberidae: Pycnoscelinae)¹

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ABSTRACT

The parthenogenetic and bisexual "forms" of the Surinam cockroach, *Pycnoscelus surinamensis* (L.) are considered sibling species, and *Blatta indica* F. is selected from the synonymy to represent the bisexual taxon from

which the parthenogenetic *P. surinamensis* undoubtedly arose. Females of *P. surinamensis* are thelytokous; males are rarely produced parthenogenetically and are nonfunctional.

Roth and Willis (1961) considered the bisexual and parthenogenetic forms of the Surinam cockroach, *Pycnoscelus surinamensis* (L.), as strains of a single species, but they suggested the possibility that the taxon *P. surinamensis* could be represented by sibling species. It was conceivable that the parthenogenetic strain females in the Indo-Malayan region had males associated with them that were different from the bisexual strain males in Hawaii. It was possible also that in Burma and Indonesia the bisexual strain had a male that was different from the male of the Hawaiian form.

Matthey (1948b) favored the hypothesis that in Malaya there was only 1 "race" of *P. surinamensis*. If the females were fertilized, they produced offspring of both sexes and if the females did not mate, they produced only females. Matthey reared a parthenogenetic strain female from Kuala Lumpur, Malaya, but apparently did not mate known parthenogenetic females. To determine whether a male is associated with the parthenogenetic strain, it should be shown that parthenogenetic *P. surinamensis* females can be fertilized by males and produce both sexes with no reduction in fertility. This phenomenon has never been demonstrated (Roth and Willis 1961).

In this paper I am reporting the results of crosses between *P. surinamensis* from different geographical areas. These crosses were made to determine whether the taxon *P. surinamensis* includes a sibling species.

MATERIALS AND METHODS

Colonies of *P. surinamensis* from 5 different geographic regions have been established and are being maintained in the U.S. Army Natick Laboratories. The cockroaches are reared on Purina laboratory chow, at 25°-27°C and 35%-50% RH. The data for these cultures are:

1. Florida parthenogenetic (Fla. ♀). Started in 1950 from 2 ♀ collected in Clearwater, Florida.
2. Hawaiian bisexual (Haw. ♂ and ♀). This strain was started in 1954, and additional specimens were obtained in 1958; males and females originated from Barber's Point and Koko Head, Oahu, Hawaii. It does not reproduce parthenogenetically.
3. Australian parthenogenetic (Aust. ♀ and ♂). Received from Dr. I. M. Mackerras, November 2, 1964. This strain was started from a female collected on Fraser Island, which is a large, well wooded, sandy island off the Queensland coast near Maryborough. The culture was begun in February 1949 at the Queensland Institute for Medical Research and some were

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eventually sent to the CSIRO, where they have been maintained. According to Mackerras (personal communication) "we thought males were extremely rare. I have a recollection that one was found, but I cannot locate this specimen now."

I found this strain to reproduce parthenogenetically, but on June 23, March 27, and April 9, 1965, 11 adult ♂ were found in the culture. The abdomens of these (Aust. ♂) were considerably darker (typical of Australian females) and the individuals were larger than Hawaiian males.

4. Indonesian bisexual (Indon. ♀). These specimens were received from Dr. S. Kadarsan, Bogor, Indonesia, in March 1965. There were 8 nymphs and 1 adult ♀ which survived shipment; several adult females and males had died. The adult female died without reproducing. Six nymphs became adult females which did not reproduce parthenogenetically. Unfortunately, no living Indonesian males were obtained, but the females were successfully crossed with Hawaiian males.
5. Indonesian parthenogenetic. Same collection data as 4.
Two nymphs became adult females that were parthenogenetic. The nymphs of this parthenogenetic clone are red. No crosses were made with these individuals.
6. Panamanian parthenogenetic. Started from a single female collected by Clyde Stephens in Chinguinola, Panama (received November 4, 1964). No crosses were made with these individuals.

In all the crosses with Hawaiian males, the spermathecae of the mated females were examined at the termination of the experiments and were found to have sperm. In the 4 crosses in which Australian parthenogenetic males were used, the spermatheca of only 1 of the mated females was examined at the end of the experiment and no sperm were present. However, spermatophores had been transferred in all 4 matings.

RESULTS

1. *Florida Parthenogenetic Clone*.—The biology of this clone has been reported, as have been the results of crossing Fla. ♀ with Haw. ♂ (Roth and Willis 1961). These mated females showed a reduction in number of eggs which hatched, and all the offspring were females that reproduced parthenogenetically. Although several Fla. ♀♀ were kept with Aust. ♂♂ (parthenogenetic), only 1 ♀ mated. Three litters were obtained, consisting of 19, 14, and 10 nymphs, respectively. Thirty-eight individuals were reared. All were females and reproduced parthenogenetically.

2. *Hawaiian Bisexual*.—The biology of this non-parthenogenetic bisexual strain was reported also by Roth and Willis (1961). The males of this strain were used in several crosses (see following). The

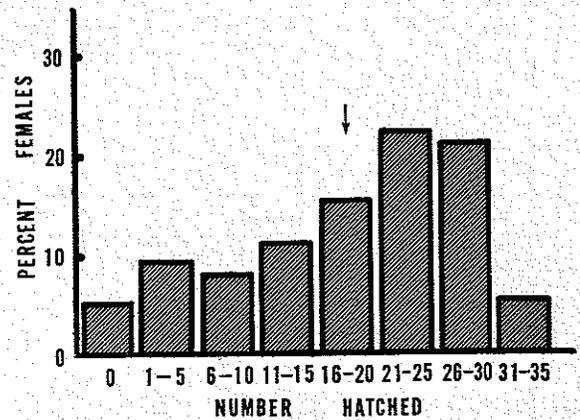


FIG. 1.—Number of eggs which hatched in the first litter in 71 unmated females of parthenogenetic *Pycnoscelus surinamensis* from Australia. Arrow points to the mean number (= 18.0) which hatched.

females did not mate with parthenogenetic males of the Australian clone, though exposed to them for long periods.

3. *Australian Parthenogenetic Clone*.—The unmated females oviposit normally in about 9–10 days after emergence. The number of eggs which hatch from the first oötheca varies considerably among females (Fig. 1). The average hatch was 18, which is almost the same (20.7) as that found in the Floridian clone (Roth and Willis 1961).

The results of 7 crosses between Aust. ♀ and Haw. ♂ are given in Table 1. The average hatch in the first litter was 12.6, slightly lower than the average hatch of the first litter in unmated females. The average hatches of the second, third, and fourth litters of mated females were 6.4, 4.9, and 2.9, respectively (for the 7 ♀ shown in Table 1). There is a drop in hatching with successive oöthecae, but it is unknown if this is due to mating, since the number hatching in successive oöthecae of unmated females was not determined. There was only 1 ♂ among the 114 adults that were reared; the females reproduced parthenogenetically.

The results of 3 crosses between Aust. ♀ and Aust. ♂ (parthenogenetic) are shown in Table 1. Only 1 female (no. 3) produced a large litter. All of the 47 offspring that were reared were females and they reproduced parthenogenetically.

4. *Indonesian Bisexual*.—The results of the study with Indonesian females are shown in Table 2. Virgin females (no. 1 and 2) did not reproduce, whereas the female (no. 3) mated to an Haw. ♂ produced young. Females 4, 5, and 6 oviposited but did not reproduce until they were mated to Hawaiian males. The oötheca usually is not retracted into the uterus by virgin females (Table 2, NR) a behavior of the bisexual strain from Hawaii (Roth and Willis 1961). Females 3–6 were mated only once. There was a reduction in fertility in successive oöthecae formed after mating. In females 3, 4, and 6, 1 or more of the oöthecae formed after mating were not retracted into

Table 1.—Results of crossing Australian females of *Pycnoscelus surinamensis* with males from Hawaii and from Australia.

No.	Age ^a (days)	Females Oö- theca no.	No. eggs in oötheca			No. reared ♂ ♀			
			Developed		Unde- vel- oped				
			Hatched	Not hatched					
<i>Australian ♀ × Hawaiian ♂</i>									
1	339	1	11	20	6				
		2	0	8	19				
		3	0	16	* ^b				
		4	1	9	7				
2	340	1	16	*	*	0	10		
		2	10	*	*	0	9		
		3	11	19	3	0	9		
		4	0	11	*	0	16		
3	368	1	18	*	*	0	16		
		2	14	*	*				
		3	0	*	*				
		4	4	16	4	0	4		
		5	1	7	2	0	1		
4	339	1	11	*	*	0	11		
		2	6	10	5	0	3		
		3	0	17	4				
		4	4	7	8	0	1		
		1	26	*	*	0	24		
5	330	2	7	*	*	0	2		
		3	14	*	*	0	12		
		4	3	*	*	0	2		
		1	6	23	16				
6	242	2	0	*	*				
		1	0	*	*				
		2	8	*	*	0	8		
		3	9	2	*	0	8		
7	315	4	8	*	*	1	2		
		<i>Australian ♀ × Australian ♂</i>							
		1	0	6	13				
		1	1	2	31	0	1		
2	365	2	0	33	8				
		1	21	*	*	0	14		
		2	25	*	*	0	20		
		3	14	9	3	0	12		
3	379	4	10	1	1				

^a At end of the experiment.

^b * Eggs not counted.

the uterus. This may have been due to a depletion of sperm; Stay and Gelperin (1966) showed that sperm in the spermathecae are necessary for normal retraction of the oöthecae in the bisexual strain of *P. surinamensis*. From these crosses 123 offspring were reared and they consisted of 62 ♂:61 ♀ (Table 2). The females reproduced only when mated.

The Indonesian females did not mate with Australian parthenogenetic males although they were exposed to them for long periods.

DISCUSSION

Facultative parthenogenesis is not uncommon in Blattaria (Roth and Willis 1956). *P. surinamensis* is the only known cockroach which is obligatorily parthenogenetic. Its parthenogenesis is apomictic (Suomalainen 1962); the eggs undergo 2 equational maturation divisions, but no chromosome reduction takes place, and the diploid number is maintained

(Matthey 1945). The females of the parthenogenetic and bisexual strains have the same number of chromosomes ($2N = 38$). The males of both strains have $2N = 37$, but the male of the bisexual strain has a lagging chromosome in the spermatogonial mitosis as well as in the second maturation division (Matthey 1948 a, b). This phenomenon was not reported in the male which developed, apparently by nondisjunction of the X-chromosome, from an unfertilized egg (Matthey 1945).

Although the number of crosses made in this study is admittedly small, the results indicate that there are 2 kinds of males associated with the taxon *P. surinamensis*. One occurs relatively rarely as a parthenogenetically produced individual; the 11 ♂ found in the Australian colony represent this type and probably developed as a result of nondisjunction of the X-chromosome. The crosses between the Australian female and Australian male and Florida female and Australian male show that these parthenogenetically produced males are nonfunctional in that all but 1 of the offspring were females; the 1 ♂ probably arose in the same manner as the 11 ♂ just mentioned. It now seems likely that the parthenogenetic female does not have a male associated with it normally in nature, and facultative parthenogenesis does not occur as suggested by Matthey (1948b). In thelytokous

Table 2.—Results of crossing Indonesian females with Hawaiian males of *Pycnoscelus surinamensis*.

No.	Age ^a (days)	Females Vir- gin or mated	Oöthecae		No. eggs hatched	No. reared ♂ ♀	
			Retracted or not retracted				
			1	249	V	1	NR
2	383	V	2	NR	0		
		V	3	NR	0		
		V	4	NR	0		
		V	5	R (50) ^b	0		
		V	6	R (28) ^b	0		
		V	1	NR	0		
		V	2	NR	0		
		V	3	R	0		
		M	1	R	40	18	16
		M	2	R	12	3	4
4	238	M	3	NR	0		
		V	1	NR	0		
		V	2	NR	0		
		M	3	R	39	12	16
		M	4	NR	0		
		M	5	NR	0		
		M	6	NR	0		
		V	1	NR	0		
5	340	M	2	R	28	9	7
		M	3	R	13	6	7
		M	4	R	13	6	2
		M	5	R	10	6	2
		V	1	NR	0		
		V	2	NR	0		
		V	3	NR	0		
		M	4	R	18	8	9
6	228	M	5	NR	0		
		V	1	NR	0		
		V	2	NR	0		
		V	3	NR	0		
		M	4	R	18	8	9

^a At termination of the experiment.

^b No. days eggs were in the uterus. Only a single egg developed in all oöthecae retracted into the uterus by virgins.

parthenogenesis "fertilization is entirely suppressed. Males are absent from the population or are only produced as occasional non-functional anomalies, frequently intersexual." (White 1964.) There is no doubt that *P. surinamensis* is thelytokous.

The second type of male is the one normally associated with the bisexual female. Based on museum collections, males in Malaya are found as frequently as females (Hebard 1929). The offspring produced by mated bisexual females in the laboratory have a sex ratio of about 1:1 (Roth and Willis 1961). The results of crosses show that although the Hawaiian male cannot successfully fertilize parthenogenetic females from Florida or Australia, it can successfully fertilize Indonesian females (producing a 1:1 sex ratio), indicating that the Hawaiian and Indonesian forms are conspecific.

Dr. M. J. D. White (1964, personal communication) commented on the *Pycnoscelus* problem as follows: "My feeling is that where there are closely related thelytokous and sexual forms, one should give them separate names. On any biological definition of the species, the thelytokous biotype is not part of the gene-pool of the sexual taxon. The real difficulty, I feel, arises where there are several or many thelytokous biotypes related to a sexual taxon. Most authors have assumed that this is evidence of evolutionary change under parthenogenetic reproduction. I am inclined to think this is a mistaken view (although I accepted it uncritically 10 years ago) and that in such situations one is usually dealing with a multiple, i.e., polyphyletic origin of thelytoky from the ancestral sexual taxon. I mention this point because it may be relevant to your *Pycnoscelus* situation. To regard a number of morphologically and perhaps cytogenetically diverse thelytokous biotypes which have arisen polyphyletically, as a single species seems undesirable. I am really not sure what I would do in such a case. The real trouble is that so little is known of the evolutionary biology of thelytoky." Mayr (1963) also has commented on parthenogenesis, as follows: "Complete parthenogenesis poses a taxonomic problem. The orthodox species criterion of interbreeding cannot be applied because each clone is reproductively isolated not only from the parental species but also from every sister clone. How to treat clones and parthenogenetic species must be decided for each

case. Where a parthenogenetic line has originated from a bisexual species by an irreversible chromosomal event (for instance, polyploidy), it is usually advisable to consider it a separate (sibling) species, even though the morphological difference is slight."

I intend to follow Mayr's (1963) and White's (1954) suggestions in treating the *P. surinamensis* complex, and propose giving the bisexual form a different name, since Linnaeus presumably named the parthenogenetic form from Surinam where males do not normally occur. Princis (1966, personal communication) differs from this opinion and believes that the *Pycnoscelus* complex (bisexual mother form and thelytokous clones) should be considered as a single species.

Princis (1964) lists 13 synonyms of *P. surinamensis* and I believe that among these are included the bisexual species. Burmeister (1839) separated *Blatta indica* F. from *Panachlora surinamensis* (L.) because the East Indian *indica* was smaller and proportionately wider and had wings that were only about half as long as those of *P. surinamensis*. Brunner (1865, p. 278-80) included *indica* as a "*Varietas minor, elytris abbreviatis*" in the synonymy of *P. surinamensis*. "From this it would appear that in 1865 at least two forms of *Pycnoscelus* were being considered as *P. surinamensis*; Fabricius' (1775) *Blatta indica* might have been the same as the Hawaiian bisexual form, although his description (p. 272) is insufficient to distinguish it from the parthenogenetic strain." (Roth and Willis 1961). The only absolutely reliable character for distinguishing between females of the parthenogenetic and bisexual species is reproduction. However, although wing and tegmina length may vary somewhat in females of both species, I have never seen parthenogenetic females with wings as short as some bisexual individuals. Parthenogenetic males undoubtedly occur rarely in nature, but when males are found they probably belong to the bisexual taxon.

The earliest synonym for *P. surinamensis* listed by Princis (1964) is the description of *Blatta indica* by Fabricius. According to Sv. G. Larson (personal communication), Fabricius' type material of *Blatta indica* in the University Museum in Copenhagen includes 2 specimens, male and female. I propose that *Pycnoscelus indicus* (F.) be used to designate the

Table 3.—Some differences between females of *Pycnoscelus surinamensis* and *P. indicus*.

<i>Pycnoscelus surinamensis</i>	<i>Pycnoscelus indicus</i>
1. Reproduces only parthenogenetically (Rarely-produced males are nonfunctional).	Reproduces only bisexually (functional males produced in about 1:1 ratio).
2. Oötheca of virgins usually retracted into the brood sac.	Oötheca of virgins usually not retracted into brood sac.
3. Female pheromone production not controlled by corpus allatum hormone. ^a	Female pheromone production under control of corpus allatum hormone. ^b
4. Usually ocelli practically touch the eyes.	Usually a distinct space between eye and ocellus.
5. Tegmina and wings usually slightly short of or extending beyond the tip of the abdomen.	Length of tegmina and wings variable but may be reduced so that several terminal abdominal segments are exposed.

^a Based on females which originated in Florida.

^b Based on females which originated in Hawaii.

bisexual relative of *P. surinamensis*. Complete morphological descriptions of the female *P. surinamensis* and of male *P. indicus* (considered as *P. surinamensis*) are given by Hebard (1917). Roth and Willis (1961) described morphological differences between individuals of restricted populations of the 2 species. The male genitalia and subgenital plate of *P. indicus* are illustrated by McKittrick (1964, p. 180-1).

In addition to the differences between the Hawaiian and Floridian species mentioned earlier, females of *P. surinamensis* produce a sex pheromone which is as effective in attracting males of *P. indicus* as is the pheromone produced by the females of *P. indicus*. This fact further emphasizes the close relationship of the 2 species and is additional evidence that the bisexual species is the sexual taxon from which the parthenogenetic form evolved. Barth (1965) has shown that sex pheromone production is controlled by the corpora allata in the bisexual species but not in the parthenogenetic; parthenogenetic females continue to produce sex pheromone even during pregnancy when their corpora allata are inactive. He explains the loss of hormonal control of sex pheromone production in parthenogenetic individuals as resulting from the fact that the female no longer requires the male for reproduction. I believe that one can look upon the production of sex attractant by the parthenogenetic female as a relic character persisting from the bisexual stock from which it arose. The loss in hormonal control may be the first step in the eventual loss of the attractant.

The principal differences between the 2 species are summarized in Table 3. The 2 morphological characters listed are not always reliable. Particularly, the lengths of the tegmina and wings in relation to the abdomen are sometimes difficult to discern because pregnancy (i.e., an oötheca in the uterus) extends the abdomen and drying (in museum specimens) shrinks the body.

The geographic area of origin of *P. surinamensis* is the Sunda Islands, i.e., the islands of the Malay Archipelago (Princis, personal communication). Since both the parthenogenetic and bisexual forms occur in Malaya (Matthey 1948a; Rehn, in Roth and Willis 1961; present paper), it is apparent that parthenogenesis already had evolved in the species' homeland. What appears to be geographic parthenogenesis in *Pycnoscelus* is undoubtedly due to the fact that a parthenogenetic species can be established much more readily than a bisexual one (where both sexes would have to be introduced) (Roth and Willis 1961, White 1964). The cases of thelytoky now met with are of recent origin (Suomalainen 1962). In geographic areas outside the country of origin of *Pycnoscelus*, the occurrence of both *P. surinamensis* and *P. indicus* could be due to a double introduction. This hypothesis is probably a fact on Hawaii, where *P. surinamensis* was first recorded as scarce in 1882 by Borimans (Hebard 1922). Rehn (in Roth and Willis 1961) believed that the Hawaiian "*P. surinamensis*" was introduced within the last century or so, from Indo-Malaya.

The "Major" and "Minor" races of *P. surinamensis* described by Roeser (1940) both have the same number of chromosomes (Suomalainen 1945) and probably represent 2 divergent biotypes of the parthenogenetic form. The fact that the morphological characters which clearly distinguish *P. surinamensis* from Florida from *P. indicus* from Hawaii do not hold up in specimens from various geographic areas can be explained on the basis of evolution occurring in different biotypes, or of *P. surinamensis* being of polyphyletic origin. The Australian parthenogenetic females are blacker (particularly the sternum) than the Floridian individuals. However, the color pattern in some individuals in the former colony may vary, and integrations from black to dark brown or reddish (typical of Florida females) are found. At present, one may consider all parthenogenetic *P. surinamensis* from different areas as 1 species, but in referring to these clones, it would be wise to indicate the geographic area in which they were collected.

The following specimens have been deposited in the U.S. National Museum:

P. indicus: 32 ♀, 8 ♂, individuals from the Natick culture which originated from Barber's Point and Koko Head on Oahu, Hawaiian Islands; 5 ♂, 11 ♀, the offspring of crosses between Bogor, Indonesia, females and Hawaiian males.

P. surinamensis: 4 ♂, 21 ♀, 5 nymphs, from the Natick culture which originated from Fraser Island, off the Queensland coast of Australia near Maryborough; 3 ♀, 7 nymphs (reddish), from Natick culture which originated in Bogor, Indonesia.

The series of *P. indicus* shows variations in color and wing length in the females and color differences in the males. The differences in size and color of the females (all of which have appeared in our Hawaiian culture during years of breeding) appear to correspond with differences in the parthenogenetic "Major" and "Minor" races described by Roeser (1940). Although the nymphs of *P. surinamensis* from Australia and Florida are usually black, occasionally reddish forms are found. The nymphs of *P. surinamensis* from Bogor are red. The nymphs of *P. indicus* are usually black, but reddish individuals are found, as well as intermediates from reddish to black. The red nymphs of *P. indicus* produce females which can reproduce only bisexually.

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