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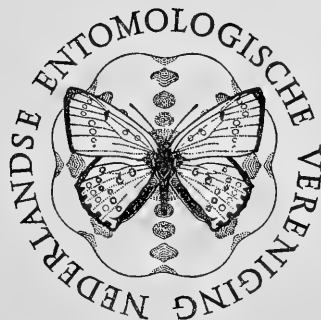
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# COURTSHIP BEHAVIOUR AS SPECIES BARRIER IN THE PARDOSA PULLATA GROUP (ARANEAE, LYCOSIDAE)

by

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## ABSTRACT

The composition of the behaviour of males of three species of the *Pardosa pullata* group — *P. prativaga* (L. Koch), *P. sphagnicola* (Dahl) and *P. pullata* (Clerck) — is described, depending on both conspecific and non-conspecific stimuli.

The isolating mechanisms between the species studied are investigated in interbreeding experiments. The relative importance of behaviour as species barrier in the *Pardosa pullata* group is discussed.

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## I. INTRODUCTION

The *Pardosa pullata* group is constituted of a number of closely related species, in morphological (Wiebes, 1959; Holm and Kronestedt, 1970; Den Hollander, 1970), as well as in ecological respect (Richter et al., 1971; Den Hollander, 1971; Den Hollander & Lof, 1972). As morphologically intermediate specimens have been found, the possibility of the occurrence of interbreeding in the field has been suggested (Locket & Millidge, 1951; Den Hollander, 1970). Under natural conditions several mechanisms may operate to prevent interbreeding (Mayr, 1969). Concerning species of the *Pardosa pullata* group Den Hollander (1971) and Den Hollander & Lof (1972) studied seasonal and habitat factors acting as barriers against interbreeding. They found that such factors do not completely isolate the species studied. Otherwise, mating behaviour as well as post-mating mechanisms may be important too in isolating the species of the *P. pullata* group.

It should be mentioned that, within the genus *Pardosa*, courtship display is very specific, and is therefore considered to act as an important barrier between the species (Bristowe & Locket, 1926). Ethological isolating mechanisms, i.e. barriers to mating due to incompatibilities in behaviour, represent the largest and most important class of isolating mechanisms in animals (Mayr, 1969). As a consequence of the biological species concept (Mayr, 1940) isolating mechanisms "are perhaps the most important set of attributes a species has, because they are, by definition, the species criteria" (Mayr, 1969).

The present paper mainly deals with courtship behaviour of the species of the *Pardosa pullata* group in the context of the importance of behaviour as an isolating mechanism. Besides, some observations on the occurrence of mechanical and post-mating isolating mechanisms between the species studied are dealt with.

## II. MATERIALS AND METHODS

### IIa. Materials

The study was carried out with three species of the *P. pullata* group, viz., *Pardosa prativaga* (L. Koch, 1870), *P. pullata* (Clerck, 1757) and *P. sphagnicola* (Dahl, 1908), which species normally occur in the Netherlands (Den Hollander, 1970; *P. prativaga*



var. *fulvipes* (Collett, 1875) stands for *P. sphagnicola*). Subadult specimens were collected from several populations in the Netherlands and France (Table 1). They were kept at low temperature, about 5° C. Before the experiments started, the spiders were transferred to room temperature. After a few days the final moult then occurred. During the experiments temperature ranged from 28-30° C and the relative humidity from 70 to 90%.

## IIb. Methods

### A. Confrontation experiments.

In these experiments each male was observed individually under various stimulus situations (Table 2). Males were tested on conspecific as well as non-conspecific substrates, both in the absence (5, resp. 1 and 3) and presence of females, being either conspecific (8, resp. 9 and 10) or non-conspecific ones (6 and 7, resp. 2 and 4) (the figures indicate the codes of the respective stimulus situations (Table 2).

The behavioral data were recorded with the help of a 20 channel event recorder

Table 1. The localities of the populations of the *Pardosa pullata* group used in the present study (cf. Den Hollander, 1971; Den Hollander et al., 1972)

Locality	Species	Experiment	
The Netherlands			
Vogelenzang, Heemstede	pra	A and B	spring, resp. autumn
Hollandse Rading, Hilversum	pul	A and B	spring, resp. autumn
Bosweítje, Rockanje	pra, pul	B	spring
De Eese, Steenwijk	sph	A and B	spring, resp. autumn
Woldberg, Steenwijk	sph	B	spring
France			
Selon, Hérault	pra	B	spring
Palavas, Hérault	pra	B	spring
Etang de Brion, Yonne	pra	B	spring
Le Pin, Yonne	pra, pul	B	spring

(Esterline - Angus) wired to two 10-key keyboards. A paper speed of 50 cm/min was used. In this way the preservation of records on frequencies and durations as well as the temporal patterning of behaviour elements was made possible. The occurrence of a behaviour event was recorded by depressing the appropriate key for the duration of that behaviour. It is evident that the accuracy of establishing durations of less than about two secs. will be small.

Three males and three females of each species were used in these experiments. In the stimulus situations 5 and 8 (Table 2) each male was tested. In the other experiments the observations were carried out with individuals which were chosen at random out of the three males and three females.

### B. Breeding experiments.

In these experiments 4-6 males were put in glass boxes together with the same number of females of the different species (non-conspecific females). One or two conspecific females were added. In these experiments the occurrence of mating and afterwards, construction and carrying of egg sacs by the females, as well as the devel-

opment of the eggs in the egg sacs and the development of the pulli emerging from the egg sacs, were recorded.

Table 2. The respective stimulus situations in which the behaviour of the males of the species studied was recorded; pra = *prativaga*, pul = *pullata*, sph = *sphagnicola*

Code	Number of experiments	<i>Pardosa prativaga</i> males		<i>Pardosa sphagnicola</i> males		<i>Pardosa pullata</i> males	
		substrates (S ♀)	females (♀)	substrates (S ♀)	females (♀)	substrates (S ♀)	females (♀)
1.	2	sph	—	pra	—	pra	—
2.	2	sph	sph	pra	pra	pra	pra
3.	2	pul	—	pul	—	sph	—
4.	2	pul	pul	pul	pul	sph	sph
5.	8	pra	—	sph	—	pul	—
6.	2	pra	sph	sph	pra	pul	pra
7.	2	pra	pul	sph	pul	pul	sph
8.	12	pra	pra	sph	sph	pul	pul
9.	2	sph	pra	pra	sph	pra	pul
10.	2	pul	pra	pul	sph	sph	pul

## IIC. The behaviour of the species studied

Courtship behaviour of Lycosid spiders was studied thoroughly by Vlijm and co-workers (Vlijm & Dijkstra, 1966; Vlijm & Borsje, 1969; Dijkstra, 1969; Vlijm, Den Hollander & Wendelaar Bonga, 1970; Dijkstra, Van der Ploeg & Koomans, in prep.). In these studies courtship behaviour is considered to be that kind of behaviour of the males which especially occurs in the presence of females of the same species.

Up till now little work has been done on the behaviour of species of the *P. pullata* group. Hallander (1967) stated that *P. pullata* does not show any courtship display and that the male directly jumps on the female to mate. However, Vlijm & Borsje (1969) observed specific movements of palps and legs as well as a special way of locomotion in the precopulatory phase of this species. Consequently these authors concluded that above mentioned behavioral elements may be considered courtship behaviour.

*P. prativaga* and *P. sphagnicola*, on the other hand, show a very distinct courtship display consisting of palpal movements comparable with those described for the *Pardosa amentata* group (Vlijm & Dijkstra, 1966), as well as special patterns of locomotion (unpublished results, e.g., film records, from the laboratory).

With the help of the following list of elements, the behaviour of males of the species studied could be satisfactorily described in the respective stimulus situations.

### A. Locomotory behaviour, non-oriented at female :

*Walking* (W) : normal locomotory activity.

*Jerky walking* (Jw) (Dijkstra, 1969) : jerky locomotion; described as "Hopping" for *P. pullata* by Vlijm & Borsje (1969).

*Searching* (S) (Vlijm & Borsje, 1969) : slow continuous locomotion in which the body is near to the substrate and the palps are continuously in contact with the substrate.

*Searching walk* (Sw) : Jerky locomotion with the body near to the substrate and the palps drumming on it.

*Stalking* (St) (Dijkstra, 1969) : slow locomotion in which the legs are moved very stealthily.

B. Locomotory behaviour, oriented at female :

*Encircling* (E) (Dijkstra, 1969) : after touching the female the male retreats and moves in a semi-circle around the female, his front remaining directed towards the female throughout.

*Hopping* (H) : first the body, and especially the abdomen, is raised, the legs being wide apart. Then, in a sudden movement ("hop"), the body is lowered between the legs, quivering violently. After this the male takes a step in the direction of the female.

*Copulation attempt* (Ca) : the male jerkily runs up to the female, lowering the abdomen to the substrate, stretching the front legs to touch the female, and tries to mount the female.

C. Oscillatory movements of abdomen and palps :

*Abdomen vibrating* (Av) (Vlijm & Dijkstra, 1966) : the tip of the abdomen violently quivers up and down, sometimes touching the substrate.

*Palp vibrating* (Pv) (Vlijm & Dijkstra, 1966) : both palps simultaneously move quickly up and down, while kept in their normal curved position.

*Palp cycling* (Pc) : the palps are, alternately, stretched and raised after which they are lowered and brought back to their normal, curved, position.

D. Single movements of legs and palps :

*Leg waving* (Lw) (Dijkstra, Van der Ploeg & Koomans, in prep.) : slow motions of the legs of first pair. They are stretched and raised and then brought back to their resting position. The tips of the legs describe an arch in this way.

*Palp waving* (Pw) (*litt. see Leg waving*) : the same motions of the palps as described for the front legs under "Leg waving". Vlijm & Borsje (1969) described Leg and Palp waving as "courting".

*Leg beating* (Lb) : one of the front legs is stretched and moved up and down rather quickly.

E. Other behaviour elements :

*Spinning* : (Sp) (Richter, 1970) : production and attachment of silk.

*Preening* (P) (Vlijm & Borsje, 1969) : drawing a leg or a palp through the chelicerae.

*Rubbing* (R) : rubbing two adjacent legs together; synonymous with Double preening (Vlijm & Borsje 1969).

Some of these behaviour elements occurred throughout the species studied, while others appeared to be restricted to one or two of the species only. Besides, comparable behavioral components do vary in structure between the respective species. This variation, however, will not be described in this paper.

### III. RESULTS

#### A. Confrontation experiments

##### A 1. Recordings of behaviour

###### A. 1.1. Frequencies and durations of the recorded behaviour elements.

Males of the species studied were tested in two stimulus situations, viz. conspecific

substrates, either without or with conspecific females (Table 2, situations 5 and 8, respectively). The experiments lasted 20 min. or, when mating occurred, till the moment of mating. In total eight experiments per species were performed on substrate only (sit. 5) and twelve with females present (sit. 8). The results are presented in Table 3.

#### 1.1.1. *P. prativaga* :

In the stimulus situation S ♀ (pra) males spend most of the period of activities (total duration) in Jerky walking, Palp cycling, Preening and Walking together (more than) 90%). Concerning Preening and to a lesser extent, Walking, this is due to the rather long duration of each period of Preening and Walking, respectively. On the other hand, the periods of Jerky walking as well as Palp cycling last much shorter. However, their frequencies are high. Thus these two activities also to a large extent contribute to the total period of activities.

In the stimulus situation S ♀ (pra) + ♀ (pra) some differences occur as compared with S ♀ (pra). The level of activity, i.e. the total duration of the recorded activities, is lower in the situation S ♀ + ♀ (604) than in S ♀ (860). In the stimulus situation S ♀ + ♀, males spend up to one third of the total period of activities in Abdomen and Palp vibrating, Hopping, Encircling and Copulation attempt together, at the cost of the remaining behaviour elements. Nevertheless Preening, Walking, Jerky walking and Palp cycling together still take up to 60% of the total period of activities.

The set of behaviour elements Abdomen and Palp vibrating, Hopping, Encircling and

Table 3. Frequencies and durations of recorded behaviour

#### *Pardosa prativaga*

Behaviour element	total duration (sec)		frequency		mean duration (sec)		range of mean dur. per exp.	total duration (sec)	
Preening	202	70	11	5	18.4	13.6	8.2—30.0	158	33
Walking	96	40	14	7	6.7	5.9	2.4—12.0	46	21
Rubbing	16	5	6	2	3.0	2.5	1.6—4.8	25	15
Spinning	7	5	6	5	1.2	1.0	1.0—1.2	6	3
Jerky walking	299	135	105	43	2.9	3.1	1.3—7.0	25	11
Searching	10	17	3	7	3.1	2.6	1.6—4.8	126	48
Searching walk	24	11	9	4	2.8	3.7	1.2—4.8	19	4
Palp cycling	204	121	114	59	1.8	2.0	1.4—2.4	55	13
Copulation attempt	—	23	—	15	—	1.5	0.8—2.6	—	2
Encircling	—	13	—	9	—	1.4	1.0—3.6	—	—
Abdomen vibrating	2	91	1	40	1.2	2.3	1.2—4.9	14	318
Palp vibrating	—	50	—	24	—	2.1	1.7—2.9	5	252
Hopping	—	23	—	10	—	2.3	1.2—4.8	—	107
Leg beating	—	—	—	—	—	—	—	66	14
Leg waving	—	—	—	—	—	—	—	16	2
Palp waving	—	—	—	—	—	—	—	1	—
Stalking	—	—	—	—	—	—	—	—	—
Total duration	860	604						562	843
Situation (Table 2)	5	8	5	8	5	8	5+8	5	8

Copulation attempt only occurs in the stimulus situation  $S\text{♀} + \text{♀}$ . These activities thus may be considered Courtship Display. The durations of the respective elements of Courtship Display are rather short and of the same length throughout. Particularly Abdomen and Palp vibrating show high frequency values as compared with other elements in the behaviour of *P. prativaga* males.

In both stimulus situations the frequencies as well as the durations of Rubbing, Spinning, Searching and Searching walk are rather small. Leg beating, Leg waving, Palp waving as well as Stalking do not occur at all in the behaviour of *P. prativaga* males.

### 1.1.2. *P. sphagnicola* :

In the stimulus situation  $S\text{♀}$  (sph) up till 80% of the total period of activities consisted of Preening, Searching, Leg beating, Palp cycling and Walking together. As in *P. prativaga*, the mean durations of Preening and Walking are rather high. In *Pardosa sphagnicola* the same holds for Searching. None of the recorded elements in the behaviour of *P. sphagnicola* males shows, as extremely high frequencies, as occur in *Pardosa prativaga* (Jerky walking, Palp cycling).

Under the stimulus situations  $S\text{♀}$  (sph) +  $\text{♀}$  (sph) the behaviour of *P. sphagnicola* males changes considerably as compared to  $S\text{♀}$  (sph). The total duration of the recorded activities increases from 562 to 843 secs. 80% of this period is spent in Adomen and

elements of males in the stimulus situations 5 and 8 of Table 2

<i>Pardosa sphagnicola</i>					<i>Pardosa pullata</i>							
frequency	mean duration (sec)		range of mean dur. per exp.		total duration (sec)		frequency	main duration (sec)		range of mean dur. per exp.		
7	2	24.0	17.2	1.2—40.8		175	101	9	5	20.3	22.0	7.2—36.0
8	4	5.5	5.0	1.2— 9.7		63	37	8	7	8.1	7.1	1.2—13.3
5	3	4.7	4.2	1.8— 7.2		12	10	3	3	3.8	4.3	1.8— 6.0
5	2	1.1	1.2	0.8— 1.8		3	1	2	1	1.3	1.3	1.2— 3.5
6	4	4.0	3.1	1.2— 7.2		25	33	4	6	6.6	8.2	1.2—10.1
14	6	9.2	8.3	1.2—26.4		99	82	8	8	12.6	10.5	3.1—34.2
7	1	2.9	3.0	1.2— 4.8		128	122	13	9	9.6	13.4	1.2—31.7
16	5	3.5	2.6	1.2—10.4		3	1	2	2	1.7	0.8	0.5— 2.4
—	2	—	1.2	1.2—18.6		—	4	—	3	—	1.6	1.2— 2.8
—	—	—	—	—		—	—	—	—	—	—	—
2	41	6.5	7.3	2.4—21.6		—	—	—	—	—	—	—
1	42	3.7	5.3	1.2—19.6		—	—	—	—	—	—	—
—	36	—	1.2	1.9— 7.2		—	—	—	—	—	—	—
13	5	4.9	3.2	1.0—12.7		39	24	7	5	5.9	5.7	1.2—24.0
6	1	2.6	2.2	1.2— 7.7		1	11	1	4	1.3	2.8	1.2— 6.6
1	—	1.0	—	1.1— 1.8		—	3	—	2	—	1.3	1.2— 1.4
—	—	—	—	—		—	4	—	1	—	4.0	1.7— 9.0
					548	433						
5	8	5	8	5+8		5	8	5	8	5	8	5+8

Palp vibrating and Hopping, while the period spent in each of the remaining behaviour elements decreases.

Abdomen and Palp vibrating as well as Hopping especially occur in the situation  $S\text{♀} + \text{♀}$  as compared with the situation  $S\text{♀}$ . Thus this set of behaviour components may be considered Courtship Display. All elements of Courtship Display show rather high frequencies as compared with the other behaviour elements. When compared to *P. prativaga* the mean durations of Abdomen and Palp vibrating are much higher in *P. sphagnicola*, that of Hopping being of the same length. Both Copulation attempt and Encircling hardly occur in the behaviour of *P. sphagnicola* males.

In both stimulus situations the frequencies and durations of Rubbing, Spinning, Jerky walking, Searching walk, Leg and Palp waving are small, whereas Stalking does not occur at all. Thus, major differences between *P. sphagnicola* and *P. prativaga* are found in Courtship Display, Leg beating, Searching and Jerky walking.

#### 1.1.3. *P. pullata* :

In both stimulus situations ( $S\text{♀}$  (pul);  $S\text{♀}$  (pul) +  $\text{♀}$  (pul)) Preening, Searching walk, Searching and Walking together take up to 80% of the total period of activities. The mean durations of all these behaviour elements are rather long. The same holds for Jerky walking, however, the frequency of this element is low, and therefore it contributes only to a small extent to the total period of activities. As in *P. sphagnicola*, none of the recorded activities show extremely high frequencies.

The situations in which conspecific females are present on the substrate ( $S\text{♀}$  (pul) +  $\text{♀}$  (pul)) the behaviour of *P. pullata* males does not change much. The level of activity is of the same height in both stimulus situations; so are the frequencies and total durations of most of the recorded elements. Copulation attempt, Leg and Palp waving as well as Stalking only or especially occur in the stimulus situation  $S\text{♀}$  (pul) +  $\text{♀}$  (pul). Although their frequencies and total durations are very small, this set of elements may be considered Courtship Display.

Rubbing, Spinning, and Palp cycling hardly occur in the behaviour of *P. pullata* males. Encircling, Abdomen and Palp vibrating as well as Hopping, elements of Courtship Display in both other species, do not occur in *P. pullata*. On the other hand, Courtship Display in *P. pullata* consists of elements which do not occur in *P. prativaga* and hardly in *P. sphagnicola*. However, *P. pullata* males spend only 5% of the total period on these activities.

In the species studied the mean duration of each behaviour element varies to a large extent, both between the respective experiments per species and within experiments. Thus, e.g., the mean duration of Preening varies between the respective experiments from 1.2 to 40.8 sec. (Table 3 : range of mean durations per experiment in *Pardosa sphagnicola*). Within the experiments the duration of Preening may vary from 1 up to 150 sec. Differences between the respective situations are small throughout the species studied, with respect to both types of variation.

#### 1.1.4. Conclusions :

In the three species studied Preening and Walking take an important part in the behaviour of the males as the mean durations of these elements are long, though their frequencies are of moderate value. Rubbing and Spinning scarcely occur in the behaviour of the males studied.

Differences between the species studied occur in the elements of Courtship Display as well as in Palp cycling, Jerky walking, Searching, Searching walk and Leg beating, both in frequencies and durations. Palp cycling and Jerky walking occur in high frequencies in *P. prativaga*. *P. sphagnicola* and *P. pullata* spend considerable periods in Searching, as the mean duration of this element is high. Both frequency and mean duration of Searching walk is higher in *P. pullata*, as compared with both other species. Leg beating does not occur in *P. prativaga*.

In *P. sphagnicola* Courtship Display takes most of the time spent by the males; *P. pullata* males spend only a very small part of time in Courtship Display. Courtship Display is rather similar in *P. prativaga* and *P. sphagnicola*. The elements of this behaviour do not occur in *P. pullata*, on the other hand elements occurring in Courtship Display of *P. pullata* hardly occur in *P. sphagnicola* and *P. prativaga*.

#### A. 1.2. The sequences of the recorded behaviour elements.

The frequencies of any of two given elements  $i$  and  $j$  in the behaviour define the number of successions of both elements, provided they are randomly distributed in that behaviour. The chance that element  $i$  occurs is put down in formula as  $e_i = n_i/N$ , in which  $n_i$  represents the frequency of element  $i$ , and  $N$  the total number of activities (sum of the frequencies of all occurring elements). In the same way  $e_j = n_j/N$ . The chance that both elements occur together  $e_{i,j} = n_i.n_j/N^2$ . The number of successions of the elements  $i$  and  $j$  will amount to  $e_{i,j}.N = n_i.n_j/N$ .

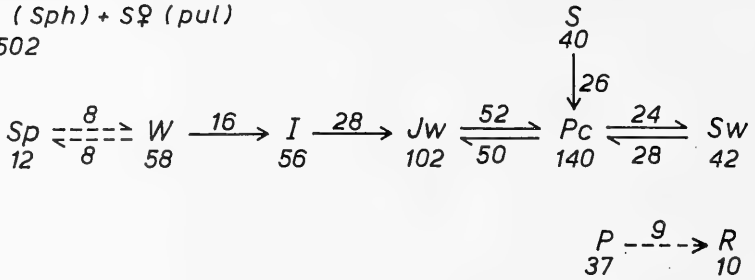
In the case that the elements  $i$  and  $j$  are not randomly distributed in the behaviour, i.e., when they are arranged in a pattern, the observed number of successions  $n_{i,j} \neq n_i.n_j/N$ .

So sequence analysis means that the observed number of successions of any pair of elements  $i$  and  $j$  ( $n_{i,j}$ ) will be compared with the expected number of successions of both elements when they were randomly distributed in the behaviour ( $e_{i,j}.N$ ) (chi-square test, one degree of freedom,  $\alpha = 0.01$ ). Behaviour patterns can be performed with the help of those successions which observed numbers exceed the expected ones.

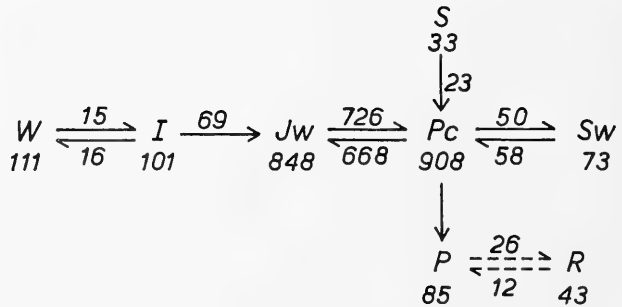
Regarding the results, two points should be taken into account. First, only changes in behaviour have been taken into consideration. So repetition of elements has not been recorded. Second, immobility, though not being behaviour, has been inserted in the sequence diagrams because preliminary observations showed that switches in behaviour (e.g. from Walking to Courtship Behaviour) often are mediated by a period of immobility (Dijkstra, 1969). Immobility is defined as those periods of at least five seconds during which the observed spider did not show overt behaviour.

Behaviour patterns have been established for three stimulus situations, viz. non-conspecific substrates, and conspecific substrates, either without or with conspecific females (Table 2 : 1 + 3, 5, 8 respectively). The observed numbers of successions of each pair of behaviour elements have been summarized irrespective of the length of the observation period. Four experiments were carried out in the stimulus situation  $S \text{ } \varnothing$  (non-conspecific). The total observation period of both *P. prativaga* ( $S \text{ } \varnothing$  (sph) +  $S \text{ } \varnothing$  (pull)) and *P. sphagnicola* ( $S \text{ } \varnothing$  (pra) +  $S \text{ } \varnothing$  (pull)) amounted to 80 min., that of *P. pullata* ( $S \text{ } \varnothing$  (sph) +  $S \text{ } \varnothing$  (pra)) to 60 min. In the stimulus situation  $S \text{ } \varnothing$  (conspecific) eight experiments were carried out, each lasting for 20 min., with each of the species studied. Twelve experiments were performed in the situation  $S \text{ } \varnothing$  +  $\varnothing$  (both conspecific). In both *P. prativaga* and *P. pullata* the length of the ob-

I. S♀ (Sph) + S♀ (pul)  
t.n.a. 502



II. S♀ (pra)  
t.n.a. 2265



III. S♀ (pra) + ♀ (pra)  
t.n.a. 1519

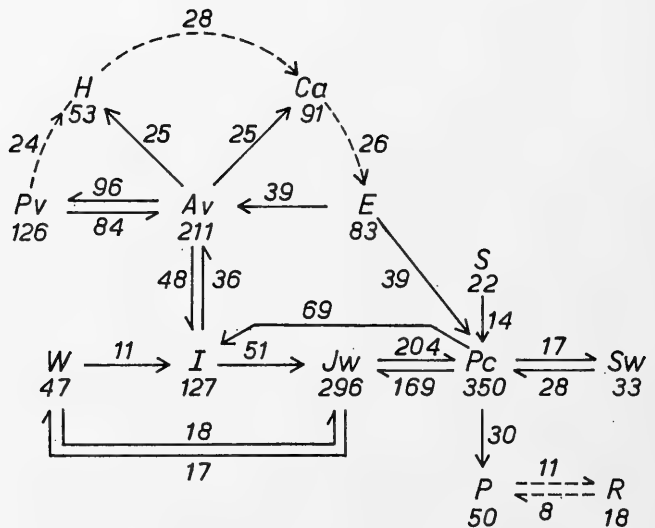


Fig. 1. The behaviour patterns of males of *P. prativaga* studied in three different stimulus situations (Cf. also caption of Fig. 3)



ervation period varied from 2.5 to 20 min. per experiment, in *P. sphagnicola* each experiment lasted 20 min. Thus the total observation period of *P. sphagnicola* males amounted to 240 min., that of *P. prativaga* males to 120 min., and that of *P. pullata* ones, to 134.5 min.

The aim of these experiments is to establish the specific events of behaviour of the respective species. Therefore a comparison is made between the behaviour patterns in the situations non-conspecific substrates (less-specific situations) (Table 2; 1, 3), conspecific substrates (5) and conspecific substrates together with conspecific females (more specific situations) (8).

Figs. 1, 2 and 3 present the behaviour patterns of the respective species.

#### 1.2.1. *P. prativaga* (Fig. 1).

In both stimulus situations without females the behaviour of *P. prativaga* males consists of a well patterned series of elements. Palp cycling takes a central position; it follows Searching, Searching walk, as well as Jerky walking. Palp cycling is followed by Searching walk and Jerky walking again, and Preening.

In the presence of females (S ♀ (pra) + ♀ (pra)) this pattern is mainly the same. Major differences concern the relation between Jerky walking and Walking and, naturally, Courtship Display. Jerky walking and Walking alternate in the latter pattern whereas they are not related at all in the former. Courtship Display is connected with the former pattern mainly through Abdomen vibrating and Immobility. The pattern of Courtship Display exists of alternating Abdomen and Palp vibrating, followed by Hopping. Hopping ends in Copulation attempt, which, when mounting does not succeed, is followed by Abdomen vibrating again, either directly or via Encircling. The cycle may then start again. Courtship Display ends, if not in mating, through both above mentioned elements in either Immobility or Palp cycling.

#### 1.2.2. *P. sphagnicola* (Fig. 2).

In contradistinction to *P. prativaga*, the elements of behaviour in *P. sphagnicola* are arranged in a cyclic pattern under conditions where males are studied on non-conspecific substrates. Besides this cyclic pattern the elements Searching and Leg waving take a distinct position.

The behaviour pattern of *P. sphagnicola* males clearly consists of two parts in the stimulus situation S ♀ (sph), one set of elements arranged around Immobility, another around Searching.

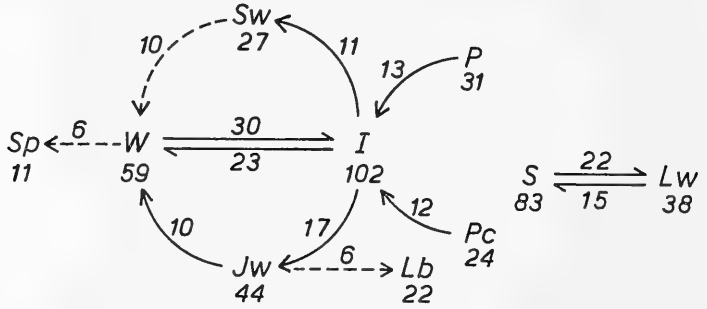
In the presence of females (S ♀ (sph) + ♀ (sph)) the males of *P. sphagnicola* are mainly engaged with Courtship Display. Under these conditions the frequencies of all other elements decrease in such a way that it is impossible to establish any relations with good confidence. Courtship Display starts through Immobility, as in *P. prativaga*. It mainly consists of both Abdomen and Palp vibrating followed by Hopping and vice versa. In some cases Hopping leads to Copulation attempt, and, when this fails Abdomen and Palp vibrating starts again. Courtship Display ends, if not in mating, through Abdomen vibrating in Immobility.

#### 1.2.3. *P. pullata* (Fig. 3).

As in *P. prativaga* the behaviour of *P. pullata* males has been patterned in a series in the stimulus situation S ♀ (sph) + S ♀ (pra), though other elements are involved than

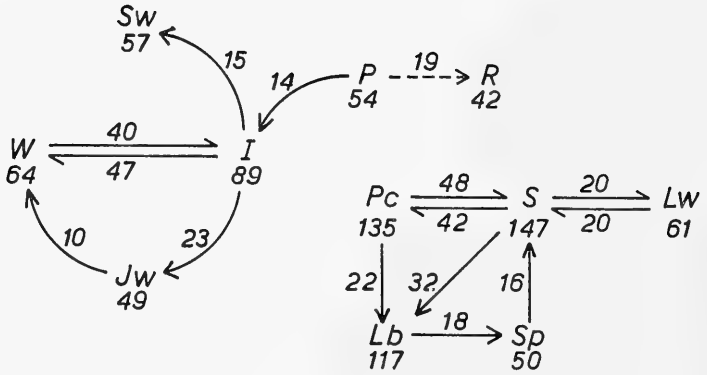
I s♀ (pra) + s♀ (pul)

t.n.a. 455



II s♀ (sph)

t.n.a. 950



III s♀ (sph) + ♀ (sph)

t.n.a. 2485

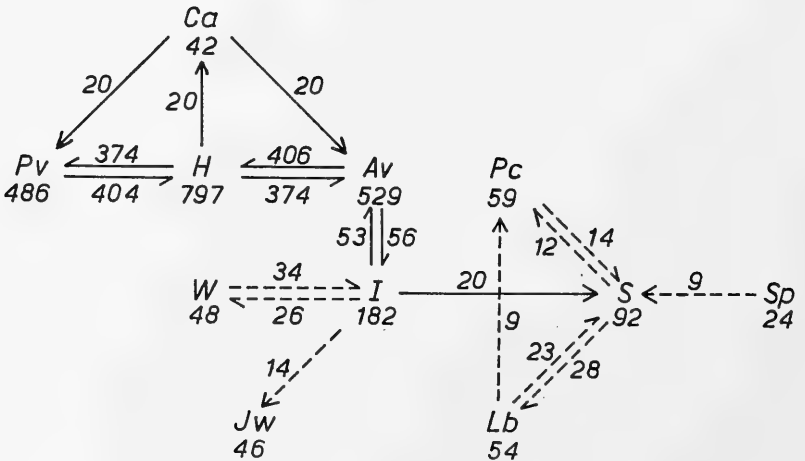
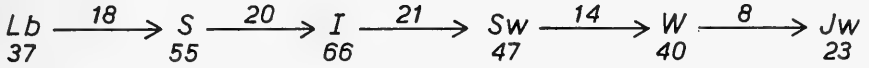


Fig. 2. The behaviour patterns of males of *P. sphagnicola* studied in three different stimulus situations. (Cf. also caption of Fig. 3)

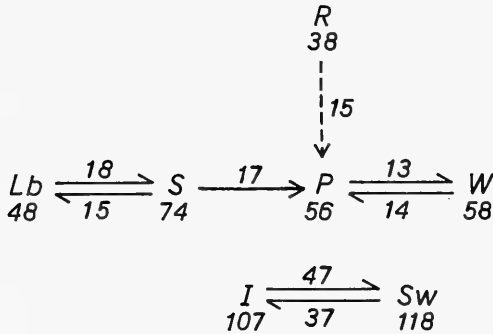
**I** S♀ (sph) + S♀ (pra)

t.n.a. 310



**II** S♀ (pul)

t.n.a. 578



**III** S♀ (pul) + ♀ (pul)

t.n.a. 467

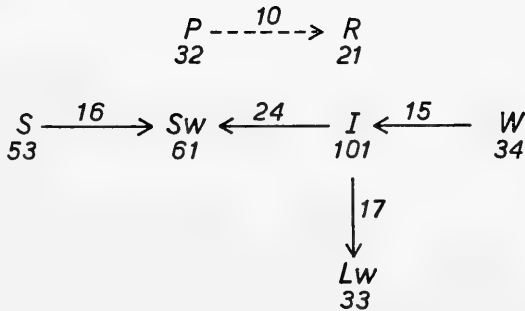


Fig. 3. The behaviour patterns of males of *P. pullata* studied in three different stimulus situations. Broken lines indicate successions showing high chi-square values, from which, however, the expected frequencies amounted to less than five, i.e., the total frequencies of either or both elements are too low for confident testing with the chi-square method. The figures on the arrows indicate the observed numbers of successions; figures below the element codes represent the frequencies of these elements. t.n.a.: the total numbers of activities.

in the former species. In the stimulus situation S♀ (pul) this series is split up into three pairs of alternating elements, viz. Immobility and Searching walk, Walking and Preening, Searching and Leg beating. However, Preening and Searching are also related to each other in that the former element follows the latter.

In the presence of females (S♀ (pul) + ♀ (pul)) the pattern again changes, consisting mainly of the arrangement of Leg waving, Walking and Searching walk

around Immobility. Courtship Display hardly occurs in this species, so it was not possible to establish the pattern of this component of behaviour with good confidence. However, as Leg waving, which is the major constituent of Courtship Display, follows on Immobility, it may be concluded that, as in the two other species, Courtship Display is connected with the remaining behavioral elements through Immobility.

#### 1.2.4. Conclusions.

These results show that the behaviour patterns are rather specific. Similarities hardly occur between the patterns of the three species, in comparable situations. Rather strict relations occur between Rubbing and Preening in each of the species, but the frequencies of both elements are low.

Major differences in pattern between the species studied concern the arrangement of the elements Immobility, Walking and Jerky walking (*P. prativaga* and *P. sphagnicola* contra *P. pullata*), as well as the strict relation between the elements Palp cycling and Jerky walking (*P. prativaga* contra *P. sphagnicola* and *P. pullata*).

### A. 2. Influence of the respective stimulus situations

#### A. 2.1. Total numbers of activities dependent on the respective external stimuli.

Table 4 presents the mean numbers of activities (= any occurrence of a behaviour element) per male per 20 min. in the respective stimulus situations. *P. prativaga* males appear to be the most active, *P. pullata* the least active.

##### 2.1.1. *P. prativaga*.

The highest numbers of activities occur on conspecific substrates (situations 5, 6, 7, 8). Addition of females, irrespective whether they are conspecific (9, 10) or non-conspecific (2, 4) to non-conspecific substrates (1, 3) increases the numbers of activities of the tested males.

##### 2.1.2. *P. sphagnicola*.

The presence of conspecific females (8, 9, 10) shows the highest numbers of activities of males as compared to the other situations. Neither conspecific substrates (5), in comparison to non-conspecific ones (1, 3) nor the addition of non-conspecific females to either conspecific (6, 7) or non-conspecific substrates (2, 4) influence the numbers of activities. An exception is only found in *P. prativaga* females in the stimulus situation S♀ (sph) + ♀ (pra) as compared to situation S♀ (sph).

##### 2.1.3. *P. pullata*.

The influences of the respective stimuli on the numbers of activities in the behaviour of *P. pullata* males are rather small.

##### 2.1.4. Conclusions.

The total numbers of activities of males of *P. prativaga* under the conditions of investigation are elicited in the same way by conspecific substrates and the presence of females on non-conspecific substrates. The numbers of activities in the behaviour of *P. sphagnicola* males only increase by the presence of conspecific females, whereas they do not seem to be affected at all in *P. pullata*.

Table 4. The total numbers of activities per male per 20 min. and the percentual deal of particular elements to these numbers in the respective stimulus situations for the species studied

Stimulus situation	Relative frequencies of behaviour elements														mean number of activities per 20 min.
	P	W	Jw	Pc	S	Sw	Ca	E	Av	Pv	H	Lb	Lw	Pw	
<i>Pardosa prativaga</i> ♂	1. sph —	12	17	26	20	8	8	—	—	1	—	—	—	—	211
	2. sph sph	5	5	31	36	14	2	2	—	1	—	—	—	—	60
	3. pul —	10	13	13	26	10	20	—	—	1	—	—	—	—	110
	4. pul pul	7	7	22	36	11	14	—	—	1	—	—	—	—	269
	5. pra —	4	6	40	40	1	3	—	—	1	—	—	—	—	250
	6. pra sph	4	4	34	42	2	5	2	—	4	2	2	—	—	235
	7. pra pul	4	2	40	40	1	3	1	—	1	—	—	—	—	230
	8. pra pra	3	3	20	22	3	2	7	4	18	10	5	—	—	138
	9. sph pra	2	8	22	27	3	2	4	3	25	5	3	—	—	190
	10. pul pra	3	—	4	25	—	3	10	9	29	9	1	—	—	76
<i>Pardosa sphaeridicola</i> ♂	1. pra —	12	24	10	4	17	12	—	—	1	1	—	13	6	82
	2. pra pra	9	14	5	11	22	15	—	—	1	—	—	19	2	87
	3. pul —	10	15	11	10	20	3	—	—	1	—	—	27	—	42
	4. pul pul	15	20	8	8	8	15	—	—	1	3	1	18	5	91
	5. sph —	8	10	8	20	16	8	—	—	2	1	—	10	8	141
	6. sph pra	5	8	4	11	13	6	—	—	14	15	10	5	3	72
	7. sph pul	9	8	8	8	11	8	—	—	9	6	4	15	8	154
	8. sph sph	1	3	2	3	4	1	—	—	27	27	23	3	1	119
	9. pra sph	5	7	9	5	1	2	—	—	23	22	17	1	—	170
	10. pul sph	2	6	5	7	9	1	—	—	14	27	18	3	3	72
<i>Pardosa pullata</i> ♂	1. pra —	17	21	2	1	22	13	—	—	—	—	—	21	—	57
	2. pra pra	12	21	9	—	21	14	—	—	—	—	—	16	1	77
	3. sph —	10	21	10	1	19	23	—	—	—	—	—	12	4	57
	4. sph sph	17	17	5	—	20	16	—	—	—	—	—	16	1	57
	5. pul —	14	15	7	4	15	25	—	—	—	—	—	12	3	66
	6. pul pra	12	22	4	3	13	26	1	—	—	—	—	15	2	62
	7. pul sph	16	24	3	3	13	17	—	—	—	—	—	8	9	56
	8. pul pul	8	10	11	4	15	17	5	—	—	—	—	9	8	46
	9. pra pul	18	16	11	—	14	22	—	—	—	—	—	10	9	34
	10. sph pul	14	24	9	—	20	11	—	—	—	—	—	9	6	123

## A. 2.2. Relative frequencies dependent on the respective external stimuli.

Table 4 also presents the fractions of the recorded behaviour elements by which they contribute to the total numbers of activities in the respective situations.

2.2.1. *P. prativaga*.

Besides influencing the total numbers of activities (2.1.1.), the respective situations vary the relative frequencies of particular elements. Frequencies of elements of Courtship Display increase in the presence of conspecific females, those of all other elements being lowered. Elements of Courtship Display are almost entirely restricted to this situation. However, conspecific substrates (S♀ (pra)) also influence the frequencies of some elements. The frequencies of Jerky walking and Palp cycling increase, those of Searching and Searching walk decrease on specific substrates (5, 6, 7) as compared to non-

conspecific ones (1, 2, 3, 4). The frequencies of Preening and Walking are lowered both on conspecific substrates (5) and in the presence of females on non-conspecific substrates (2, 4).

*P. pullata* females or substrates affect the behaviour of *P. prativaga* males in the same way as *P. sphagnicola* ones do. An exception is found in Searching walk, the frequency of which is relatively high in the situations  $S\text{♀}$  (pul) and  $S\text{♀}$  (pul) + ♀ (pul).

### 2.2.2. *P. sphagnicola*.

Also in this species the relative stimuli influence the frequencies of the respective behaviour elements differentially. As in *P. prativaga*, conspecific females increase frequencies of elements involved in Courtship Display, those of all other elements being lowered, especially of Preening, Walking, Searching, Searching walk and Leg beating. The other elements are hardly influenced by the respective situations. The same influences, though to a lesser extent, can be established in the stimulus situations  $S\text{♀}$  (sph) + ♀. Especially the influences of *P. prativaga* females upon the behaviour of the males is similar to that with conspecific females. In these situations particularly the frequencies of Walking, Searching walk and Leg beating decrease, whereas those of Abdomen and Palp vibrating and Hopping increase.

The frequencies of Walking, Searching walk and Leg beating, decrease and that of Palp cycling increased with conspecific substrates (5) as compared to non-conspecific ones (1, 3). Adding non-conspecific females to non-conspecific substrates does not influence the behaviour of *P. sphagnicola* males.

Thus the behaviour of *P. sphagnicola* males is especially influenced by the stimulus situations  $S\text{♀}$  + ♀ (sph) as well as  $S\text{♀}$  (sph) + ♀ (pra) in stimulating Courtship Display. The frequencies of the remaining behavioral activities are decreased in these situations.

### 2.2.3. *P. pullata*.

The tested stimulus situations have a small influence on the relative frequencies of particular behaviour elements of *P. pullata* males, as was the case with the total numbers of activities (cf. 2.1.3.).

Independent of the nature of the substrates, conspecific females (8, 9, 10) only affect the frequencies of Leg beating (decreasing) and Leg waving (increasing). More elements are involved in the situation  $S\text{♀}$  (pul) + ♀ (pul): the frequencies of Palp waving and Copulation attempt increase whereas those of Walking and Preening decrease (8).

Conspecific substrates (5, 6, 7, 8) increase the frequency of Palp cycling and decrease that of Searching. The remaining elements are scarcely affected. In the stimulus situation  $S\text{♀}$  (pul) + ♀ (sph) the behaviour of males shows differences in the same way as in the situation  $S\text{♀}$  (pul) + ♀ (pul) regarding the elements Leg beating, Leg waving and Palp waving. Thus, in *P. pullata* males, the occurrence of the complete set of elements involved in Courtship Display (Copulation attempt, Palp and Leg waving) is almost restricted to the situation  $S\text{♀}$  (pul) + ♀ (pul).

### 2.2.4. Conclusions.

Males of the species studied react in different ways on the presented stimulus situations, with respect to both the total numbers of activities and the frequencies of particular elements.

Courtship Display is elicited in *P. sphagnicola* by the less specific stimuli, in *P. pullata* by the most specific ones. The presence of females on conspecific substrates as well as conspecific females, independent on the nature of the substrates, stimulate *P. sphagnicola* males to Courtship Display. Complete Courtship Display of *P. pullata* males is stimulated by conspecific females on conspecific substrates only. In *P. prativaga* conspecific females stimulate Courtship Display, independent the nature of the substrates.

On the other hand, in *P. prativaga* conspecific substrates as well as the presence of females influence particular elements in the behaviour of the males. In both other species almost only conspecific females have this effect.

### A. 3. Conclusions of confrontation experiments.

The results of these experiments have shown that the behaviour of each of the species studied is rather specific, both in quantitative and qualitative respects. Generally Courtship Display, the most specific part of behaviour, especially occurs in situations in which conspecific females are present. Thus it may be concluded that the behaviour of the species studied can be important as species barrier.

## B. Breeding experiments

### B. 1. Mating and egg sac construction.

The results of the breeding experiments are summarized in table 5. Any differences between breedings with specimens from the respective collecting sites (Table 1) could not be established.

Matings occurred in all breedings except pul ♂ × pra ♀. Although matings have not been observed in the breedings pul × sph, (vice versa) it is evident that they had occurred, as the females constructed egg sacs in which developing eggs could be established.

In all breedings except pul ♂ × pra ♀ the females constructed egg sacs. The numbers of egg sacs in the breedings sph × pul (vice versa), however, were small. Only those egg sacs have been taken into account which were carried by the females during a normal period of development of the eggs till the emergence of the pulli, which lasts (under laboratory conditions) 15 - 20 days.

Many females constructed egg sacs which were abandoned after a few days. In these

Table 5. The occurrence of matings, the numbers of egg sacs constructed, the numbers of egg sacs with developing eggs, as well as the numbers of egg sacs from which pulli emerged in six cross breedings of the species studied

number of experiments	total number of females	breeding	occurrence of matings	number of egg sacs	egg sacs with developed eggs	egg sacs from which pulli emerged
4	19	pra ♂ × pul ♀	+	12	10	8
3	12	pul ♂ × pra ♀	—	—	—	—
4	19	pra ♂ × sph ♀	+	11	—	—
3	14	sph ♂ × pra ♀	(+)	9	4	3
4	24	pul ♂ × sph ♀	+	2	1	—
3	17	sph ♂ × pul ♀	(?)	2	2	2

egg sacs, the eggs always had been decayed. They were not taken into account, as, probably, they were constructed by females which had not mated (cf. Kessler, 1969).

## 2. Emergence of pulli.

The eggs in the egg sacs of *P. pullata* females from breedings pra ♂ × pul ♀ developed normally. From eight out of twelve egg sacs pulli emerged. The same holds for breedings sph ♂ × pra ♀, though in this case from three out of nine egg sacs pulli emerged. On the contrary, eggs in the egg sacs of *P. sphagnicola* females from breedings pra ♂ × sph ♀ did not develop at all. As matings had occurred it may be concluded that mechanical or postmating barriers isolate *P. prativaga* males from *P. sphagnicola* females. The precise nature of the barrier-system is yet unknown. Probably fertilization of the eggs did not occur, as no development at all of the eggs could be established (sperm transfer could not be directly established).

In cross-breedings of *P. sphagnicola* and *P. pullata* a rather limited number of egg sacs were constructed. In breedings sph ♂ × pul ♀ the eggs (only two egg sacs were constructed) developed normally and pulli emerged in a normal way. In the reciprocal breedings the eggs developed in only one of two egg sacs produced, but no pulli did emerge. In these breedings probably, therefore, postmating factors prevent interbreeding, as it is likely that in the cross-breeding pul ♂ × sph ♀ fertilization of the eggs did occur (development of eggs in one of the two egg sacs).

In conclusion, pulli could be obtained from three out of six breedings: pra ♂ × pul ♀; sph ♂ × pra ♀; sph ♂ × pul ♀. These results allow two conclusions: first, every species interbreeds with every other species in only one of the two reciprocal ways; and second, *P. pullata* males as well as *P. sphagnicola* females do not interbreed with any of the other species studied, whereas *P. pullata* females as well as *P. sphagnicola* males interbreed with both other species.

## 3. Breeding of pulli.

The obtained hybrid juveniles were reared in glass jars provided with a layer of plaster of Paris which was kept moistened. They were fed *Drosophila melanogaster* mutant vestigial. The pulli grew rapidly till about four moults had occurred. Afterwards many specimens died, especially during the moults. As the same phenomena occurred in control breedings of both *P. prativaga* and *P. pullata*, the difficulties in breeding juveniles must be a methodical question. As a consequence only a few juveniles reached the adult stage (1 ♀ pra ♂ × pul ♀; 1 ♀ sph ♂ × pra ♀).

## 4. Conclusions.

The results show that premating barriers do not occur between *P. prativaga* and *P. sphagnicola*, however mechanical or postmating barriers prevent the production of juveniles from breedings pra ♂ × sph ♀. *P. sphagnicola* is virtually isolated from *P. pullata* by premating factors. However, this isolation is not complete. In addition, postmating factors are effective in breedings pul ♂ × sph ♀, but they do not operate in the reciprocal breedings (sph ♂ × pul ♀). In one of the cross-breedings of *P. prativaga* and *P. pullata* premating factors completely prevent interbreeding (pul ♂ × pra ♀), whereas in the reciprocal breeding (pra ♂ × pul ♀) barriers are completely absent. Thus behaviour is only of minor importance in isolating the species studied.



## IV. GENERAL CONCLUSIONS AND DISCUSSION

## 1. General conclusions.

The behaviour of males of the species studied shows qualitative as well as quantitative differences. Males of the three species react differentially to different stimulus situations, both in the total numbers of activities as well as in the relative frequencies of particular activities. Complete Courtship Display in *P. pullata* males is only elicited in the situation  $S\text{♀}(\text{pul}) + \text{♀}(\text{pul})$ . Conspecific females, independent of the nature of the substrates, elicit Courtship Display in *P. prativaga*. In *P. sphagnicola*, besides these situations, also conspecific substrates with females, irrespective of their nature, evoke Courtship Display.

Under laboratory conditions every species interbreeds with every other species in only one of the two reciprocal ways.

## 2. Discussion with regard to behaviour composition.

Walking and Preening occur in moderate frequencies throughout the species studied. The mean durations of these activities, however, last longer than that of most others. Thus both Walking and Preening contribute an important part to the total period spent. The predominant behaviour elements differ in the three species. Palp cycling and Jerky walking dominate in the behaviour of *P. prativaga* males, Searching and Courtship Display do so in those of *P. sphagnicola*. *P. pullata* males are mainly engaged in Searching and Searching walk.

*Walking and Preening.*

In the behaviour patterns of the species studied the position of Preening is fixed to a small extent only. Walking, however, contributes, together with Jerky walking and Immobility, an important part to the patterns of both *P. prativaga* and *P. sphagnicola*. In *P. prativaga* both elements are dependent in a similar way on the respective stimulus situations. Conspecific substrates as well as the presence of females lower their frequencies. In *P. sphagnicola* conspecific females only lower the frequency of Preening, that of Walking being changed also by conspecific substrates. Conspecific females on conspecific substrates lower the frequencies of both elements in the behaviour of *P. pullata* males.

*Palp cycling and Jerky walking.*

Palp cycling and Jerky walking are closely related in the behaviour pattern of *P. prativaga*; they are elicited by similar stimuli. Conspecific substrates and, to a lesser extent, in non-conspecific females the frequencies of Palp cycling and Jerky walking increase, in conspecific females they decrease. In both *P. sphagnicola* and *P. pullata* the frequencies are much lower as compared with *P. prativaga*. In both species the elements concerned are not connected at all with the behaviour patterns. In *P. prativaga* as well as in *P. sphagnicola* Jerky walkings is associated with Walking and Immobility. Whereas in *P. prativaga* Palp cycling closely relates to Jerky walking, it is more connected with Searching and Leg beating in *P. sphagnicola*. In the pattern of *P. pullata* the positions of both elements are less fixed. In both *P. sphagnicola* and *P. pullata* Palp cycling is elicited to some extent by conspecific substrates (as in *P. prativaga*), Jerky walking, however, seems not to be related to any special stimulus situation.

*Searching and Searching walk.*

Searching and Searching walk contribute an important part to the behaviour of

*P. pullata* males, although their frequencies being of moderate values only, the mean durations are rather long. In the pattern Searching especially relates to Leg beating, Searching walk is associated with Immobility. The respective stimuli exert only small changes in both elements. Conspecific substrates lower Searching to some extent, Searching walk does not seem to be changed by any stimulus situation. The frequencies of Searching and Searching walk are rather low in *P. prativaga*. In the behaviour pattern both elements are connected with Palp cycling. Conspecific substrates, as well as conspecific females lower the frequencies of both Searching and Searching walk. In *P. sphagnicola* the frequency of Searching is also low, that of Searching walk, however, is rather high. In pattern Searching relates to Palp cycling (as in *P. prativaga*) and to Leg beating (as in *P. pullata*). The position of Searching walk is to some extent comparable to that in *P. pullata*. Conspecific females lower the frequencies of both elements, only Searching walk is also changed by conspecific substrates (as in *P. prativaga*).

#### Courtship Display.

In appropriate situations Courtship Display dominates in the behaviour of *P. sphagnicola* males. The particular elements arrange a fixed pattern and behave similarly towards the respective stimulus situations. Generally, Courtship Display is connected with the other activities in the patterns through Immobility and is elicited by conspecific females only. However, in *P. sphagnicola* non-conspecific females occurring on conspecific substrates also evoke Courtship Display. Comparable activities contribute to Courtship Display in *P. prativaga* and in *P. sphagnicola*. In *P. prativaga* Courtship Display never dominates the behaviour of the males. Courtship elements of both *P. prativaga* and *P. sphagnicola* hardly occur in *P. pullata*. On the other hand, this species shows Courtship Display, the elements of which hardly occur in both former species. Courtship Display takes a very small part in the behaviour of *P. pullata* males only.

One of the elements of Courtship Display in *P. pullata*, Leg waving, also occurs in *P. sphagnicola*. However, in this species conspecific females lower its frequency and the position in the patterns is different. Leg waving as well as Leg beating do not occur in *P. prativaga*. The frequency of Leg beating is of the same level in both *P. sphagnicola* and *P. pullata*. In the pattern of both species it is close to Searching. Similar stimuli lower its frequency in both species, viz., conspecific females. Conspecific substrates also lower Leg beating to some extent in *P. sphagnicola* only.

#### 3. Discussion with regard to interbreeding.

In the context of interbreeding, Courtship Display and its eliciting factors are important. Courtship Display dominates in *P. sphagnicola* and is elicited in rather un-specific situations too. In *P. prativaga* and especially in *P. pullata* Courtship Display never dominates the behaviour of the males and only occurs in specific situations. Thus it may be concluded that the behaviour of *P. sphagnicola* males presents the weakest factor in preventing interbreeding as compared to that of both *P. prativaga* and *P. pullata*.

Indeed, in breeding experiments *P. sphagnicola* males mated with females of both other species, especially *P. prativaga* females. However, matings occur in all breedings except pul ♂ × pra ♀. In all cases matings result in egg sac construction. Hybrid juveniles have been obtained in only three out of six breedings, viz., pra ♂ × pul ♀, sph ♂ × pra ♀ and sph ♂ × pul ♀. Behavioral factors isolate *P. pullata* males

from *P. prativaga* females, whereas postmating or mechanical factors isolate *P. sphagnicola* females from both *P. prativaga* and *P. pullata* males. In the barrier between *P. pullata* and *P. sphagnicola*, however, behavioral factors are involved to some extent too.

#### 4. Discussion with regard to isolating mechanisms.

Preceding studies have shown that seasonal, as well as habitat factors operate in isolating the species studied. *P. sphagnicola* exclusively occurs in peat-moor swamps (Dahl, 1908; Holm & Kronestedt, 1970) whereas both *P. pullata* and *P. prativaga* occur in less specific habitats (Dahl, 1908; Wiebes, 1959), although differences occur (Den Hollander & Lof, 1972). Both *P. prativaga* and *P. pullata* occur in populations of *P. sphagnicola*, though in very small numbers, especially *P. prativaga*. True mixed populations of *P. prativaga* and *P. pullata*, on the other hand, do occur. Thus *P. sphagnicola* is isolated from *P. prativaga* and, to a lesser extent, from *P. pullata*, by habitat.

*P. prativaga* males are isolated completely from *P. pullata* females by seasonal factors, as *P. pullata* females have already mated and are constructing their egg sacs when *P. prativaga* is going through its last moult and becoming adult. Adult males of both *P. sphagnicola* and *P. pullata* occur in the same period as unmated females of the other species (Den Hollander, 1971).

Thus habitat isolation prevents interbreeding between *P. sphagnicola* and both *P. prativaga* and *P. pullata*. Furthermore, *P. sphagnicola* females are isolated from males of both other species by mechanical or postmating barriers. The habitat barrier between *P. sphagnicola* and *P. pullata* is not complete. However it is compensated by the existence of, though not complete, behavioral barriers. Behavioral barriers only prevent cross breedings of *P. prativaga* females and *P. pullata* males, the reciprocal breedings being prevented by seasonal barriers.

These results show that specificity of Courtship behaviour of wolf spider males does not imply that it should play an important role in isolating species. It is more likely that only then when other barriers are broken down, e.g. when two species become syntopical, the existing differences in behaviour are embraced to evolve reproductive isolation.

## V. SUMMARY

1. Species of the *Pardosa pullata* group (*P. pullata*, *P. prativaga* and *P. sphagnicola*) were studied as to specific differences in behaviour of the males towards both conspecific and non-conspecific substrates and females.
2. Qualitative, as well as quantitative differences occur between the behaviour of males of the respective species.
3. Males of the species studied react differentially to the presented stimulus situations.
4. In the laboratory every species interbreeds with every other species in only one of the two reciprocal ways. Under natural conditions these cross-breedings mostly are prevented by seasonal and habitat factors.
5. It is concluded that behavioral factors are of minor importance in isolating the species of the *P. pullata* group. However, differences in behaviour have been evolved to species barriers in sympatric situations.

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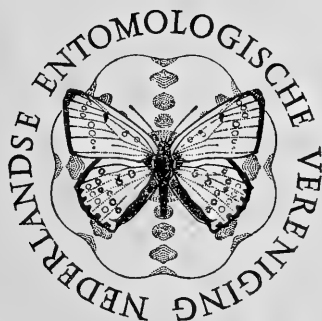
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# A COMPARATIVE STUDY OF THE PRODUCTION OF EGGS IN EIGHT PARDOSA SPECIES IN THE FIELD (ARANEAE, LYCOSIDAE)

by

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## ABSTRACT

The egg production of eight common *Pardosa* species in the Netherlands, estimated from field samples, is described. Samples were taken on the same spot during five years for six species (1966—1970). In 1968 some species were sampled extensively in several parts of the Netherlands. Intra- and interspecific differences in egg production were found to be related to the size of the mother spiders. Factors influencing intraspecific differences in size of the spiders are discussed.

## INTRODUCTION

The relation between food consumption and egg production in spiders has been dealt with by Turnbull (1962) in *Linyphia triangularis*. Data on Lycosid spiders in general are scarcely known (cf. Edgar, 1968, 1971). Kessler (1971) studied this relationship in four species of *Pardosa* under experimental conditions. These results, however, should be compared with data on natural populations. This paper deals with data on egg production of eight species of *Pardosa* in the field, estimated from samples taken in natural populations. The results are discussed in relation to data from the literature as well as in relation to experimental data (Kessler, 1971; Turnbull, 1962, 1965).

## MATERIAL AND METHODS

All samples were made by hand-collecting female spiders carrying egg sacs. Care was taken to collect specimens in the period when all females were carrying egg sacs, viz., in the middle of the reproductive period, so that a sample is representative for all females in the population.

Eight species were sampled in 1968 in different localities throughout the country, six species were sampled from 1966 to 1970 yearly in the same locality.

A description of the habitat of the species concerned in the Netherlands is given by Richter (1970).

It is only possible to collect spiders in sufficient quantities when the weather is bright. This seriously narrows down the time available for sampling. Moreover, the period in which the females are carrying the egg sacs is about the same for all species (the middle of May until the end of June). For these reasons some samples in the series are missing or incomplete.

In each sample a number of spiders were collected which were missing one or more legs. The egg sacs of these specimens are not considered in this paper. The same holds

for egg sacs containing egg sac parasites (Hymenoptera). The latter are dealt with elsewhere (Kessler & Fokkinga, 1973).

Every specimen collected was kept separately, so that relations between mother spider and offspring could be studied.

A positive correlation between size of the mother spider and number of offspring has been demonstrated in the genus *Pardosa* by Petersen (1950). In order to investigate this phenomenon interspecifically one should either calculate regression lines for each species or express the number of eggs as a ratio of spider size. The latter method is used in this paper because the calculations are simple and the method gives a more direct insight, when comparisons are made interspecifically. The dryweight of carapaces, including the legs, is used as an estimate for spider size. Carapaces were dried in an oven at 60° C.

For statistical method Duncan's new multiple range test with Kramers modification for unequal sample size was used ( $\alpha = 0.05$ ).

## RESULTS

### I. COMPARISON OF THE SPECIES

In 1968, the eight common species of *Pardosa*, viz., *Pardosa amentata* (Clerck), *P. lugubris* (Walck.), *P. pullata* (Clerck), *P. prativaga* (L. Koch), *P. nigriceps* (Thorell), *P. purbeckensis* F.O.P.-Cambridge, *P. monticola* (Clerck) and *P. palustris* (L.), were sampled in order to compare the species as to the amount of egg production.

The data on numbers of eggs per egg sac (1), the dryweight of the carapaces (2) and the numbers of eggs per mg carapace dryweight (3) are shown together in table 1 and are discussed separately in the following chapters.

#### a. Number of eggs

The mean numbers of eggs in the egg sacs range from 86.2 in *P. amentata* to 26.6 in *P. monticola*. In Graph 1 the frequencies are shown; Graph 2 gives the range of the values and the means for all species together. Three separate groups can be distinguished (though sometimes a considerable overlap has been found).

<i>P. amentata</i>	± 85 eggs
<i>P. palustris</i> , <i>P. prativaga</i> and <i>P. purbeckensis</i>	± 50 eggs
<i>P. lugubris</i> , <i>P. pullata</i> , <i>P. nigriceps</i> and <i>P. monticola</i>	± 30 eggs

In some egg sacs undeveloped eggs were found. They are easily recognized, even at very early stages in the development of the egg batch, by a brownish colour (normal eggs are white). Table 1 illustrates that the number of undeveloped eggs is never high. The great variability is due to the fact, that in most egg sacs only 1 or 2 undeveloped eggs are found, whereas in a few others more than half of the eggs are undeveloped.

#### b. Size of spiders (carapace dryweight)

The differences in carapace dryweight between the species are rather small, with the exception of *P. amentata* (Table 1). None of the species does show any overlap in values with *P. amentata* (Graph 1). In this group of species *P. monticola* and *P. pullata* can

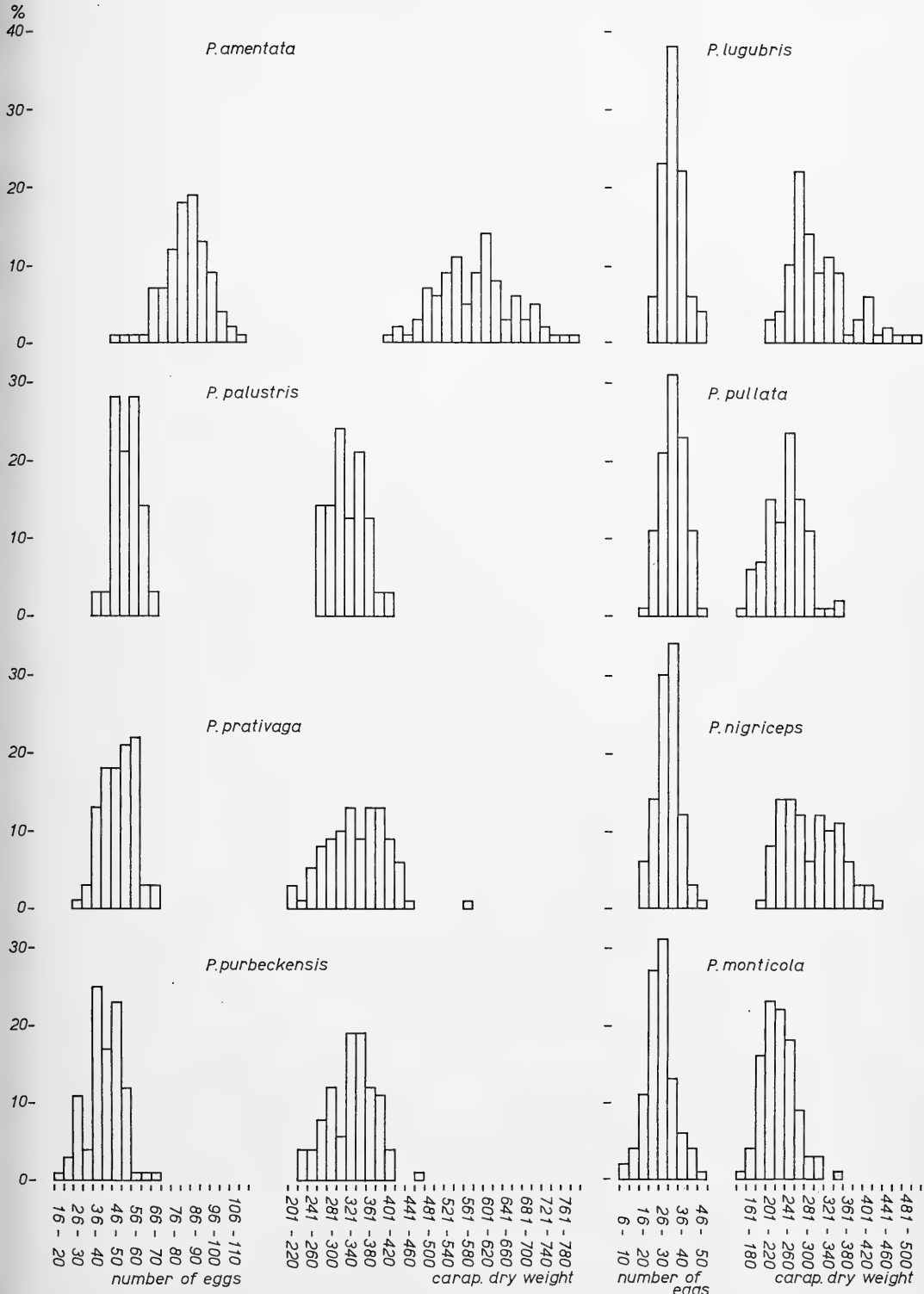
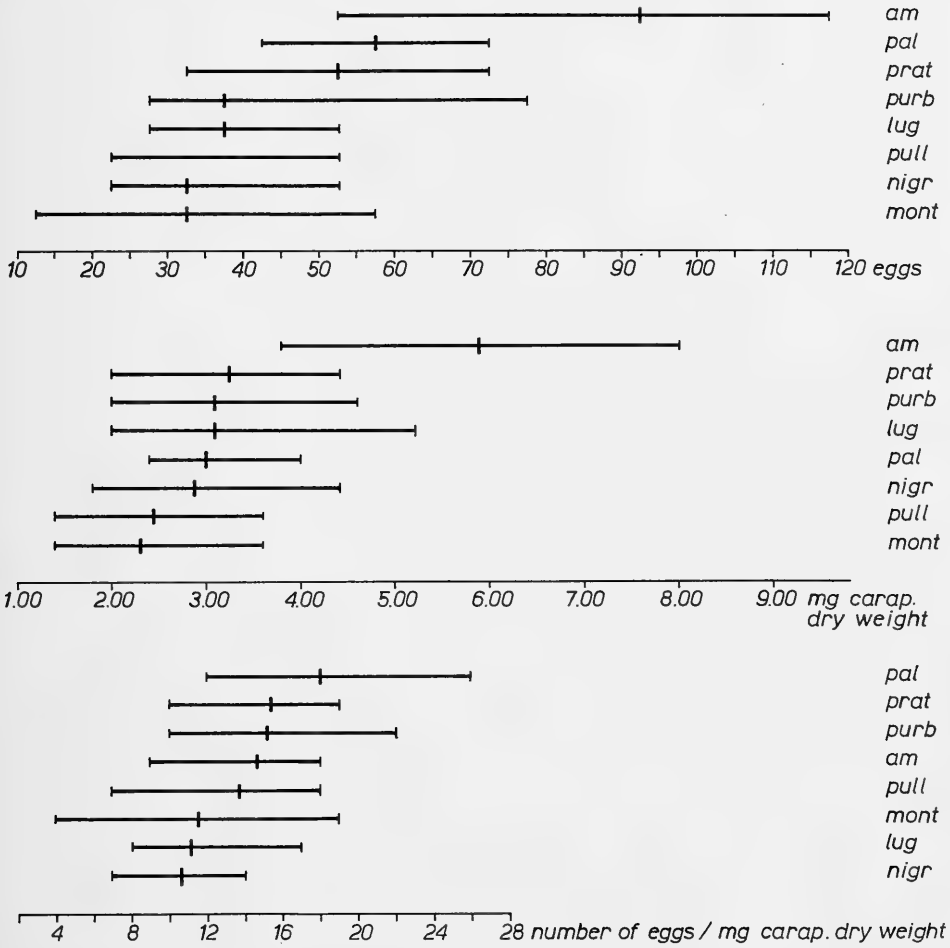


Table 1. Comparison of the egg production and size of eight species of *Pardosa* in 1968. Means and standard deviations are given. In table 1a the statistical significance of the differences in mean values are given. The names of the spiders represent the values. Any two values not flanked by the same line are significantly different. (am = *P. amentata*, pal = *P. palustris*, prat = *P. prativaga*, purb = *P. purbeckensis*, lug = *P. lugubris*, pull = *P. pullata*, nigr = *P. nigriceps*, mont = *P. monticola*)

Spider species	Number of specimens	Number of eggs	Dryweight of carapace in mg	Number of eggs per mg carapace dryweight	Number of egg sacs containing undeveloped eggs	Mean number of undeveloped eggs in these egg sacs
<i>P. amentata</i>	91	86.2 ± 12.9	5.90 ± 0.81	14.7 ± 1.6	19	3.1 ± 3.3
<i>P. palustris</i>	29	54.2 ± 6.9	3.03 ± 0.36	18.0 ± 2.4	6	2.3 ± 2.8
<i>P. prativaga</i>	78	49.3 ± 8.3	3.25 ± 0.63	15.4 ± 2.2	20	2.2 ± 1.2
<i>P. purbeckensis</i>	75	47.1 ± 8.9	3.12 ± 0.49	15.2 ± 2.5	46	3.6 ± 2.6
<i>P. lugubris</i>	90	33.9 ± 6.1	3.11 ± 0.63	11.1 ± 1.8	7	2.9 ± 3.7
<i>P. pullata</i>	81	33.1 ± 6.1	2.44 ± 0.43	13.7 ± 2.1	8	1.4 ± 1.1
<i>P. nigriceps</i>	73	30.4 ± 5.6	2.92 ± 0.58	10.6 ± 1.6	7	2.1 ± 1.9
<i>P. monticola</i>	97	26.6 ± 7.7	2.29 ± 0.36	11.6 ± 2.9	8	1.3 ± 0.5

Table 1a. For legends see table 1

Number of eggs	Dryweight of carapace	Number of eggs per mg carapace dryweight
am	am	pal
pal	prat	prat
prat	purb	purb
purb	lug	am
lug	pal	pull
pull	nigr	mont
nigr	pull	lug
mont	mont	nigr



Graph. 2. Range of values and means of number of eggs per egg sac, carapace dryweight and number of eggs per mg carapace dryweight of eight *Pardosa* species. (For further explanation see table 1.)

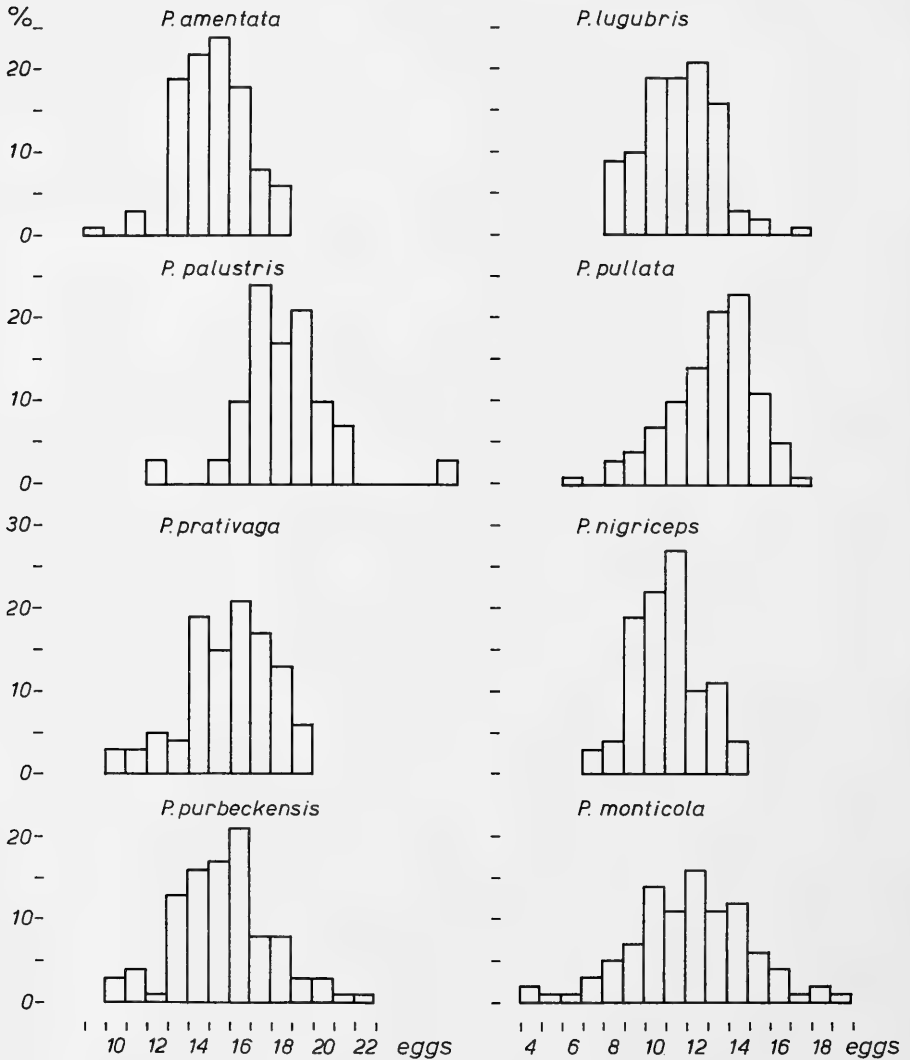
be distinguished by their carapace weight (2.3 and 2.4 versus  $\pm 3$  mg). Furthermore it should be noted that in most species different size groups are found (Graph 1).

Probably these differences are caused by the presence of spiders born from the first egg sacs as well as from the second egg sacs of last year.

c. Number of eggs per mg carapace dryweight

The data in table 1, Graph 2, and Graph 3, show that any differences in the values of number of eggs per mg carapace dryweight are not conspicuous. This leads to the conclusion that in general the size of the spider species determines the number of offspring.

An exception is found in *P. palustris*. In this species, under field conditions, considerably more eggs are produced per unit of size than in the other species. This is in



Graph 3. Frequency diagrams of the number of eggs per milligram carapace dryweight of eight *Pardosa* species

agreement with the data of Kessler (1971), which showed that under experimental conditions *P. palustris* produces more eggs per unit of size than the other investigated species, because the eggs are lighter.

## II. COMPARISON OF SAMPLES FROM DIFFERENT LOCALITIES IN THE SAME YEAR

Samples from different localities in 1968 (Fig. 1) were available from *P. amentata*, *P. pullata*, *P. purbeckensis*, *P. nigriceps*, *P. monticola* and *P. prativaga*. The results are shown in table 2.



Fig. 1. The geographic position of the different sampling localities in the Netherlands in 1968 (1 = Schiermonnikoog, 2 = Weerribben (*P. prativaga*), 3 = IJsselmeerpolder, 4 = Surroundings of Amsterdam (*P. amentata*), 5 = *Hollandsche Rading*, 6 = Oostvoorne)

a. Number of eggs.

In *P. amentata* the mean number of egg in locality 4 is relatively low (62.9). The difference between the other three localities (72.9—86.2) are not conspicuous. The localities 1, 2 and 3 are situated in the normal habitat of *P. amentata* in the Netherlands, viz. along ditches in meadows. Locality 4 is a piece of wasteland with heaps of black earth along a ditch. The density of *P. amentata* is relatively high there. In this locality the same number of specimens as at the other localities was collected in a much shorter period.

In *P. pullata* only locality 5 shows a very low number of eggs per egg sac (24.5). These specimens were collected on small, newly formed dunes, near the beach of the Frisian island Schiermonnikoog. The other localities (1 to 4) are situated on Schiermonnikoog and in *Hollandsche Rading*.

In *P. purbeckensis* two groups can be distinguished, on account of the number of eggs: spiders from localities 1 and 2 (65.0 and 58.1 eggs) and from 3 and 4 (47.1 and 42.8 eggs). Localities 3 and 4 are situated in the normal habitat of the species, viz., salt marshes between tidal creeks on Schiermonnikoog. Locality 1 is situated in a recently made polder in the IJsselmeer; locality 2 on the island Oostvoorne, where a tidal salt marsh is enclosed by a dike.

In *P. nigriceps* the only difference between the localities is their geographical position:

Table 2. Data on egg sac samples from different localities in 1968. Any two values not flanked by the same line are significantly different

Spider species	Locality	Number of eggs	Dryweight of carapace	Number of eggs per mg carapace (dryweight)	Number of specimens
<i>P. amentata</i>	1	86.2 ± 12.9	5.90 ± 0.81	14.7 ± 1.6	91
	2	78.0 ± 10.8	5.80 ± 0.97	13.5 ± 1.0	18
	3	72.9 ± 14.8	5.87 ± 1.08	12.5 ± 2.2	44
	4	62.9 ± 9.2	5.33 ± 0.67	11.9 ± 1.5	146
<i>P. pullata</i>	1	33.1 ± 6.1	2.44 ± 0.43	13.7 ± 2.1	81
	2	30.0 ± 5.8	2.26 ± 0.44	13.3 ± 1.6	21
	3	28.3 ± 6.1	2.03 ± 0.37	13.9 ± 2.0	86
	4	26.6 ± 3.9	2.04 ± 0.30	13.0 ± 1.7	23
	5	24.5 ± 6.7	1.93 ± 0.15	12.8 ± 3.5	8
<i>P. purbeckensis</i>	1	65.0 ± 10.2	4.00 ± 0.82	16.3 ± 2.5	13
	2	58.1 ± 13.6	3.71 ± 0.38	15.7 ± 2.6	14
	3	47.1 ± 8.9	3.12 ± 0.49	15.2 ± 2.5	75
	4	42.8 ± 9.4	3.00 ± 0.46	14.3 ± 2.4	72
<i>P. nigriceps</i>	1	35.5 ± 4.7	2.96 ± 0.41	13.0 ± 1.1	94
	2	30.4 ± 5.6	2.92 ± 0.58	10.6 ± 1.6	73
<i>P. monticola</i>	1	30.8 ± 7.7	2.38 ± 0.46	12.9 ± 2.8	39
	2	26.6 ± 7.7	2.29 ± 0.36	11.6 ± 2.9	97
<i>P. prativaga</i>	1	59.3 ± 9.7	3.54 ± 0.54	16.8 ± 2.0	28
	2	49.3 ± 8.3	3.25 ± 0.63	15.4 ± 2.2	78



Oostvoorne (1) versus Schiermonnikoog (2). The same holds for *P. monticola*: Hollandse Rading (1) versus Schiermonnikoog (2).

In *P. prativaga* locality 1 is the normal habitat of the species in the eastern part of the Netherlands, while locality 2 is the same as locality 2 of *P. purbeckensis* (Oostvoorne).

b. Size of spiders (carapace dryweight).

As the localities in table 2 are arranged according to decreasing mean number of eggs, it is easy to see in column 2 of table 2 that the dryweight of the carapace decreases in relation to the number of eggs. The same applies here as to the mean number of eggs in the different species (c.f. paragraph a).

c. Number of eggs per mg carapace dryweight.

In general the number of eggs per mg carapace dryweight shows the same trend as the dryweight of the carapace and the number of eggs, except in *P. pullata*, where there are no significant differences in the values (table 2).

A decreasing number of eggs corresponds with a decrease in size and a decrease in number of eggs per mg carapace dryweight. It seems that there is a correlation between size and number of eggs per unit of size. This correlation, however, could not be demonstrated in separate samples. This implicates that the values for carapace dryweight and number of eggs per mg carapace dryweight vary independently of each other. This does not mean that the reason why spiders in some localities stay smaller and produce less eggs per unit of size cannot be found in the correlation between size and number of eggs per unit of size.

### III. COMPARISON OF SAMPLES FROM THE SAME LOCALITIES IN SUBSEQUENT YEARS

From some localities — the specific habitats of the species concerned — each year, from 1966 to 1970, a sample of females with egg sacs was taken. This was done for *P. amentata*, *P. pullata*, *P. nigriceps*, *P. purbeckensis*, *P. monticola*, *P. lugubris* and *P. palustris* (the last species only in 1966 and 1968). The results are shown in table 3.

a. Number of eggs.

It is clear from table 3, that in general the mean number of eggs in a population is kept at a fairly constant level. In each species there are no significant differences in numbers of eggs in different years. Most striking is the situation in *P. pullata* and *P. lugubris* where in 4 out of 5 and 3 out of 4 years, respectively, almost the same mean numbers of eggs were found. *P. amentata* is more or less an exception since the numbers of eggs agree for two years at the most. In the case of *P. palustris* no conclusions can be drawn because of lack of data.

However, it is clear that in some years either comparatively high or low values occur. From column 6 in table 3, it is concluded that there are no specific "good" or "bad" years for the whole group of species.

b. Carapace dryweight.

A constancy in carapace dryweight during the years has been found. This seems to agree with the data on the mean number of eggs, although they are not directly

Table 3. Data on egg production during subsequent years (in the last three columns the statistical significance of the difference in mean values is given). Two values not flanked by the same line are significantly different

Spider species	Year	Number of eggs	Dryweight of carapace mg	Number of eggs per mg carapace (dryweight)	Number of specimens	Number of eggs	Carapace dryweight	Number of eggs per mg carapace dryweight
<i>P. amentata</i>	1966	74.4 ± 14.0	5.00 ± 0.98	15.0 ± 1.9	72	1968 86.2	1968 5.90	1966 15.0
	1967	81.5 ± 12.4	5.78 ± 0.65	14.2 ± 1.8	77	1970 84.3	1967 5.78	1970 14.9
	1968	86.2 ± 12.9	5.90 ± 0.81	14.7 ± 1.6	91	1967 81.5	1969 5.69	1968 14.7
	1969	73.7 ± 13.1	5.69 ± 0.80	12	12	1966 74.4	1970 5.69	1967 14.2
	1970	84.3 ± 14.5	5.69 ± 0.81	14.9 ± 1.9	56	1969 73.7	1966 5.00	
<i>P. pullata</i>	1966	33.9 ± 7.6	2.25 ± 0.33	15.3 ± 2.6	59	1966 33.9	1968 2.44	1966 15.3
	1967	33.8 ± 7.0	2.36 ± 0.46	14.2 ± 2.5	102	1967 33.8	1970 2.43	1967 14.2
	1968	33.1 ± 6.1	2.44 ± 0.43	13.7 ± 2.1	81	1970 33.4	1967 2.36	1968 13.7
	1969	28.9 ± 5.6	2.29 ± 0.27	12.8 ± 1.8	45	1968 33.1	1969 2.29	1970 13.6
	1970	33.4 ± 6.6	2.43 ± 0.43	13.6 ± 1.8	46	1969 28.9	1966 2.25	1969 12.8
<i>P. nigriceps</i>	1966	34.9 ± 5.6	3.30 ± 0.54	10.8 ± 2.0	99	1967 37.8	1966 3.30	1967 11.9
	1967	37.8 ± 5.8	3.20 ± 0.60	11.9 ± 1.7	113	1966 34.9	1967 3.20	1970 11.3
	1968	30.4 ± 5.6	2.92 ± 0.58	10.6 ± 1.6	73	1970 31.9	1968 2.92	1969 11.2
	1969	31.5 ± 5.5	2.88 ± 0.50	11.2 ± 2.0	48	1969 31.5	1969 2.88	1966 10.8
	1970	31.9 ± 5.2	2.88 ± 0.43	11.3 ± 1.6	40	1968 30.4	1970 2.88	1968 10.6
<i>P. purbeckensis</i>	1966	51.5 ± 11.4	3.43 ± 0.65	15.1 ± 2.2	87	1966 51.5	1966 3.43	1968 15.2
	1967	45.7 ± 10.7	3.24 ± 0.48	14.2 ± 2.8	49	1968 47.1	1967 3.24	1966 15.1
	1968	47.1 ± 8.9	3.12 ± 0.49	15.2 ± 2.5	75	1967 45.7	1968 3.12	1967 14.2
	1969	45.5 ± 8.0	3.54 ± 0.50	12.8 ± 1.9	50	1969 45.4	1969 3.54	1969 12.8
	1970	30.0 ± 9.2	2.76 ± 0.62	9.9 ± 1.9	50	1970 30.0	1970 2.76	1970 9.9
<i>P. monticola</i>	1966	36.7 ± 7.7	2.47 ± 0.38	14.9 ± 2.6	77	1966 36.7	1969 2.52	1966 14.9
	1967					1970 33.9	1966 2.47	1970 13.7
	1968	26.6 ± 7.7	2.29 ± 0.36	11.6 ± 2.9	97	1969 33.7	1968 2.29	1969 13.4
	1969	33.7 ± 9.8	2.52 ± 0.55	13.4 ± 3.9	23	1968 26.6	1970 2.19	1968 11.6
1970	33.9 ± 9.4	2.19 ± 0.33	13.7 ± 2.2	43				

Table 3 (continued)

Spider species	Year	Number of eggs	Dryweight of carapace mg	Number of eggs per mg carapace (dryweight)	Number of specimens	Number of eggs	Carapace dryweight	Number of eggs per mg carapace dryweight
P. lugubris	1966	40.2 ± 7.7	3.25 ± 0.71	12.5 ± 1.7	92	1970 40.5	1970 3.63	1966 12.5
	1967					1966 40.2	1966 3.25	1970 11.4
	1968	33.9 ± 6.1	3.11 ± 0.63	11.1 ± 1.8	90	1969 39.8	1968 3.11	1968 11.1
	1969	39.8 ± 6.7			36	1968 33.9		
P. palustris	1970	40.5 ± 8.2	3.63 ± 0.64	11.4 ± 2.4	43			
	1966	42.5 ± 8.1	2.83 ± 0.43	15.2 ± 2.1	85	1968 54.2	1968 3.03	1968 18.0
	1968	54.2 ± 6.9	3.03 ± 0.36	18.0 ± 2.4	29	1966 42.5	1966 2.83	1966 15.2

Table 4. Data on second egg sacs, compared with data on first egg sacs from the same locality. Any two values not flanked by the same line are significantly different

Spider species	Stage	Number of eggs	Dryweight of carapace	Number of eggs per mg carapace dryweight	Number of specimens	Number of eggs in second egg sac as % of the first egg sac
P. amentata	1st egg sac	84.3 ± 14.5	5.69 ± 0.81	14.9 ± 1.9	56	64.5
	2nd egg sac	54.4 ± 13.3	5.74 ± 1.08	9.7 ± 2.5	39	
P. pullata	1st egg sac	33.4 ± 6.6	2.43 ± 0.43	13.6 ± 1.8	46	58.4
	2nd egg sac	19.5 ± 5.4	2.41 ± 0.62	8.1 ± 1.9	17	
P. nigriceps	1st egg sac	31.9 ± 5.2	2.88 ± 0.43	11.3 ± 1.6	40	52.7
	2nd egg sac	16.8 ± 4.4	2.58 ± 0.53	6.6 ± 1.6	33	
P. monticola	1st egg sac	33.9 ± 9.4	2.19 ± 0.33	13.7 ± 2.2	43	64.3
	2nd egg sac	21.8 ± 6.4	2.15 ± 0.46	9.9 ± 2.1	19	

comparable. "Good" or "bad" years for size mostly do not coincide with "good" or "bad" years for egg production.

c. *Number of eggs per mg carapace dryweight*

This value is also rather constant in all species. Striking are the extremely high values of *P. amentata* in 1966 and *P. pullata* in 1966. In both cases this high value compensates the low value in carapace dryweight, resulting in a normal number, in *P. pullata* even the highest number, of eggs. This is not the case in *P. purbeckensis* in 1970, where the effect of a low value in carapace dryweight on egg production is strengthened by a low value in number of eggs per mg carapace dryweight.

In general there is no correlation between carapace size and number of eggs per mg carapace dryweight, as can be easily seen in comparing columns 7 and 8 of table 3.

#### IV. SECOND EGG SACS

In a few species samples of spiders with second egg sacs could be taken. The data are compared with samples of the first egg sac from the same locality (table 4). The number of eggs in the second egg sac is about 50 to 60 % of the number in the first egg sac. The size of the spiders (except *P. nigriceps*) is the same in first and second egg sac samples. Thus it may be concluded that the production per mg carapace dryweight is much lower for the second egg sac.

#### V. EVALUATION OF THE RESULTS

A summary of the data on egg production of the *Pardosa* species concerned in this paper is given in Graph 4 where the ranges of mean values from all the samples are shown for the eight species of *Pardosa*.

The differences in egg production between the species are mainly caused by differences in size. Larger species produce more eggs than smaller species.

This does not seem to hold when a species produces eggs which weigh less. In this case (c.f. *P. palustris*) more eggs are produced than should be expected on account of the size.

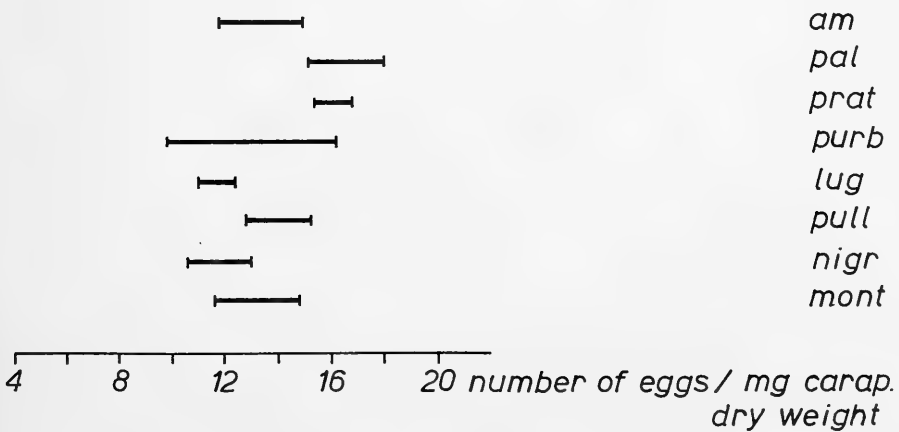
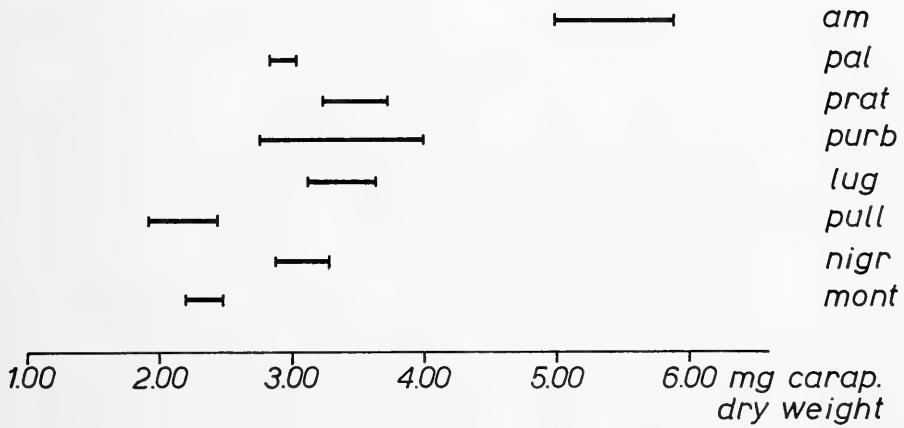
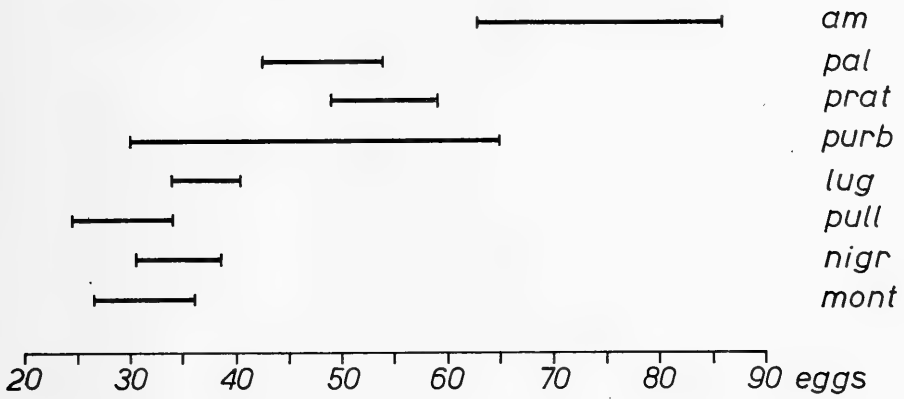
#### Intraspecific differences.

Differences in subsequent years in the same locality.

Any differences occurring in egg production can be caused by climate, habitat or food.

Climate. — In general the period of growing up for all species as well as their breeding periods, coincide. Therefore, the influence of good or bad weather conditions should be manifest in all species in the same way. As this is not the case, it can be concluded that no clear influence of climatic conditions can be observed.

Habitat. — In the successive years the habitats studied remained constant. This is also clear from the fact that no trend in egg production, indicating a gradual change in habitat in the course of the years, could be demonstrated. Differences in egg production, therefore, cannot be caused by differences in habitat conditions.



Graph 4. Ranges of mean values of number of eggs per egg sac, carapace dryweight and number of eggs per mg carapace dryweight, based on all samples that are discussed in this paper

Food. — Two components can be distinguished in relation to egg production:

- 1) Availability of the food: the total quantity of food that is available.
- 2) Accessibility of the food: that part of the total quantity of food that can be obtained by spiders.

#### Availability of the food.

One should distinguish between two periods in the life-time of a spider: the period of growing up and the egg-ripening period during the breeding season. Differences may occur in quantity of food available during the time of growing up as compared to the quantity of food available during the egg-ripening period. Large quantities of food during the time of growing up will result in large spiders. However, when during the egg-ripening period the quantity of available food is small, relatively few eggs per unit of size will be produced (e.g. *P. purbeckensis* in 1969 in table 3).

It is also possible, that small specimens produce much more per unit of size than the larger specimens, indicating that the food situation is better during the breeding season than during the time of growing up (e.g. *P. amentata* in 1966 in table 3).

#### Accessibility of the food.

Differences in density of the spiders can be of importance here, as higher densities of spiders will mean a smaller amount of food for every individual. Though no pertinent observations have been made on this point, there are no reasons to assume that there are considerable differences in density from year to year.

If there is enough food available the possibility remains that the animals periodically lack opportunities to catch food. Under high temperatures ( $\pm 40^{\circ}$  C) the spiders become inactive and this diminishes the chance of meeting prey. At the same time metabolic processes continue and, at a certain moment, the animals are due to produce an egg sac (Kessler, 1969). At low temperatures ( $\pm 10^{\circ}$  C) the spiders are inactive too, and although metabolic processes are retarded then, they do not stop entirely. This causes the same effect, though on a lesser scale, as in the forementioned case.

The same reasoning probably holds for the period between two moults. The length of time between two moults is, as is the case with the egg-ripening period, mainly determined by temperature. Food plays a minor role in this process (Turnbull, 1965).

In conclusion we may state, that in the same habitat in different years, differences in size of the spiders and differences in egg production per unit of size are caused by differences in food intake of the spiders. In general this does not lead to considerable differences in the mean number of eggs per egg sac.

#### Differences between localities in 1968.

As all three factors mentioned, viz., climate, habitat and food, might be of influence, they are evaluated here.

Climate. — There are certain differences in macroclimate between the different localities (e.g. Schiermonnikoog in the north of the Netherlands, Oostvoorne in the south). It is not clear if these differences are also reflected in differences in microclimate between the localities.

Habitat. — The clear difference in habitat in some localities, (e.g. *P. purbeckensis*

in salt marshes and in new polders; *P. amentata* in waste land and along ditches in meadows; table 2 also shows clear differences in egg production.

Food. — It is assumed that any differences in climate and difference in habitat structure in most cases only can have influence on egg production via food.

It is evident that not in all places the egg potential of the species is realized in an optimal way. This provides an opportunity to evaluate habitats as suitable or unsuitable for the development and the egg production of *Pardosa* species. However, it is not clear whether a large size and a high egg production can be considered an advantage or a disadvantage for the population of a species (e.g. *P. amentata* in a piece of waste land, table 2; the egg production and the size show low values, whereas the density of the population is rather high).

#### Second egg sac.

Not all species construct a second egg sac, at least not in large quantities. The meaning of the second egg sac for the survival of the species is not clear.

The lower number of eggs in second egg sacs compared with first is probably caused by a lower potential number of eggs for the second egg sac. This can be deduced from laboratory experiments (unpublished data), where the spiders consumed less food during the second egg-ripening period, as compared with the first egg-ripening period, under the same experimental conditions.

#### General conclusions.

There are specific differences in size. The size determines the egg potential of the spider. The size is determined by the quantity of food consumed by the spider. This is influenced by the geographical position of the habitat (differences in climate) and differences in habitat structure.

For the effectuation of the egg potential (egg production per unit of size) the same can be said. However, differences in weight of the eggs can decrease or increase the egg potential of a species as compared to other species.

In determining size and effectuation of egg potential, food is the most important factor.

## VI. DISCUSSION

Dahl (1908) gives some data on number of eggs per egg sac in *Pardosa* species, with references to several authors. Wiebes (1959) describes the number of eggs in *Pardosa* species, and Den Hollander (1971) and Richter et al. (1971) do the same especially with regard to *P. pullata* and *P. praivaga* in the Netherlands. Graefe (1964) gives some information on a few *Pardosa* species from Germany and Petersen (1950), on some species from Sweden. Edgar (1971) produces data on numbers of eggs in *P. lugubris* in Scotland. The data are summarized in table 5. There is a wide variety in number of eggs produced in a species. Partly this may be caused by the fact that some authors did not study enough specimens in definite populations to gain reliable results.

Furthermore it should be noted that the data are not discussed with reference to the size of the spider which carried egg sacs. From the present study it is clear that any

Table 5. Number of eggs per egg sac, data from literature (data from the present paper are derived from the mean values found in different populations of the species)

Spider species	Number of eggs per egg sac	Author	Country
<i>P. amentata</i>	60—70	Dahl (Sundevall)	Sweden
	± 50	Dahl (Blackwall)	England
	75—100	Dahl (Becker)	Belgium
	60	Dahl (Henking)	Germany
	50—70	Wiebes	Netherlands
	34	Graefe	Germany
	60—85	Kessler (present paper)	Netherlands
<i>P. pullata</i>	25	Dahl (Blackwall)	England
	36	Dahl (de Lessert)	Switzerland
	25—30	Wiebes	Netherlands
	26—44	Den Hollander	Netherlands
	30—37	Richter	Netherlands
	27	Petersen	Sweden
	25—35	Kessler (p.p.)	Netherlands
<i>P. prativaga</i>	33	Graefe	Germany
	42—52	Den Hollander	Netherlands
	47—52	Richter	Netherlands
	36	Petersen	Sweden
	50—60	Kessler (p.p.)	Netherlands
<i>P. lugubris</i>	50	Dahl (Blackwall)	England
	40—70	Dahl (Becker)	Belgium
	25—30	Wiebes	Netherlands
	24	Graefe	Germany
	37	Edgar	Scotland
	35—40	Kessler (p.p.)	Netherlands
<i>P. nigriceps</i>	± 30	Wiebes	Netherlands
	30—40	Kessler (p.p.)	Netherlands
<i>P. monticola</i>	± 50	Dahl (Sundevall)	Sweden
	50—60	Dahl (Blackwall)	England
	30—40	Dahl (Becker)	Belgium
	± 40	Wiebes	Netherlands
	39	Graefe	Germany
	25—35	Kessler (p.p.)	Netherlands
<i>P. palustris</i>	± 40	Wiebes	Netherlands
	42	Petersen	Sweden
	45—55	Kessler (p.p.)	Netherlands
<i>P. purbeckensis</i>	30—65	Kessler (p.p.)	Netherlands

study dealing with egg production in *Pardosa* species in relation to their geographic distribution should account for the size of the spiders at the same time.

In a former paper (Kessler, 1971) I reported on the relation between food consumption and egg production of some *Pardosa* species under experimental conditions



Table 6. Comparison between experimental data on egg production (Kessler, 1971) and range of mean numbers from field samples (present paper)

Spider species	Experiments			Field samples	
	Number of eggs	Carapace dryweight	N	Number of eggs	Carapace dryweight
<i>P. amentata</i>	85.4	7.65	10	62.9—86.2	5.00—5.90
<i>P. lugubris</i>	46.8	4.59	4	33.9—40.5	3.11—3.63
<i>P. palustris</i>	63.0	4.38	4	42.5—54.2	2.83—3.03
<i>P. monticola</i>	51.0	4.64	4	26.6—36.7	2.19—2.47

in the laboratory. The spiders were kept separately in glass jars and were given an abundant food supply of *Drosophila melanogaster*.

The results of these experiments show much higher values in egg production than found in the field samples. Table 6 summarizes these differences. The most striking is the large size of the spiders in the experiments. The higher amount of eggs produced must be considered a natural consequence of this larger size. The question is why these animals were so much larger than the animals in the field samples. They have been caught in the same localities in which the field samples were collected. All experimental animals, however, were kept for some weeks in the laboratory before moulting to adults. During that time they were also given an abundant food supply. This can account for their larger size, assuming that in nature, during the period before moulting to adults (very early spring), they are not able to catch abundant food. There is evidence (Turnbull, 1962, 1965), that spiders when given small amounts of food go on growing and moulting, although the period between two moults is much longer and the spiders stay smaller. These observations indicate that, under field conditions, indeed food may be a limiting factor in egg production, directly or via the size of the spiders. In the same paper (Kessler, 1971) the reaction was described of *Pardosa* species on increasing food shortages after moulting to adult.

It was clear that all four species (viz., *P. amentata*, *P. lugubris*, *P. palustris* and *P. monticola*) adapt their egg production to the food supply. However, *P. amentata* and *P. monticola* showed a quicker reaction than *P. palustris* and *P. lugubris*. The egg-ripening period, viz., the length of the period between moulting and egg laying, proved to be mainly dependent on "climate", not on food.

The species concerned also showed the tendency to produce lighter eggs under conditions of food shortage. This phenomenon slightly compensated the lower amount of egg biomass produced.

Combining the results of Turnbull (1962, 1965), my experimental results (Kessler, 1971) and the field data from the present paper, it can be stated that:

1. The size of the adult spider is dependent on the quantity of food available during the developmental period. Conditions of climate and habitat probably influence the availability of food during this period.

2. The quantity of food available during the egg-ripening period then determines the effectivity of the potential number of eggs, that can be deposited according to size. By a decrease in weight of the individual eggs the potential number of eggs can be increased. The amount of egg production in combination with the size of the adult

spiders can give an indication of the suitability of the particular locality where the species is sampled.

Den Hollander (1971) states that, although there is a rather sizable difference in number of eggs in the first egg sac between *P. pullata* and *P. prativaga*, the difference is annihilated by the fact that the species with fewer eggs in the first egg sac (*P. pullata*) produces a second egg sac more often than *P. prativaga*. No direct data on the other species in this paper are available, but indirect data (e.g. the much greater effort to sample second egg sacs of *P. amentata* compared with *P. nigriceps*) indicate that this phenomenon may be of common interest in spiders of the genus *Pardosa*.

Before speculating on the meaning of the higher number of eggs in the first egg sac in bigger species, more data on the second egg sac of *Pardosa* species should be available.

### SUMMARY

The egg production of eight *Pardosa* species (Araneae, Lycosidae) in the Netherlands is described on the basis of field samples. The eggs are deposited in an egg sac, which is carried around by the female spider on the spinnerets.

The first egg sac seems to be the most important one for reproduction, although some species sometimes produce a second egg sac, containing much less eggs than the first. The mean number of eggs in the first egg sac ranges from  $\pm 86$  in *Pardosa amentata* to  $\pm 25$  in *Pardosa monticola*. The number of eggs produced is dependent on the size of the spiders.

Intraspecific differences occur as to the number of eggs and size of the spiders between populations from different localities in the same year. In the same locality no obvious differences in egg production could be found in subsequent years in different species.

It is concluded that differences in size and differences in egg production between populations are mainly caused by differences in food intake of the spiders.

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# HYMENOPTEROUS PARASITES IN EGG SACS OF SPIDERS OF THE GENUS *PARDOSA* (ARANEIDA, LYCOSIDAE)

by

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With 2 text-figures, 4 graphs and 3 plates

## ABSTRACT

The occurrence of two hymenopterous egg parasites, *Gelis* spec. (Ichneumonidae) and *Acolus krygeri* Kieffer (Proctotrupidae), in egg sacs of spiders of the genus *Pardosa* (Araneida, Lycosidae) in the Netherlands is described.

*Gelis* spec. develops in the spider egg sac. All spider eggs are either eaten or destroyed by the larvae. Only a small proportion of *Pardosa* egg sacs is parasitized by *Gelis*:  $\pm 140$  out of  $\pm 5000$  egg sacs. In some species and at some sampling sites the degree of parasitism can be rather high, up to 42.6%.

*Acolus krygeri* develops in a single spider egg. Only a proportion of spider eggs in an egg sac is parasitized, the other eggs develop into young spiderlings normally.

*Acolus krygeri* occurs in the Netherlands only on the Frisian island Schiermonnikoog. This species parasitizes mainly egg sacs of *Pardosa nigriceps* (Thorell), viz., to about 70%, with a mean number of 10 parasites per sac; this means that 30 to 60% of the spider eggs are attacked. To a lesser extent egg sacs of *P. pullata* (Clerck) are attacked.

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## INTRODUCTION

In order to study the egg production of spiders of the genus *Pardosa* (Lycosidae) in the field, a large number of female spiders carrying egg sacs have been collected. In some samples a number of eggs sacs contained larvae of a hymenopterous parasite, *Gelis* spec. (Hymenoptera, Ichneumonidae). In other samples, collected on the Frisian island Schiermonnikoog, larvae of *Acolus krygeri* Kieffer (Hymenoptera, Proctotrupidae) were found in spider eggs. A study of the interrelation between parasites and spiders was initiated, in order to establish the effect of parasitism on egg production in spiders of the genus *Pardosa*. The results of this study are presented in this paper.

### Life history of *Pardosa* in the Netherlands

In early spring the juvenile spiders moult to the adult stage (March-April). About one month later the females construct egg sacs, which are carried around on the spinnerets (May-June). Again after about one month the juvenile spiders emerge. The females can produce a second egg sac (July-August), and very seldom, a third one. Most of the juvenile spiders reach the penultimate stage before winter. For more detailed description of the life history of *Pardosa* may be referred to Vlijm et al. (1963).

Eight species of the genus *Pardosa* can be found in reasonable numbers in the Netherlands: *P. amentata* (Clerck), *P. lugubris* (Walckenaer), *P. pullata* (Clerck), *P. prativaga* (L. Koch), *P. nigriceps* (Thorell), *P. purbeckensis* F.O.P.-Cambridge, *P. monticola* (Clerck), and *P. palustris* (Linnaeus).

### The parasites

As is said above, we have to deal with two types of egg parasites.

#### 1. *Gelis* spec. (Hymenoptera, Ichneumonidae).

The members of the genus *Gelis* are ant-like insects; the females are wingless, the males have wings; their length is 2 to 2.5 mm (Pl. I Fig. A1 and A2). The species are rather difficult to identify, and therefore they are dealt with as a genus. The larvae develop in spider egg sacs in such a way, that no spiderlings can emerge from the parasitized egg sac; the larvae consume all the spider eggs or, if not all eggs in the sac are eaten, the remaining eggs are destroyed by the prepupae.

## 2. *Acolus krygeri* Kieffer (Hymenoptera, Proctotrupidae, Scelioninae).

These are rather small insects (length  $\pm$  1.2 mm). The females are wingless, the males have wings (Pl. I Fig. B1). The larvae develop in a single spider egg. Non-parasitized spider eggs develop normally. The species was recorded by Kryger from Denmark, obtained from eggs sacs of *Lycosa* spec., especially *Lycosa picta* (the latter is probably synonymous with *Arctosa perita* Latreille).

## MATERIAL AND METHODS

All samples of *Pardosa* females with egg sacs were collected by hand on sunny days. In this way one only catches spiders, that are active upon the vegetation. However, there is reason to believe that on sunny days nearly all females are out on the vegetation, exposing their egg sacs to the sun.

The parasites used for experimental purposes were obtained by collecting *Pardosa* females with egg sacs from localities, where in former years a reasonable number of egg sacs were found to be parasitized. The spiders were kept in cages and as soon as parasites emerged, these were transferred to small glass jars and supplied with water and honey. The temperature was kept at 20 to 25°C.

Previously a number of *Pardosa* females were retarded in their development by keeping them under low temperature conditions. Thus they constructed their first egg sac after the emergence of the first egg sacs of spiders in the field, and just in time to supply the parasites in the experiments with fresh spider egg sacs.

## RESULTS

### 1. *Gelis* spec.

#### A. Field observations

Larvae of *Gelis* spec. have been found in egg sacs of all *Pardosa* species in the Netherlands, except in *P. palustris*.

In table 1 all available data are presented. It is evident from this table that the degree of parasitism is highly variable among the different *Pardosa* species. In nearly 35% of the samples *Gelis* larvae were found. The degree of parasitism of *Gelis* in *Pardosa* egg sacs in general is not very impressive. Only 139 out of 5116 egg sacs were found to be parasitized. On 65% of the sampling sites, however, we never found parasitized egg sacs, even though a high number of sacs were collected on these sites.

When we consider the number of parasitized egg sacs in those samples where parasites were found, it is evident that the degree of parasitism can be rather high (Table 2). The highest parasitism (e.g. 42.6% in *P. amentata*) was found in samples of second egg sacs. Moreover, in *P. purbeckensis* and *P. pullata* only the second egg sac was found to be parasitized. It is not clear whether the first egg sac in these two species is not parasitized at all. More likely the number of parasitized egg sacs is so low, that they have not been met with in the samples. It should be noted that we did not succeed in taking samples of second egg sacs of all species and on all sampling sites.

Table 1. General impression of the occurrence of *Gelis* larvae in egg sacs of species of *Pardosa* at different sampling sites

Spider species	Number of egg sacs	Number of samples	Number of samples with parasitized egg sacs	Number of sampling sites	Total number of parasitized egg sacs
<i>P. amentata</i>	1006	16	9 (56.3%)	6	53
<i>P. lugubris</i>	601	6	3 (50.0%)	3	31
<i>P. pullata</i>	791	17	6 (35.3%)	2	13
<i>P. prativaga</i>	147	2	1 (50.0%)	2	12
<i>P. nigriceps</i>	1324	18	5 (27.8%)	2	9
<i>P. purbeckensis</i>	609	11	2 (18.2%)	3	20
<i>P. monticola</i>	445	7	1 (14.3%)	3	1
<i>P. palustris</i>	493	3	- -	2	-
Total	5116	81	28 (34.6)	12 <sup>1)</sup>	139

1) Some sampling sites are the same for several species

Table 2. Mean percentage of parasitism in samples of *Pardosa* species, where *Gelis* larvae were found

	Mean % of parasitized egg sacs	Number of samples	Highest and lowest % found
<i>P. amentata</i>	9.7	9	42.6 — 0.7
<i>P. lugubris</i>	8.1	3	22.6 — 2.0
<i>P. pullata</i>	8.9	6	16.7 — 2.1
<i>P. nigriceps</i>	3.7	5	5.9 — 1.8
<i>P. purbeckensis</i>	14.7	2	25.7 — 3.7
<i>P. monticola</i>	2.0	1	2.0
<i>P. prativaga</i>	8.0	1	8.0

These considerations do suggest that *Gelis* presumably is much more widespread than is indicated in table 1.

Number of larvae in the spider egg sac.

The interrelation between the number of spider eggs per egg sac and the number of larvae of *Gelis* is shown in table 3. The size of spiders with parasitized egg sacs did not differ from that of spiders with normal egg sacs. Thus there is no reason to assume that the parasitized egg sacs contained different numbers of spider eggs, this number being correlated with the size of the mother spider (cf. Petersen, 1950). Moreover, the number of eggs could be counted when the *Gelis* larvae were very young, and this

Table 3. Mean number of *Gelis* larvae per egg sac found in samples of the first (1) or second (2) egg sac of different *Pardosa* species, and the calculated mean number of spider eggs available to one *Gelis* larva in the different samples

Spider species	First or second egg sac	Mean number of spider eggs per egg sac	Mean number of <i>Gelis</i> larvae in parasitized egg sacs	Number of spider eggs available to one <i>Gelis</i> larva	Number and percentage of parasitized egg sacs in the sample
<i>P. pullata</i>	2	16.0	1.8 $\pm$ 1.17	8.9	6 (21.6)
<i>P. purbeckensis</i>	2	26.7	3.1 $\pm$ 0.87	8.6	18 (26.1)
<i>P. amentata</i>	2	49.7	4.9 $\pm$ 1.94	10.1	23 (42.6)
<i>P. lugubris</i>	1	40.5	5.1 $\pm$ 2.35	7.4	19 (22.6)
<i>P. amentata</i>	1	74.4	6.6 $\pm$ 4.28	11.3	7 ( 6.7)
<i>P. prativaga</i>	1	48.9	7.0 $\pm$ 2.37	6.4	12 (10.2)
<i>P. amentata</i>	2	54.1	7.6 $\pm$ 3.10	7.1	7 (13.0)
<i>P. amentata</i>	1	65.7	10.3 $\pm$ 3.24	6.4	8 ( 8.9)

number did not differ from the numbers in non-parasitized egg sacs. However, as a rule, it is not possible to count the number of spider eggs in a parasitized egg sac. Therefore the mean number of spider eggs in not parasitized egg sacs of the same samples is chosen as an estimate of the spider eggs available to the larvae in a parasitized egg sac.

There clearly is a relation between the number of host eggs and the number of *Gelis* larvae. It is striking, that the number of larvae is highest, when the percentages of parasitized egg sacs in the samples are lowest. This is, however, a consequence of the fact, that second egg sacs, containing fewer eggs than the first egg sacs, have a higher degree of parasitism. The number of eggs available to one *Gelis* larva ranges from 6.4 to 11.3.

Table 4. Mean number of old and young *Gelis* larvae per egg sac in one sample of *Pardosa lugubris* and one sample of *P. prativaga*

Spider species	Young larvae	Number of egg sacs	Old larvae or pupae	Number of egg sacs
<i>P. lugubris</i>	4.7 $\pm$ 1.88	12	5.6 $\pm$ 2.38	11
<i>P. prativaga</i>	6.5 $\pm$ 2.43	6	7.5 $\pm$ 2.43	6

In two samples of *Pardosa lugubris* and *P. prativaga*, collected in the same period, it was possible to compare egg sacs with very young *Gelis* larvae (in that stage the spider eggs are not yet damaged), with egg sacs containing old larvae or pupae. The results are shown in table 4. The mean numbers of old and young larvae were not significantly different in those samples. Therefore it may be concluded, that the number of *Gelis* eggs, deposited in one egg sac, is proportional to the number of spider eggs in these egg sacs.

## B. Laboratory observations

A number of spiders carrying egg sacs was collected in the field and kept in cages. Every day the cages were searched for parasites. A total number of 49 specimens was collected that way : 28 ♂ and 21 ♀ (Table 5). The slight predominance of males over

females is not statistically significant. The parasites were kept in glass tubes, together with a small sponge soaked in water and honey.

After emergence the males and females mated very soon (duration of the copulation: 5 - 10 minutes); consequently, the females were able to lay eggs within 1 or 2 days after emergence.

Table 5. The number of *Gelis* males and females emerged from different samples of *Pardosa amentata* females with egg sacs, collected in the field

Spider species :	Number of egg sacs	Total number of <i>Gelis</i> in the sample	
		♂	♀
<i>P. amentata</i>	30	4	6
	90	10	5
	70	7	3
	11	4	3
	40	3	4
Total	—	28	21

#### Parasitizing of the spider egg sac.

When a *Pardosa* spider carrying a fresh egg sac is put in a tube together with a *Gelis* female, the latter becomes very active. After about 10 minutes the *Gelis* female jumps on the egg sac, walks around on the surface of the egg sac for a few minutes and then pierces the egg sac with her ovipositor (Pl. I Fig. B2). The eggs are mostly deposited at the edge of the egg sac, where the two halves of the sac are joined together (for a description of the egg sac, cf. Vlijm et al., 1963). After egg laying the *Gelis* female leaves the egg sac or sometimes pierces the sac at another point. The number of parasite eggs found in the egg sacs in these experiments varied between 1 and 7.

An easier method to obtain parasitized egg sacs is to remove the sac from the female spider and put it in a tube with the parasite. It takes less time then for the parasite to mount the egg sac than in the case of a spider running around with its egg sac. After being parasitized, the egg sac be returned to the owner; in all cases it was readily accepted by the female spider.

#### Development of the *Gelis* larvae.

The development of the larvae was studied by keeping larvae separately with some spider eggs, which were replaced by fresh ones every two days, in "cages" (small glass rings with some moist plaster of Paris on the bottom and sealed with a piece of filter paper, Fig. 1). The results were compared with data of larvae developing normally

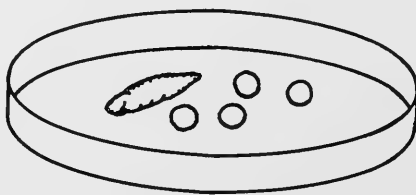


Fig. 1. Glass "cage" with one *Gelis* larva and some spider eggs

within a spider egg sac. This procedure had to be followed since the *Gelis* larvae are lost for the experiment when egg sacs are opened for inspection and determination of the development of the larvae. Moreover, in the small cages one can easily assess the feeding rate of the larvae.

In a temperature range from 20 - 25°C the total development took from 16 - 20 days. The development of the spider eggs under these conditions takes about 20 - 25 days (Table 6; Pl. II). Only in the active larval stage spider eggs are eaten. This stage lasts 2 - 3 days. During this time the larvae consumes on the average 7 spider eggs (min. 5 eggs; max. 13 eggs). This is in agreement with data from the field samples (Table 3).

The development of the larvae in the normal egg sacs and in the glass cages proved to be the same under these temperature conditions. The larvae destroy all the spider eggs in the egg sac. If not all eggs are eaten, the remaining eggs are smashed by the prepupae. When the imago is ready to emerge it bites a hole in the wall of the egg sac, or emerges out of holes bitten by the mother spider to release the juvenile spiders,

Table 6. Duration of the stages in the development of *Gelis*

Time in days	Larval stage	Size of the larva in mm	
1 — 3	egg	0.5 x 0.1	Pl. II A1
3 — 4	active larva	0.7 x 0.1 to 1.1 x 0.4	Pl. II A2
5	active larva	1.1 x 0.4 to 3.5 x 1.4	Pl. II B1
6	full grown larva	3.5 x 1.4	Pl. II B2
7, 8, 9, 10	prepupa (silkspinning)		Pl. II C1
10 — 16 — 20	pupa		Pl. II C2
16 — 20	imago		

even though the latter are not present any more. This phenomenon has not yet been studied in detail.

#### Behaviour of the spider towards the parasite.

When a *Gelis* female is sitting on a spider egg sac, the spider does not seem to notice: it shows no reaction at all. When a spider meets a moving *Gelis* specimen it is sometimes grabbed, but in all cases observed, the spider immediately released the parasite undamaged. The spider takes care of a parasitized egg sac in a normal way, even when it becomes seriously deformed when the larvae are in the pupal stage. Even in the field one can easily recognize a parasitized egg sac at this stage.

#### Conclusions

1. On the whole the parasitism by *Gelis* is not very important in reducing natality in *Pardosa* spiders: only 139 egg sacs out of 5116 contained *Gelis* larvae, Table 1. However, in some localities and especially in the second egg sac it can be important; e.g. 42.6% of the egg sacs were found parasitized in a sample of the second egg sac of *Pardosa amentata*, Table 3.

2. The number of parasites emerging from a spider egg sac is dependent on the

size of the egg sac; from 1.8 larvae in the second egg sac of *Pardosa pullata*, containing 16.0 spider eggs, up to 10.3 larvae in the first egg sac of *Pardosa amentata*, containing 65.7 spider eggs, Table 3.

3. The parasite adapts the number of eggs laid to the size of the spider egg sac; regulation of the numbers of parasites is therefore determined by the female parasite and not by competition between larvae (conclusion 2 and table 4).

4. The ratio ♂/♀ does not differ statistically from 1.

5. It is possible, at least under laboratory conditions, to raise the larvae of *Gelis* to the adult stage outside the spider egg sac, provided enough food is presented in the form of spider eggs.

6. A *Gelis* larva needs about 7 eggs of a *Pardosa* spider to complete its development, under laboratory conditions. In the field the spider eggs available to a single *Gelis* larva range from 6.4 to 11.3

7. The development of *Gelis* from egg to the adult stage takes about the same time as, or is somewhat shorter than, the development of the spider eggs into juvenile spiders.

8. No conclusions can be drawn on the hibernation of *Gelis* spec.

#### Discussion

A number of authors have described the occurrence of *Gelis* spec. in egg sacs of several spider species. A list of reference on all spider parasites is given by Eason et al. (1967). They state that the records of spider parasites mainly consists of brief and incomplete accounts. More recently, Horstmann (1970) extensively studied the ecology of Ichneumon flies in Schleswig-Holstein. He described two species of *Gelis*, *G. micrurus* and *G. pumilus*, both parasitizing egg sacs of Linyphiid spiders, while *G. micrurus* also parasitizes *Pardosa* egg sacs. Both species have more than one generation per year. *Gelis micrurus* parasitizes Linyphiid egg sacs, when *Pardosa* egg sacs are not available any more. In Linyphiid egg sacs there is one larva (Solitärparasit), whereas in *Pardosa* egg sacs there are more than one (Gregärparasit).

In our study no separate species of *Gelis* are distinguished. It is possible, that some of the differences found must be ascribed to specific differences. The mean number of spider eggs and the mean number of *Gelis* larvae per egg sac were calculated for each sample of egg sacs. A positive correlation between the mean number of these eggs and mean number of *Gelis* larvae per sac was demonstrated in comparing all samples of *Pardosa* egg sacs. Within a sample, however, no correlation between size of the egg sac and number of *Gelis* larvae was found. It is possible to estimate the original number of spider eggs in the parasitized egg sac by the size of the corresponding spider. This might mean that in different *Pardosa* species and in different localities, we are dealing with different *Gelis* species or subspecies, adapted to the size of the spider egg sac which is normally available to them. However, from laboratory experiments there is an indication that *Gelis* individuals bred from egg sacs from one locality and sampled at the same time, deposit more eggs in *Pardosa amentata* egg sacs, with a high number of eggs, than in *Pardosa monticola* egg sacs, with a much lower number of eggs.

The observation of Horstmann that the larvae of *Gelis micrurus* are solitary in the small Linyphiid egg sacs and gregarious in *Pardosa* egg sacs points in the same direction. As indicated by Horstmann, *Gelis micrurus* parasitizes Linyphiid egg sacs when *Pardosa*



egg sacs are not available. It is not clear whether one generation of *Gelis micrurus* parasitizing Linyphiid egg sacs and the other generation(s), *Pardosa* egg sacs, or whether there is a gradual shift to other egg sacs.

In this context it is of importance to study the behaviour of *Gelis* spec. in connection with egg sacs of other spider species.

## 2. *Acolus krygeri* Kieffer

### A. Field observations

As already remarked above, *Acolus krygeri* has been found in the Netherlands only on the Frisian island Schiermonnikoog; samples from other Frisian islands were not available and our observations therefore only refer to *Pardosa* species found on that island: *P. nigriceps*, *P. pullata*, *P. purbeckensis* and *P. monticola*.

*Acolus krygeri* is practically restricted to *P. nigriceps* and *P. pullata* as host species (Table 7A). It is seldom found in egg sacs of *P. monticola* and *P. purbeckensis* (Table 7B). *Acolus* seems to be restricted to the typical habitat of *P. nigriceps* on Schiermonnikoog. This is a dense vegetation of *Carex arenaria* and *Salix repens* in a dune area

Table 7A. Occurrence of *Acolus* larvae in egg sacs of *Pardosa* species. Samples from the habitat of *P. nigriceps*

<i>Pardosa</i> species	First (1) or second (2) egg sac	Number of egg sacs	Parasitized egg sacs	%
<i>P. nigriceps</i>	1	359	227	63.2
<i>P. nigriceps</i>	2	801	564	70.5
<i>P. pullata</i>	1	22	10	45.5
<i>P. pullata</i>	2	124	57	46.0

Table 7B. Occurrence of *Acolus* larvae in egg sacs of *Pardosa* species. Samples from the typical habitat of the spider concerned

<i>Pardosa</i> species	First (1) or second (2) egg sac	Number of egg sacs	Parasitized egg sacs	%
<i>P. pullata</i>	1	146	11	7.5
<i>P. purbeckensis</i>	1	97	4	4.1
<i>P. monticola</i>	1	50	6	12.0

(Vlijm & Kessler-Geschiere, 1967). The data in Table 7A refer to specimens found in this habitat. The data in Table 7B are based on specimens sampled in other habitats, mostly bordering on the habitat of *P. nigriceps*. The data in Table 7 are based on samples from several places on Schiermonnikoog and from several years.

Table 8 shows the percentages of parasitism in 1968 and 1969 at the same sampling site, both for the first and second egg sacs.

Table 9 shows the differences in percentage of parasitism between sampling sites in 1968 for the second egg sac.

Because of the small numbers of *P. pullata* found in the samples (habitat of *P. nigriceps*!), this could be done only for *P. nigriceps*. It is clear that there are no

conspicuous differences in percentages of parasitism, neither between the first and second egg sacs nor in the different localities (sampling sites). These data are confirmed by additional samples of either the first or the second egg sac of *P. nigriceps* from other years.

#### Number of larvae in the spider egg sac.

Although in several egg sacs all spider eggs were parasitized, this generally is the case with only a portion of the eggs. The non-parasitized eggs develop into young spiderlings in a normal way.

There is a relation between the size of the spider egg sac and the number of parasites found (Table 10), which is especially clear for the second egg sac. It is striking, that

Table 8. Differences in percentage of parasitism in egg sac samples of *Pardosa nigriceps* on the same sampling site in 1968 and 1969

	First egg sac		Second egg sac	
	N	%	N	%
1968	85	63.5	70	78.6
1969	53	64.2	21	61.9

although the mean number of spider eggs in the first egg sac is much higher than in the second, the mean number of parasites is the same for both egg sacs: about 10. This means that in the first egg sac about 30% of the spider eggs is parasitized, whereas in the second egg sac this percentage is about 60% (Table 11). This is also found for egg sacs of *Pardosa pullata* (Table 11), although the percentage of parasitism in the samples is much lower here: about 45% (Table 7A). If we compare all samples of second egg sacs of *Pardosa nigriceps* with a degree of parasitism lower than 70%, with the samples where the percentage of parasitism is higher, we see that a lower percentage of parasitism results in a lower mean number of parasites per egg sac (Graph 1).

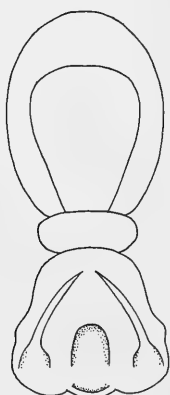


Fig. 2. First stage larva of *Acolus krygeri*

However, the difference is not very conspicuous. The number of parasites in parasitized egg sacs ranges from 1 to 42. The frequencies are given in Graph 2. It is clear from this figure, that the same mean number of parasites in the first and second egg sac is reached

Table 9. Differences in percentage of parasitism in the second egg sac of *Pardosa nigriceps* on several sampling sites

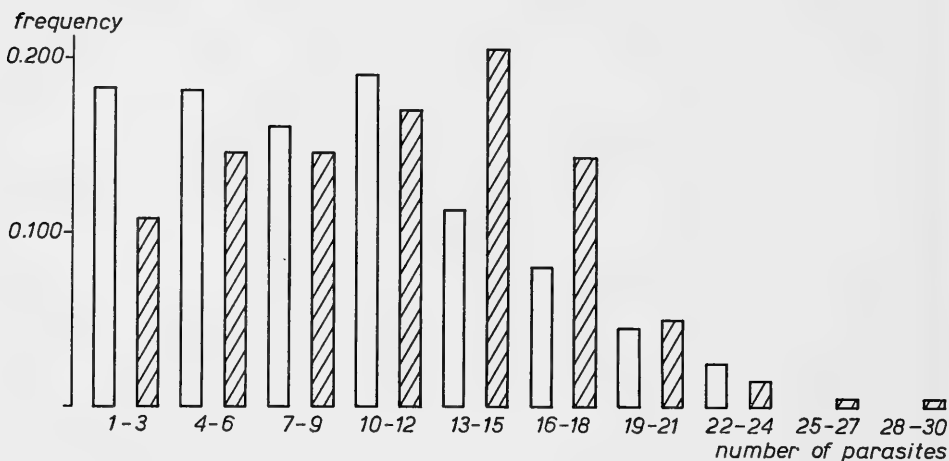
Sampling site	Number of egg sacs	Percentage of parasitized egg sacs
1	70	78.6
2	60	60.0
3	47	76.1
4	30	70.0
5	54	77.8
6	51	74.5
7	55	69.1
8	41	82.9
9	41	92.9

Table 10. Relation between size of the egg sac (number of eggs per egg sac) and the number of parasites per egg sac for *Pardosa nigriceps*; A, data on first egg sac, B, second egg sac

		A														
size of the egg sac (number of spider eggs)		4-6	7-9	10-12	13-15	16-18	19-21	22-24	25-27	28-30	31-33	34-36	37-39	40-42	43-45	46-48
mean number of parasites per egg sac							7.8	10.6	8.0	9.3	9.8	10.8	9.6	12.3	12.8	23.4
N							5	10	27	42	54	38	28	12	6	5
% parasitized eggs in the egg sac							39.0	46.0	30.8	32.1	30.6	30.9	25.3	30.0	28.8	49.8
		B														
mean number of parasites per egg sac		3.6	5.8	6.6	8.7	10.4	11.9	14.1	15.3	16.0						
N		5	12	60	114	151	117	70	26	8						
% parasitized eggs in the egg sac		72.0	72.5	60.0	62.2	61.2	59.5	61.3	58.8	55.2						

Table 11. Mean number of spider eggs and mean of *Acolus* larvae per egg sac in first and second egg sacs of *Pardosa nigriceps* and *Pardosa pullata* from one sampling site

Host species	First or second egg sac	N	Mean number of spider eggs in the egg sac	Mean number of parasites in parasitized egg sacs	N	% of parasitized eggs in the egg sac
<i>P. nigriceps</i>	1	359	32.0 $\pm$ 6.01	9.9 $\pm$ 6.94	227	30.9
<i>P. nigriceps</i>	2	801	17.0 $\pm$ 4.65	10.4 $\pm$ 5.67	564	61.2
<i>P. pullata</i>	1	22	30.0 $\pm$ 5.65	10.7 $\pm$ 3.11	10	35.6
<i>P. pullata</i>	2	124	17.1 $\pm$ 5.12	8.6 $\pm$ 5.59	57	50.6



Graph 1. Frequency distributions of number of parasites (*Acolus*) per egg sac in samples with a degree of parasitism less than 70% (white: N = 183; M =  $9.2 \pm 5.76$ ) and samples with a higher degree of parasitism (hatched: N = 894; M =  $11.0 \pm 5.54$ )

in a similar way. It seems that it is not so much dependent on the size of the egg sac, but on other phenomena. In Graph 3 the frequencies of the parasitized egg sacs are compared with the frequencies of the total number of parasitized and non-parasitized egg sacs together. Within the groups of first or second egg sacs there is an even chance for every egg sac, not dependent on size, to become parasitized. *Acolus*, therefore, does not seem to discriminate between large and small egg sacs.

In about 20 cases a spider egg appeared to contain 2 larvae of *Acolus*, this is a very low percentage: about 0.5%.

#### Laboratory observations

##### Sex ratio.

To determine the sex ratio of *Acolus* two samples of *Pardosa nigriceps* second egg sacs were collected in the field. The spiders with egg sac were kept separately in glass tubes. After emergence the parasites were collected and counted. The results are shown in table 12. There is a dominance of females over males. This ratio fluctuates when we consider the numbers of parasites emerging from an egg sac. When there are only a few parasites in the egg sac the males predominate (Table 13).

Mating occurs within a day after emergence. The parasites were provided with water and honey; it is not clear whether the females need food to develop the eggs. In other experiments, where no honey or sugar were provided the females were able to parasitize spider eggs successfully.

##### Parasitizing of the egg sac.

A female spider with a fresh egg sac was put in a glass tube, together with some female *Acolus* specimens, which had already mated. When the egg sac comes in reach of the parasite, the animal takes a crouching position with bent hind legs. This reaction can also be provoked by approaching the animal with the tip of the finger or a pencil.

It then jumps on the egg sac and walks around, tapping the surface of the egg sac with the antennae. Every now and then it stops and pierces the egg sac with the ovipositor (Pl. III Fig. A1). The length of the ovipositor is only 0.4 mm, the spider eggs have a diameter of 1 mm or more, consequently only spider eggs at the surface of the egg sac

Table 12. Number of males and females of *Acolus* emerged from egg sacs of *Pardosa nigriceps*

Sample	Number of egg sacs	Number of males	Number of females	Ratio ♂/♀
1	28	105	212	0.495
2	20	49	105	0.467

are within reach of the parasite. After 10-30 minutes the parasite leaves the egg sac and walks around in the glass tube, after which it may again jump on the egg sac. This is the more easily observed when the egg sac is removed from the female spider and thus stays in the same place.

In this way egg sacs of *Pardosa nigriceps* as well as those of *Pardosa amentata* were successfully parasitized. All egg sacs less than 5 days old, were successfully parasitized; in two cases where the parasite was apparently parasitizing egg sacs of 7 and 10 days old, no parasites emerged.

#### Development of the *Acolus* larvae.

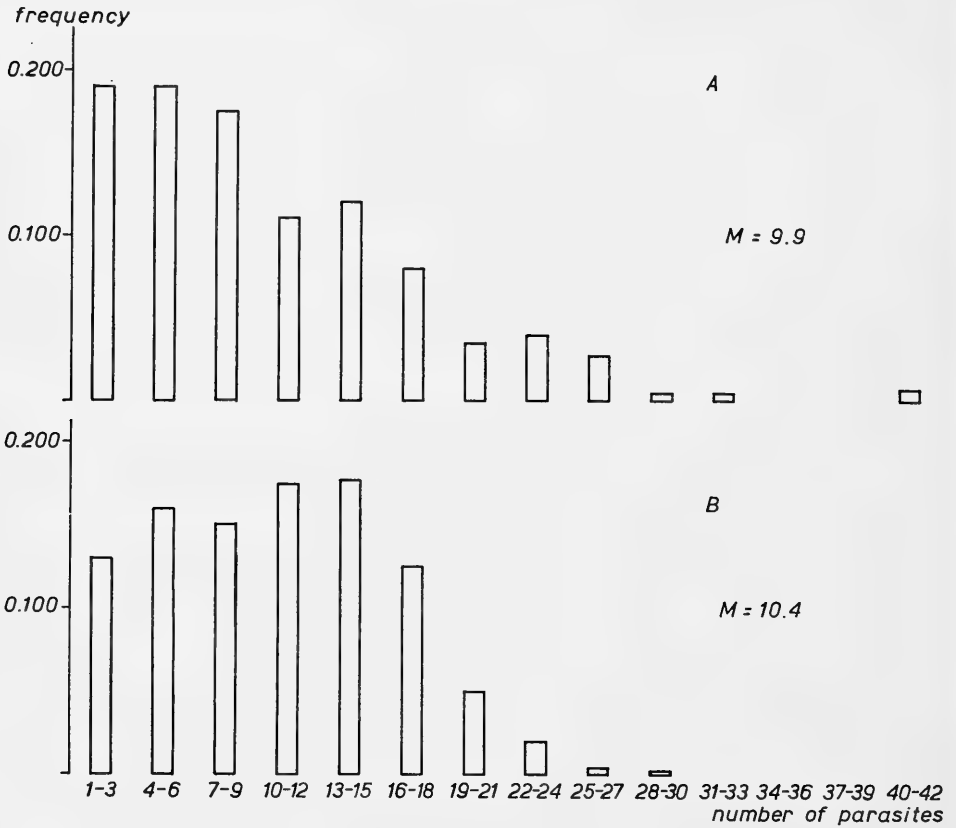
The embryonic development of the parasites was studied by immersing the parasitized spider eggs in paraffin oil, following the technique by Holm (1940) for observing the development of living spider embryos. The egg membrane becomes transparent which makes the larvae of the parasite easily visible.

Controls were made by opening parasitized spider egg sacs of the same age and studying the parasitized eggs in alcohol. The paraffin oil proved to have no effect on the embryonic development of the larvae. At temperature conditions of 25°C the total development took 18-21 days in the following scheme:

day 1 - 3	egg stage	
day 4	1st stage larva	pl. III A2
day 5	2nd stage larva	pl. III B1
day 6 - 7	3d stage larva (prepupa)	pl. III B2
day 8 - 21	pupa	

During the first 3 days no details in the development of *Acolus* could be observed with the techniques used. The first stage larvae have a curious shape (Fig. 2), probably adapted to floating in the fluid of the spider egg. The active larval stage takes only two days, during which time most of the contents of the spider egg are eaten by the larva. After this active stage the larva becomes immobile; then follows the prepupal and pupal stages in which no clear observations on the development could be made. The longevity of the adult under laboratory conditions was about 14 days.

The influence of different temperatures upon the length of the larval development is shown in table 14. Compared with the development of the spider embryos the development of *Acolus* is short. The total number of parasites out of 20 experimental egg sacs was 174, a mean of 9.1 parasites per egg sac.



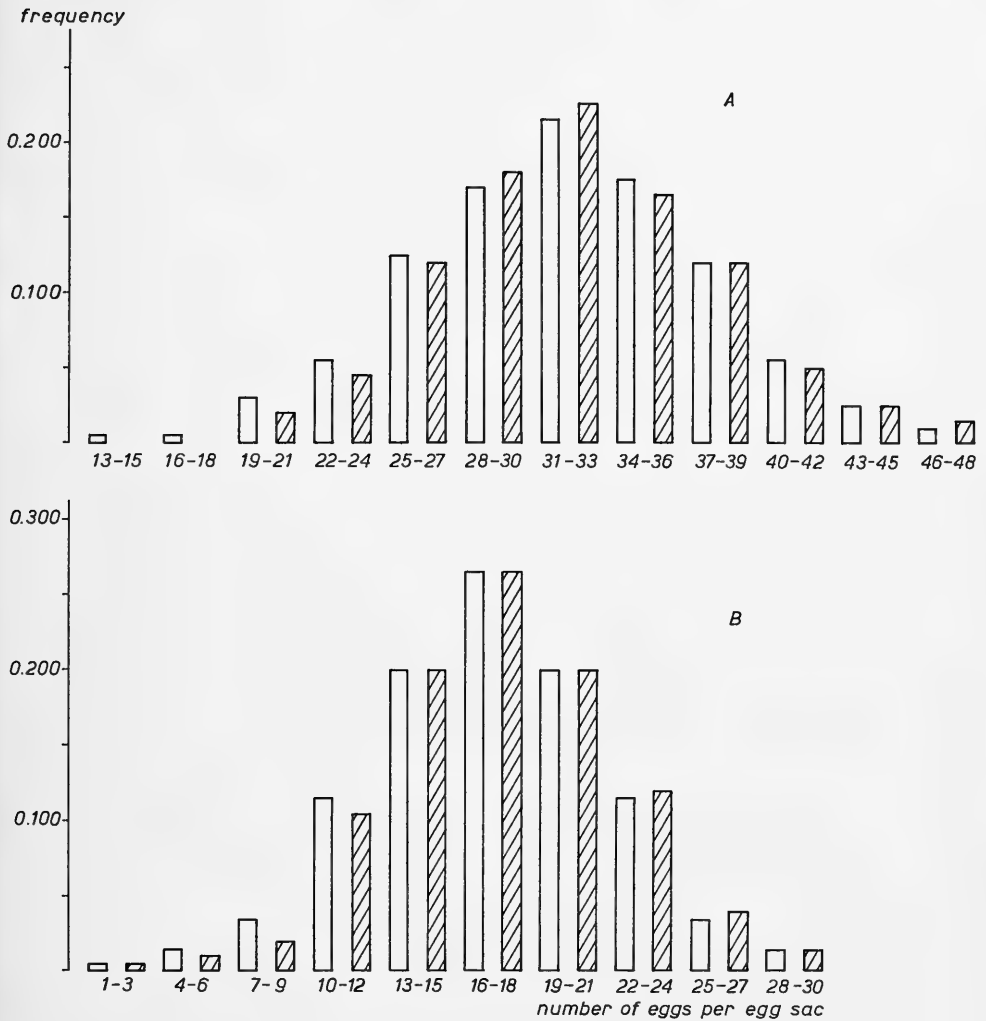
Graph 2. Frequency distributions of the number of parasites per egg sac in A : the first egg sac and B : the second egg sac of *Pardosa nigriceps*

#### Number of larvae per female parasite.

To learn about the egg-potential of *Acolus*, 35 female spiders with a fresh egg sac were put separately in glass tubes, each with a female *Acolus*. This resulted in a mean number of 11.7 parasites per egg sac emerging from 35 egg sacs (minimum 1, maximum 28). The mean number of spider eggs in these egg sacs was 16.4. The frequency is shown in Graph 4.

#### Actual time of parasitizing in the field.

During the period of time when female *Pardosa nigriceps* construct egg sacs some samples were taken to determine the actual time of parasitizing of the egg sacs in the field. Table 15 gives the results. On June 2, when only a fraction of the spiders had their egg sacs already constructed, the percentage of parasitism was relatively low. Very soon afterwards the percentage of parasitism reached a maximum. The mean number of parasites per egg sac in the samples was fairly constant.



Graph 3. Frequency distributions of number of eggs per egg sac: white: parasitized and non-parasitized egg sacs together, hatched: parasitized egg sacs; A = first egg sac, B = second egg sac of *Pardosa nigriceps*

### Conclusions

1. The occurrence of *Acolus krygeri* on the Frisian island Schiermonnikoog is practically restricted to the habitat of *Pardosa nigriceps*: low dunes with a dense vegetation of *Carex arenaria*.

2. In this habitat *Acolus* is able to parasitize both the first and second egg sacs of *P. nigriceps* for about 70%. For the second egg sac of *P. pullata* this percentage is only about 45%.

3. The mean number of parasites in a parasitized egg sac is about 10. This means that

in the first egg sac of *P. nigriceps* about 30% of the spider eggs in a parasitized egg sac contain larvae of *Acolus*, in the second egg sac this percentage is about 60%.

4. As a result of parasitism the first egg sac of *P. nigriceps* yields on the average about 75% of the potential number of spiderlings. For the second egg sac this percentage is about 60%.

Table 13. Ratio ♂/♀ arranged following the number of specimens emerging from one egg sac. The samples are the same as in table 12

Number of parasites emerging	Sample 1 ratio ♂/♀	N	Sample 2 ratio ♂/♀	N
1 — 5	1.667	26	0.941	33
6 — 10	0.238	8	0.889	17
11 — 15	0.427	157	0.327	65
16 — 20	0.537	126	0.300	39

### Discussion

Although there is a wider range of data on *Acolus krygeri*, the relationship between *Acolus* and *Pardosa* remains obscure. No data on the relation between *Acolus* and *Pardosa* are available in literature. It is not clear in the first place whether an egg sac is parasitized only once or more than once by one or by more females of *Acolus*. Considering the results shown in Graph 4 it is evident that one female *Acolus* is able to lay up to 28 eggs (in other experiments even 44 eggs) in one egg sac, but in some cases it parasitizes not more than a single spider egg in an egg sac. These data can explain the wide range of number of parasites per egg sac found in the field.

Table 14. Length of development of *Acolus* larvae under different temperature conditions

Temperature	Length of development in days
20°C	25 — 28
25°C	18 — 21
30°C	12 — 14
35°C	8

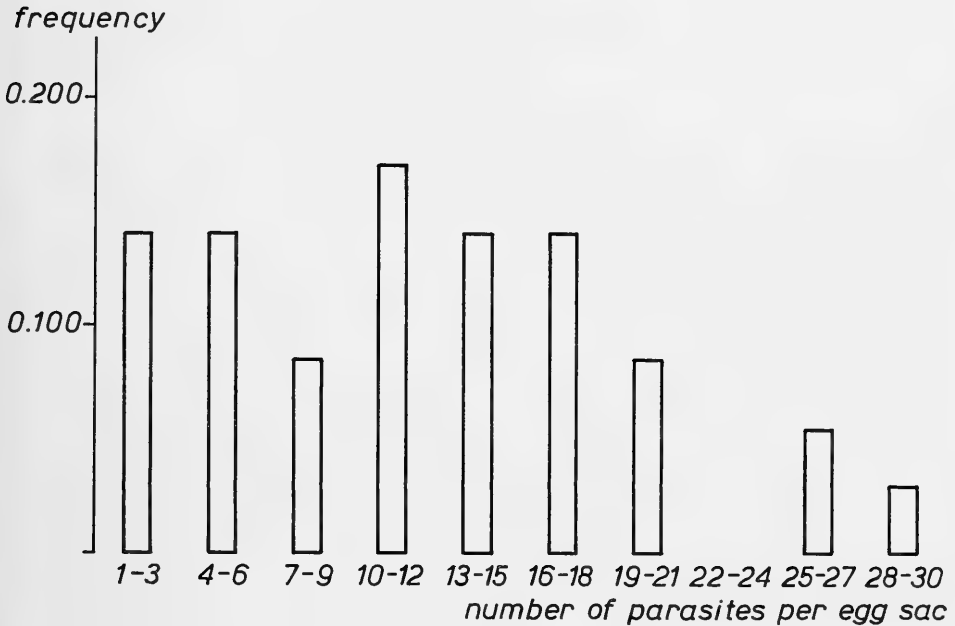
Parasites apparently may discriminate (cf. Salt, 1936) between parasitized and unparasitized hosts. If this is true for *Acolus* then the parasite may consider an egg sac with some parasitized eggs unsuitable and pay no further attention to it. However, it is also possible that the parasite distinguishes only between parasitized and non-parasitized eggs. In that case an egg sac with a few parasitized eggs can be parasitized again by another parasite.

If egg sacs can be parasitized more than once, this may be expected to happen especially when the density of parasites is highest. The data in Graph 1 suggest that in samples with a high degree of parasitism, probably due to a high density of parasites, the egg sacs are parasitized more often than in samples with a relatively low percentage of parasitism. This results in a higher mean number of parasites per egg sac in the former case.

Another problem arises from the fact that sometimes all or nearly all spider eggs in



an egg sac are parasitized. The length of the ovipositor is only 0.4 mm, while the spider eggs measure at least 1 mm. If the eggs are laid directly in the spider eggs, only eggs near the surface of the egg batch can be reached. There are, however, so many egg sacs with all spider eggs parasitized (in the second egg sac of *P. nigriceps* in about 5%



Graph 4. Frequency distribution of number of parasites per egg sac (explanation in text)

of all the cases all eggs are parasitized; in about 10% of the cases all eggs minus 1 are parasitized), that another possibility must be thought of. The explanation might be that the ovipositor is extendable during egg-laying. Or the parasite eggs are laid in or on the egg sac and the larvae crawl inside the egg sac and so settle in a single egg. This latter assumption, however, is highly improbable. In the laboratory experiments the spider eggs were removed from the egg sac immediately after parasitizing and put in paraffin oil. Nevertheless these eggs produced full-grown parasites.

When all samples are considered together, no distinct differences in mean number of parasites per spider egg sac become apparent. No simple explanation can be given for this. We know that the population of parasites is able to attack 60-80% of the spider egg sacs, while they deposite on the average 10 eggs in an egg sac. Furthermore there is evidence, both from field and laboratory observations, that *Pardosa* egg sacs can only be parasitized when they are not more than a few days old. Probably the period during which spider eggs can be parasitized is the limiting factor. However, it cannot yet be understood how this operates in detail.

More data on density of host and parasite are not yet available. In this context it is

Table 15. Percentage of parasitism of *Pardosa nigriceps* egg sacs by *Acolus*. The samples were taken on the same sampling site

Date	Sample size	Number of parasitized egg sacs (between brackets: %)	Mean number of parasites per parasitized egg sac
2-6-70	23	7 (30.4)	9.9 ± 7.95
4-6-70	14	9 (64.3)	8.4 ± 7.25
5-6-70	25	16 (64.0)	10.3 ± 5.19
9-6-70	17	13 (76.5)	12.9 ± 7.66
15-6-70	41	29 (70.7)	11.1 ± 8.07

important that the locomotory activity of female *Pardosa* after egg sac construction is considerably lower than before (Vlijm & Richter, 1966).

Eason et al. (1967) describe an egg parasite: *Idris* spec. (Hymenoptera, Scelionidae) reared from *Pardosa lapidicina* egg sacs.

The incidence of parasitized eggs in the egg sacs ranged from 63% to 94%, an average of 28 parasites per egg sac, which averaged 35 spider eggs. The parasites only attacked egg sacs that were less than 72 hours old and could not be induced to oviposit in a second egg sac. Moreover this parasite could not be induced to oviposit in the egg of any spider other than *Pardosa lapidicina*, not even in those of its congener, *P. milvina*. The larval development of the parasite took 21 to 22 days, which coincided with the length of time that the eggs and first instar spiderlings of *Pardosa lapidicina* remain in the egg sac. The parasites were dependent on the female spider as it had to open the egg sac, otherwise the parasites could not emerge. The authors state: "Presumably most or all of the eggs on the periphery of the mass, those that touch the egg sac covering are parasitized, and those in the centre are spared probably due to the limitation in length of the parasite's ovipositor".

Although there is a general resemblance with our observations on *Acolus krygeri*, there are many differences. A coincidence is that *Idris* spec. as well as *A. krygeri* in general do not parasitize all spider eggs in an egg sac. Eason (1966) established that the female *Pardosa lapidicina* tends to destroy her egg sac at the end of the incubation period if no living spiderlings are ready to emerge. In that case it is important for the parasite to leave part of the spider eggs untouched.

The behaviour of *Pardosa nigriceps* and *P. pullata* towards their egg sac seems to be different from that of *P. lapidicina*. If no living spiderlings emerge at the proper time, the egg sac is abandoned; the parasites can emerge then by biting holes in the wall of the sac.

### 3. The occurrence of *Acolus krygeri* and *Gelis* spec. together

In 1968 a number of egg sacs were collected, that contained *Acolus krygeri* and *Gelis* spec. together. In total 15 egg sacs (9 of *P. nigriceps* and 6 of *P. pullata*) contained *Gelis* larvae. Ten of these (66.7%) contained both *Gelis* and *Acolus* larvae. The mean number of *Gelis* larvae per egg sac was 1.9, the mean number of *Acolus* larvae was 11.5. In the egg sacs with *Gelis* larvae alone the mean number of larvae was 2.2. No spiderlings were found in the egg sacs. As indicated before, the mean number of larvae in egg sacs with *Acolus* alone is about 10.

### Conclusions

1. In the group of egg sacs parasitized by *Gelis* the percentage of parasitism by *Acolus* is comparable with the percentage of parasitism in the whole of egg sacs. This means that *Gelis* is not able to recognize an egg sac already parasitized by *Acolus*, or vice versa.

2. It seems that the larvae of *Gelis* cannot consume spider eggs already parasitized by *Acolus*, for when there were spider eggs left in the sacs, these were in all cases parasitized by *Acolus*.

### GENERAL DISCUSSION

Some aspects of the biology of both parasites (*Gelis* and *Acolus*) had little or no attention in our studies. Problems of hibernation, density and the successive generations have not been dealt with. "The wealth of material concerning spider parasites is composed principally of brief and incomplete accounts which are widely scattered in the literature" (Eason et al., 1967).

The present study as a whole can be seen as an attempt to study the relation between egg parasites and spiders more closely. This is only possible when there is at least a substantial knowledge about the biology of one of the partners in this relationship. In our department much work has been done on the biology of *Pardosa* spiders, and therefore, from our knowledge of spider species, we gained some insight in the biology of the parasites. It is evident that knowledge about spider parasites may help to understand the biology of the spiders.

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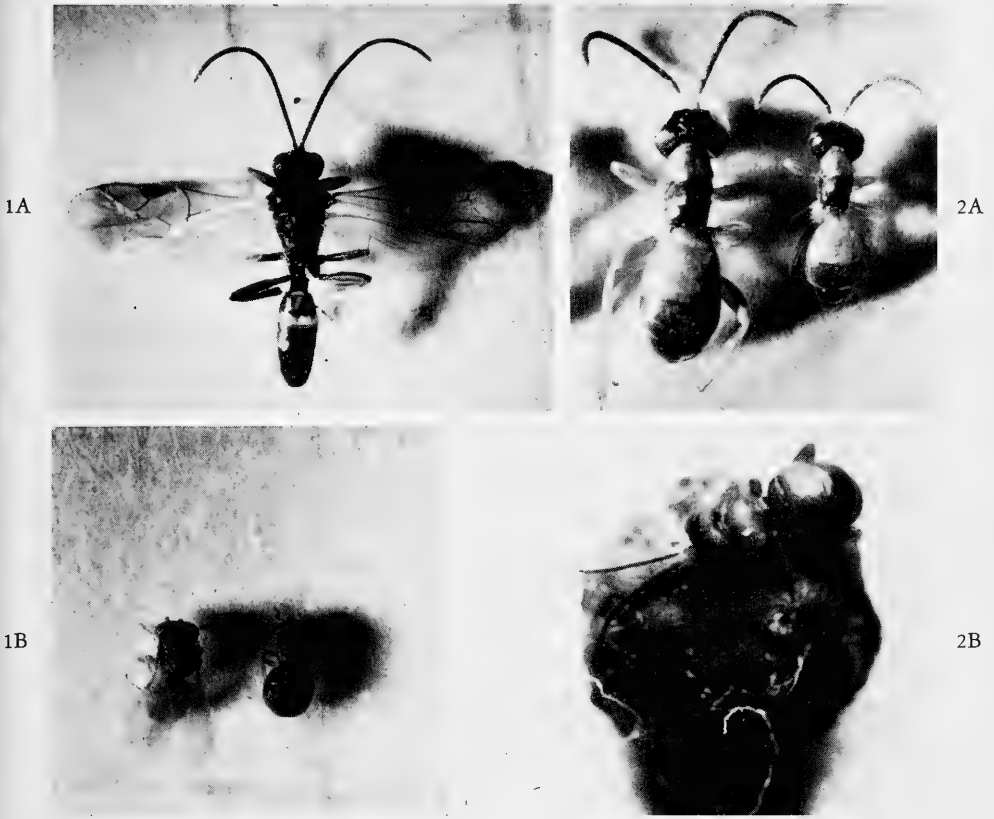


Plate 1. Hymenopterous parasites from *Pardosa* egg sacs. A 1, *Gelis* sp. male: A 2, Females of *Gelis* sp.; B 1, *Acolus krygeri*, male and female; B 2, Female *Gelis* parasitizing an egg sac

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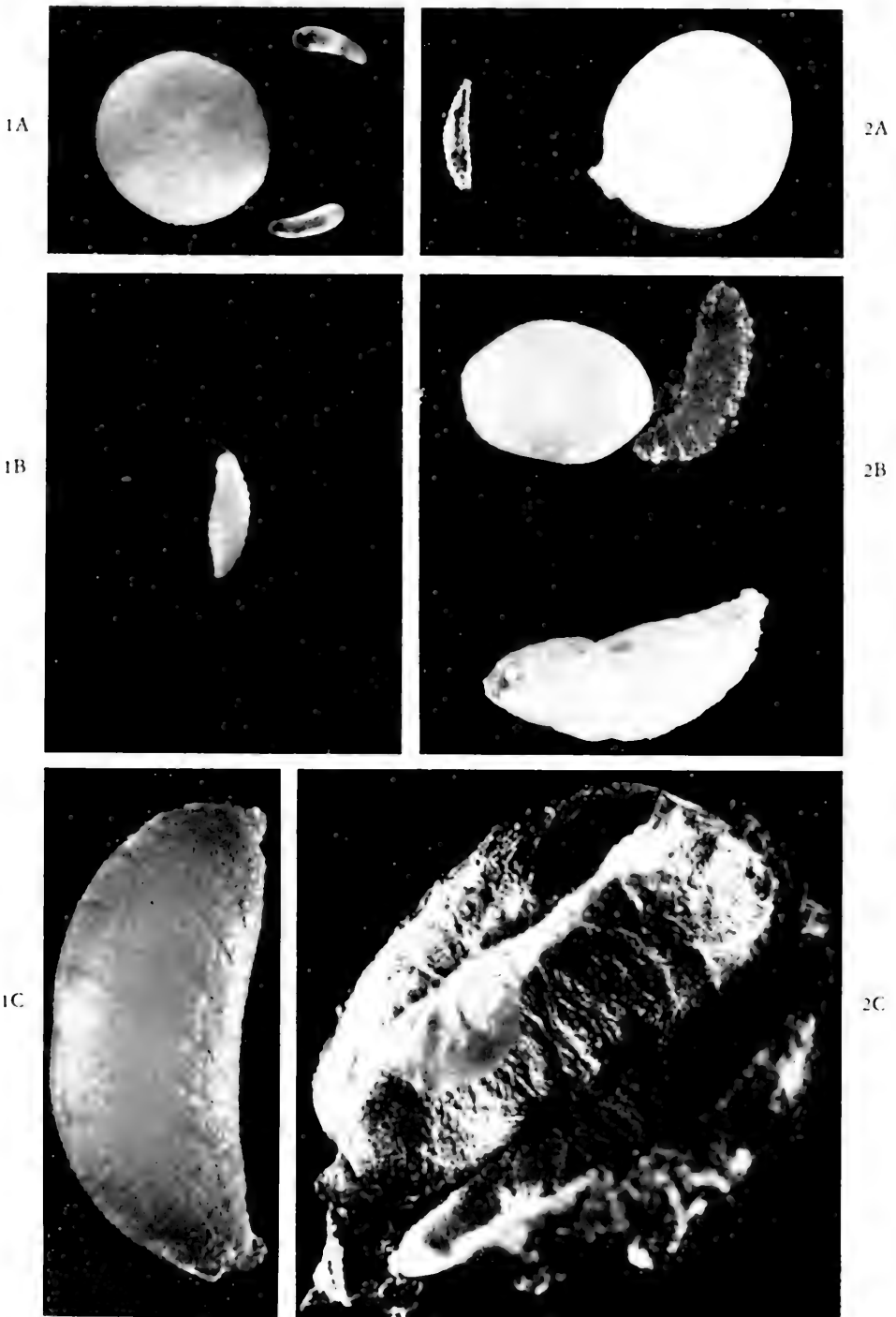


Plate 2. Development of *Gelis* sp. larvae. 1 A, Spider egg with two *Gelis* eggs; 2 A, 1 B, 2 B, Successive stages of active *Gelis* larva; 1 C, Prepupa; 2 C, *Gelis* pupae inside a spider egg sac, the covering of the egg sac is partly removed

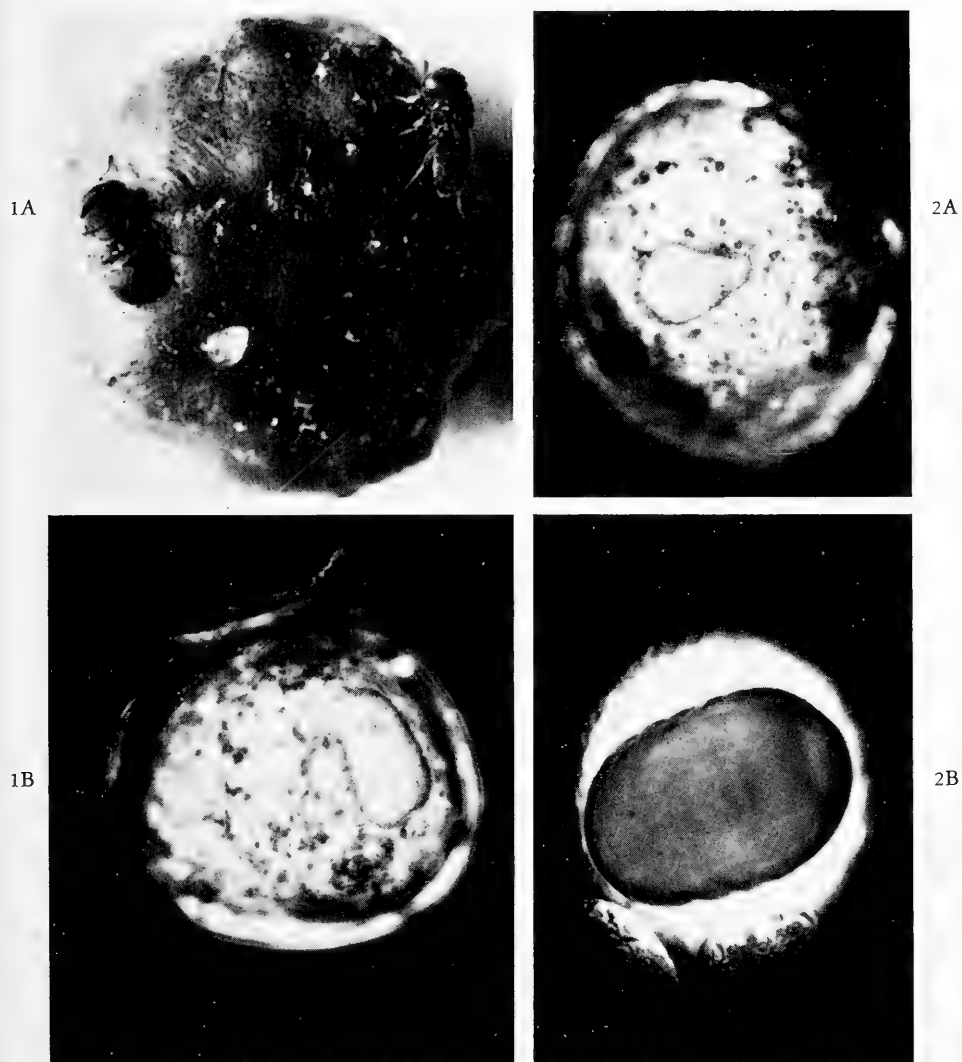


Plate 3. *Acolus krygeri*. 1 A, Female parasitizing a spider egg sac; 2 A, First stage larva of *Acolus* inside a spider egg; 1 B, Second stage larva of *Acolus* 2 B, Prepupa of *Acolus*





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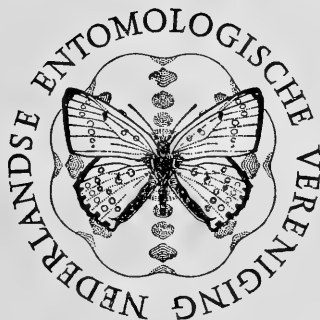
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## PARASITIC MITES OF SURINAM

### XI. FOUR NEW SPECIES OF THE GENUS PSORERGATOIDES FAIN, 1959, (PSORERGATIDAE: TROMBIDIFORMES)<sup>1)</sup>

by

F. S. LUKOSCHUS <sup>2)</sup>,

P. G. ROSMALEN <sup>2)</sup>,

and

A. FAIN <sup>3)</sup>

#### ABSTRACT

Four new species of genus *Psorergatoides* Fain, 1959, itch mites of bats are described and figured in detail. *P. glossophagae* sp. n. was collected from *Glossophaga soricina*; *P. indicicola* sp. n. from *Saccopteryx bilineata* and *S. canescens*; *P. artibeii* sp. n. from *Artibeus lituratus fallax* and *P. molossi* sp. n. from *Molossus molossus* and *M. ater*. The most important data for all the known species of the genus are given in several tables. Histological investigations indicate low grade pathogenicity. Host-parasite list is added.

#### INTRODUCTION

This study is a continuation of investigations on Psorergatidae, itch mites of bats from Europe, Africa, Venezuela, New Guinea, and Burma (Fain, 1959a, b, Lukoschus, 1967).

In observations of Surinam bats one of us (F.L.) succeeded in finding new species, deviating in many characteristics from those of the Old World. They are described below.

#### 1. *Psorergatoides glossophagae* spec. nov.

**F e m a l e** (holotype): Shape of body as in other species of genus. Length including gnathosoma 172  $\mu$ , average for 20 paratypes measured 177  $\mu$  (166—191), width 151  $\mu$ , in paratypes  $\emptyset$  153  $\mu$  (143—179). **V e n t e r** (Fig. 1). Cuticle soft. Epimerae I and II fused. Ventral setae (*v s*) 5—6  $\mu$ , distance between ventral setae 15  $\mu$  (15—20). Genital opening (*V u*) 10  $\mu$ , lying between two adanal lobes, each of which carries a pair of terminal setae (*t s*) of 24  $\mu$  (20—25). The legs are inserted ventrolaterally. Legs with five free segments. All trochanters (*T r*) have a small ventral spur, more sclerotized than basal part of segment, and one seta of 8  $\mu$ . Femora (*F e*) of all legs with small prominent ventral spur and only one posterolateral seta of 12  $\mu$  on femora I—III, and 14  $\mu$  on femur IV. Genua (*G*) with a very small postero-lateral seta. Tibiae (*T i*) with a club-like spine antero-ventrally (Fig. 2) and dorso-median seta (Fig. 3). Tarsi (*T a*) with a 16  $\mu$  long dorso-anterior (*d a*) and 16  $\mu$  long dorso-posterior seta (*d p*). Spines on tarsi two-

<sup>1)</sup> Investigation conducted by Dr F. Lukoschus with the aid of Grant W 83—1 by the Netherlands Foundation for the Advancement of Tropical Research (WOTRO).

<sup>2)</sup> Zoological Institute, Catholic University of Nijmegen, the Netherlands.

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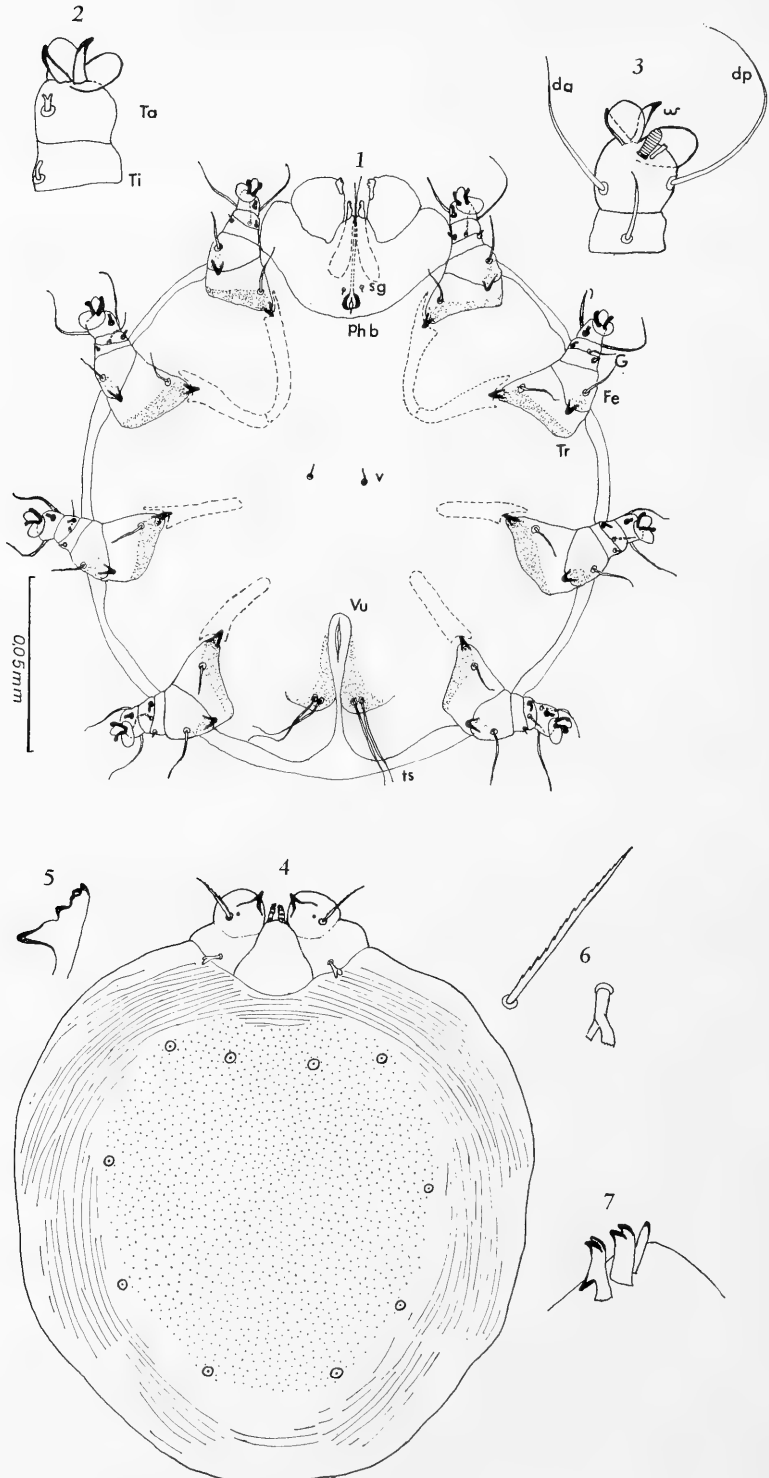


Fig. 1—7. *Psorergatoides glossophagae* sp. n. Female. 1, holotype ventrally; 2, leg I tarsus and tibia ventrally; 3, leg I dorsally; 4, holotype dorsally; 5, chelicera of a squashed paratype in lateral view; 6, gnathosoma and palptibia setae; 7, palptarsus of a squashed paratype

pointed. Two one-pointed claws and two-lobed empodium are inserted ventrally to the end of tarsi. Tarsi I and II dorsally with two solenidia (*w*), the dorsomedial bulbous, lateral solenidion lying inside a fold of the epidermis. *Dorsum* (Fig. 4). Dorsal shield sclerotized and distinctly punctured, soft parts striated. Length of dorsal shield  $117\ \mu$ , in paratypes  $\emptyset 118\ \mu$  (110—124), width  $103\ \mu$ , paratypes  $\emptyset 103\ \mu$  (99—106). Four pairs of point-like lateral setae and a pair of antero-paramedian setae on the shield. *Gnathosoma* ventrally with short subgnathosomal setae (*sg*) in front of an oval-shaped pharyngeal bulb, dorsally with two-lobed, dentated  $5\text{--}6\ \mu$  long gnathosoma setae (Fig. 6). Palps two-segmented. Palptibia dorsally with a strong  $16\ \mu$  saw-like posterior seta, point-like anterior seta and conical dorsal spur. Palptarsus with two claws and a spine (Fig. 7) inserted medio-ventrally. Chelicerae with dentated digitus fixus (Fig. 5) directed dorsally and stinging bristles.

**Male (allotype):** Shape and body like in other *Psorergatoides*-species. Length including gnathosoma  $170\ \mu$ , average in 20 paratypes  $169\ \mu$  (156—179), width  $135\ \mu$ , in paratypes  $\emptyset 131\ \mu$  (117—140). *Venter* (Fig. 8). Like female, but with only one median tubercle without terminal setae. Setation of legs somewhat shorter than in female, measurements in table II. *Dorsum* (Fig. 9). Dorsal shield sclerotized and distinctly punctured with median longitudinal furrow behind genital opening. Four pairs of point-like lateral setae evenly spaced along lateral border of shield and two pairs of short setae near genital opening, anterior pair  $8\ \mu$  apart, posterior  $8\ \mu$  apart. Penis simple, pointed,  $24\ \mu$  long, in paratypes  $\emptyset 24\ \mu$  (19—29); penis sheath  $13\ \mu$ , in paratypes  $13\text{--}16\ \mu$ .

### Developmental stages

**Egg:** Thin-shelled, almost round  $\emptyset 104\ \mu$  (97—111).

**Larva** (Fig. 10): Disc-shaped with three pairs of two-segmented legs. Length average in 9 specimens measured  $120\ \mu$  (104—143), width  $\emptyset 109\ \mu$  (97—127). Cuticle soft, in some specimens with indistinct irregular striation. Epimerae short, indistinct, trochanters without ventral spur, segments femur to tarsus fused, forming a flattened unit with two trifid claws. Ventro-posterior spur of this unit is homologous with femoral spur of adults. Gnathosoma (Fig. 11) almost as large as in adults with palptibia seta of  $8\ \mu$ .

**Protonymph** (Fig. 12): Length including gnathosoma (measurements of 6 specimens)  $\emptyset 111\ \mu$  (94—123), width  $\emptyset 96\ \mu$  (89—114). Disc-shaped like larva, but with four pairs of two-segmented legs. Gnathosoma (Fig. 13) with  $10\ \mu$  long palptibia seta.

**Deutonymph** (Fig. 14): Length (measurements of 3 specimens)  $\emptyset 150\ \mu$  (142—163), width  $121\ \mu$  (116—114). Legs I and II with distinct solenidia. Gnathosoma (Fig. 15) with palp-tibia seta of  $12\ \mu$ .

**Type host:** *Glossophaga soricina* (Pallas, 1766).

**Type locality:** Leonsberg, Surinam, 27.XII.1969.

**Pathology:** The mites live in the epidermis of the wing, causing hyperkeratosis and hypertrophy of connective tissues. Parasitized places of wing membrane are uncoloured, thickened and not foldable.

**Deposition of types:** Holotype ♀ and allotype ♂ in Rijksmuseum van Natuurlijke Historie Leiden, coll. nr P 1222—3. Paratype ♀ and ♂: Muséum National d'Histoire Naturelle, Paris, coll. nr 55 J 6—7; British Museum (Natural History) Lon-

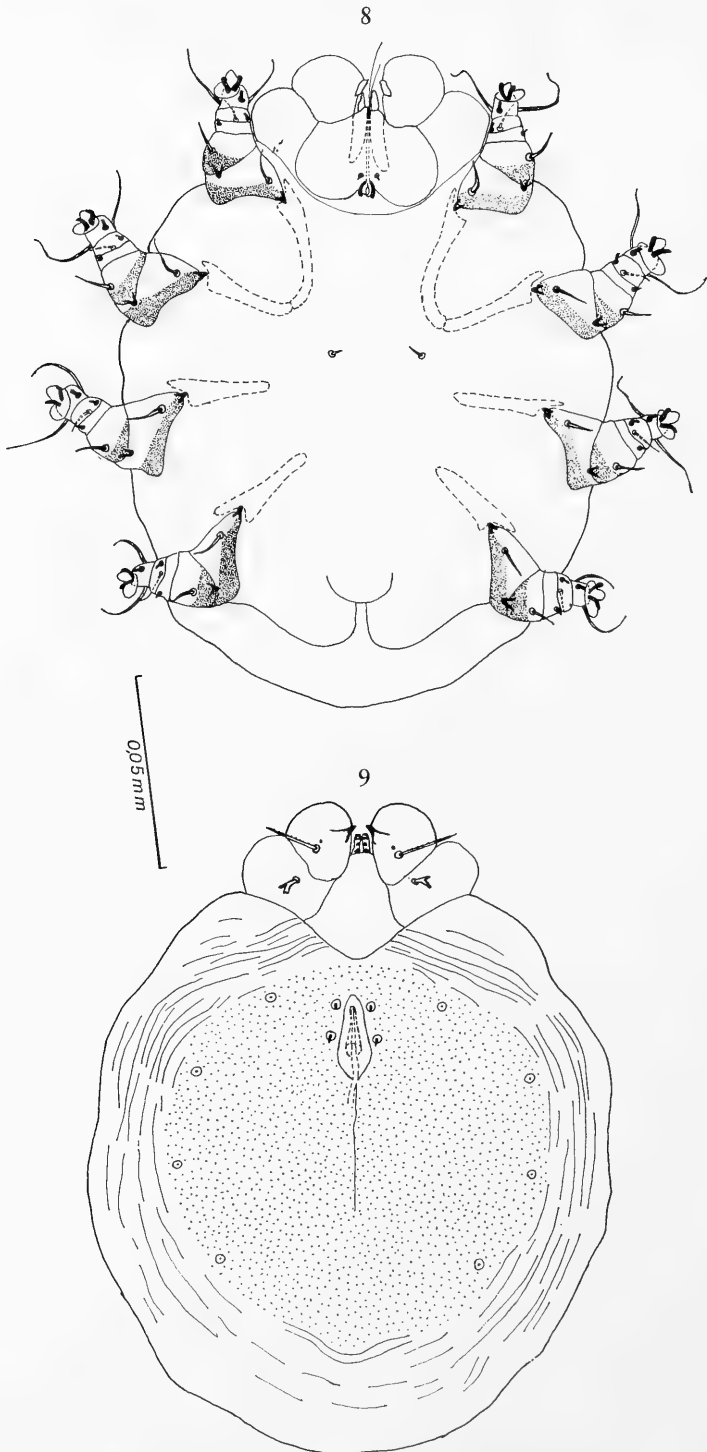


Fig. 8—9. *Psorergatoides glossophagae* sp. n. Male. 8, allotype ventrally and 9, dorsally



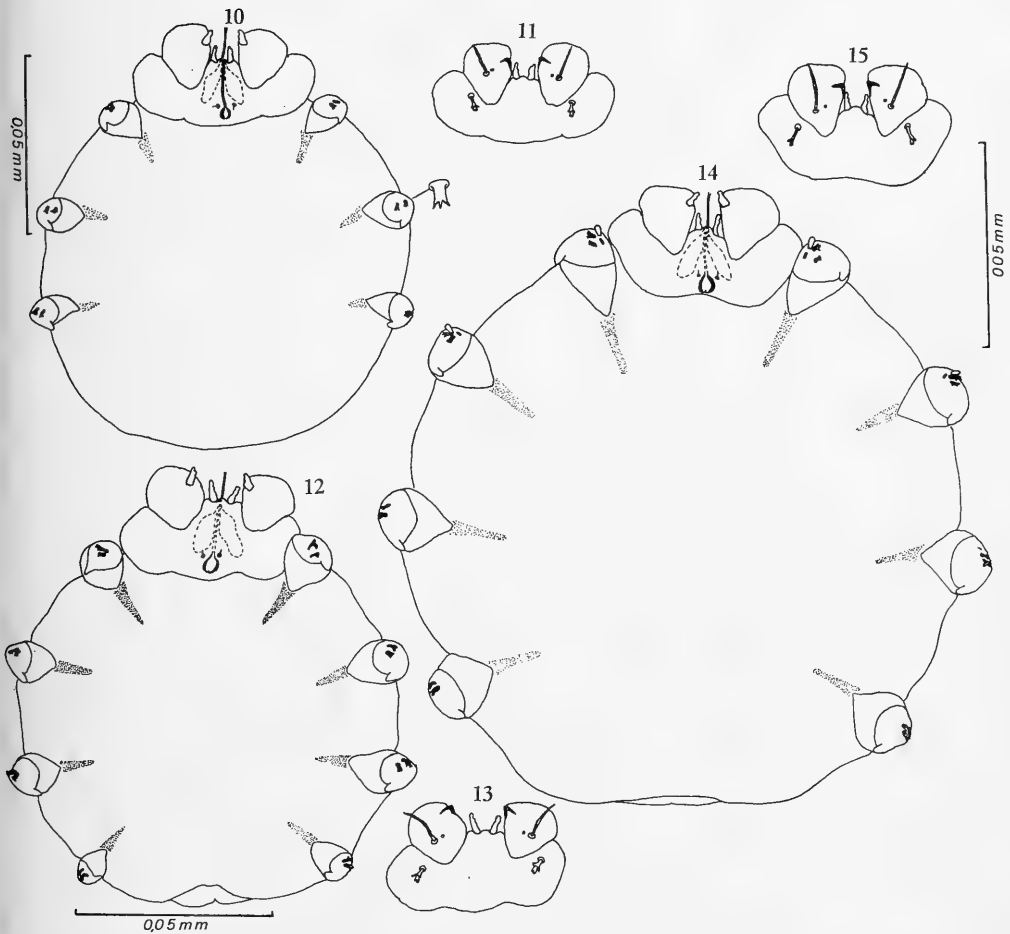


Fig. 10—15. *Psorergatoides glossophagae* sp. n., developmental stages. 10, Larva ventrally; 11, gnathosoma of larva dorsally; 12, protonymph ventrally; 13, gnathosoma of protonymph dorsally; 14, deutonymph ventrally; 15, gnathosoma of deutonymph dorsally

don, coll. nr 1971/169—170; National Collection of Surinam, Paramaribo; Field Museum of Natural History, Chicago; Institute of Acarology, Columbus, Ohio; Smithsonian Institution, U.S. National Museum, Washington; Institut Pasteur, Cayenne 71.04—05.06; Institut de Médecine Tropicale Prince Léopold, Antwerpen; Zoologisches Staatsinstitut und Zoologisches Museum, Hamburg A 28/71; Zoologisch Laboratorium, Nijmegen.

2. *Psorergatoides indicicola* spec. nov.

Female (holotype): Shape like in other species of genus *Psorergatoides*, however remarkable by the two-pointed tarsal claws and the absence of ventral setae, genu setae and spine of tibiae. Length including gnathosoma 177  $\mu$ , average in 20 paratypes 170  $\mu$  (156—186), width 149  $\mu$ , in paratypes  $\varnothing$  144  $\mu$  (136—154). Venter (Fig. 16). Cuticle soft, unstriated. Epimerae I straight without connection to epimerae II. Ventral

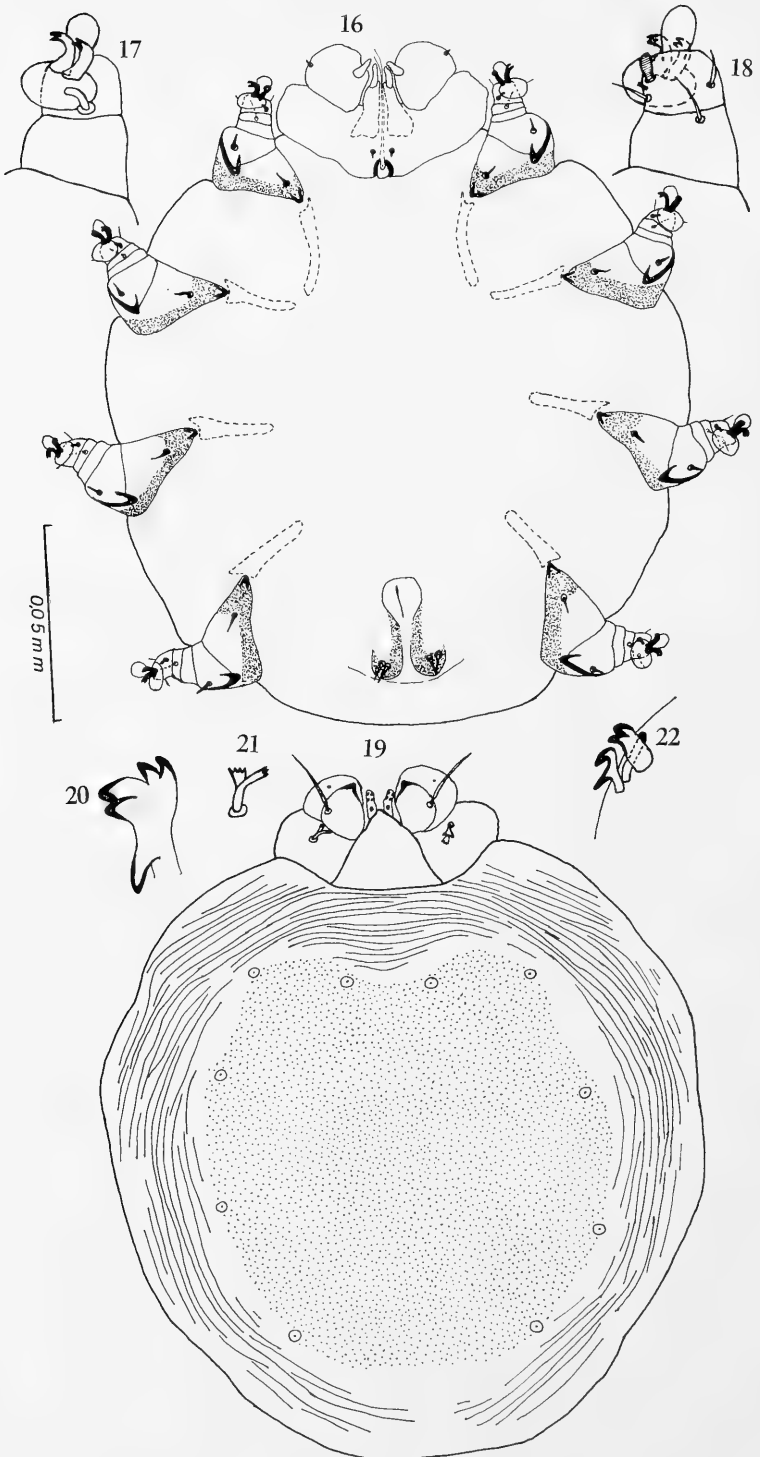
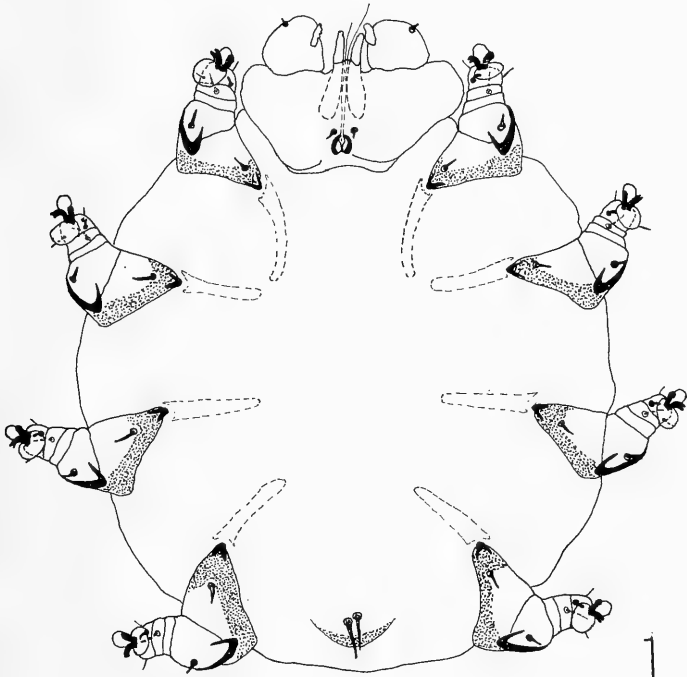


Fig. 16—22. *Psorergatoides indicicola* sp. n. Female. 16, holotype ventrally; 17, leg I ventrally; 18, leg I dorsally; 19, holotype dorsally; 20, chelicera of a squashed paratype in lateral view; 21, gnathosoma seta; 22, palptarsus of a squashed paratype

23



24

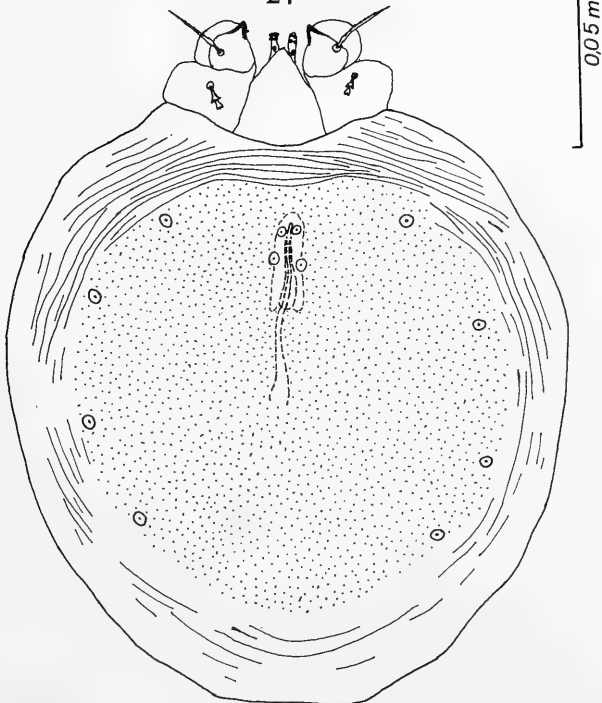


Fig. 23—24. *Psorergatoides indicicola* sp. n. Male. 23; allotype ventrally; 24, dorsally

setae lacking in all paratypes. Trochanteres with very small ventral spur and short ( $4 \mu$ ) seta. Femora with distinct ventrolateral spur and one seta of  $3-4 \mu$ . All genera without seta. Tibiae without spine and  $4 \mu$  long dorsal seta (Fig. 17, 18). Tarsi with short setae *d a* 4, *d p* 4, club-shaped tarsal spine (without two points, as usual in genus). Tarsal claws distinctly two-pointed, two-lobed empodium and two solenidia on tarsi I and II. Vulva  $10 \mu$  between two adanal lobes, each carrying a pair of very short ( $4-6 \mu$ ) terminal setae. Dorsum (Fig. 19). Dorsal shield sclerotized and punctured with encaved anterior border. Shield length  $119 \mu$ , in paratypes  $\emptyset 112 \mu$  ( $102-124$ ), width  $108 \mu$ , in paratypes  $104 \mu$  ( $94-113$ ). Five pairs of point-like setae almost evenly spaced along lateral and anterior border. Soft parts of dorsum striated. Gnathosoma like in *P. glossophagae*. Gnathosoma setae (Fig. 21) bilobed with dentated borders,  $6 \mu$ , palptibia seta saw-like  $18 \mu$ . Palptarsi with two two-pointed claws and a blunt spine (Fig. 22). Chelicerae with five-pointed dorsally directed digitus fixus (Fig. 20) and stinging bristles.

Male (allotype) (Fig. 23): Shape like female, but one subterminal sclerotized tubercle with two terminal setae. Length including gnathosoma  $150 \mu$ , width  $130 \mu$ . 20 paratypes measured length  $\emptyset 154 \mu$  ( $143-166$ ), width  $126 \mu$  ( $105-140$ ). Measurements in table II. Dorsum (Fig. 24). Genital opening surrounded by unpunctured shield with two pairs of genital setae. Distance anterior setae  $3 \mu$ , posterior setae  $7 \mu$ . Pointed penis of  $43 \mu$  ( $34-51$ ) with sheath of  $18-22 \mu$ .

Developmental stages like in *P. glossophagae* but larvae and nymphs without femoral spurs.

Egg: almost globular, average of 6 measurements  $103 \mu$  ( $95-116$ ).

Larva: length  $\emptyset$  of 8 specimens  $111 \mu$  ( $93-122$ ), width  $\emptyset 96 \mu$  ( $81-107$ ).

Protonymph: length  $\emptyset 136 \mu$  ( $127-145$ ), width  $\emptyset 109 \mu$  ( $104-119$ ) (6 specimens).

Deutonymph: length  $\emptyset 158 \mu$  ( $150-168$ ), width  $\emptyset 133 \mu$  ( $127-145$ ) (5 species).

Type host: *Saccopteryx canescens* (Thomas, 1901).

Type locality: Lelydorp, Surinam, 25.II.1970.

Pathology: The mites were found only within epidermis around the end of second digit. Epidermis was found uncoloured and strongly thickened.

Deposition of types: Holotype and allotype: Leiden coll. nr P 1224-5. Paratypes: Paris coll. nr 55 J 8-9; London coll. nr 1971/152-3, Hamburg A 30/71; Washington; Antwerpen, Cayenne 71.07, 08, 09, 010, Columbus, Chicago, Paramaribo, Nijmegen.

Specimens from *Saccopteryx bilineata*: On four specimens of the closely related species *Saccopteryx bilineata* (Temminck, 1838) also at the end of the second digit mites were found, which morphologically cannot be separated from *Psorergatooides indicicola*. Measurements for comparison are given in table III. We consider them to be conspecific.

### 3. *Psorergatooides artibeii* spec. nov.

Female (holotype): General shape like *P. glossophagae*, but with remarkable long tarsal setae and extremely long setae on tibia I in females. Length including gnathosoma  $156 \mu$ , in 17 paratypes measured  $\emptyset 151 \mu$  ( $133-179$ ), width  $127 \mu$ , in paratypes  $\emptyset 119 \mu$  ( $108-143$ ). Venter (Fig. 25). Cuticle soft, epimerae I slightly bowed outwards, not connecting with epimerae II. The pair of ventral setae ( $5-6 \mu$ ) very variable in distance

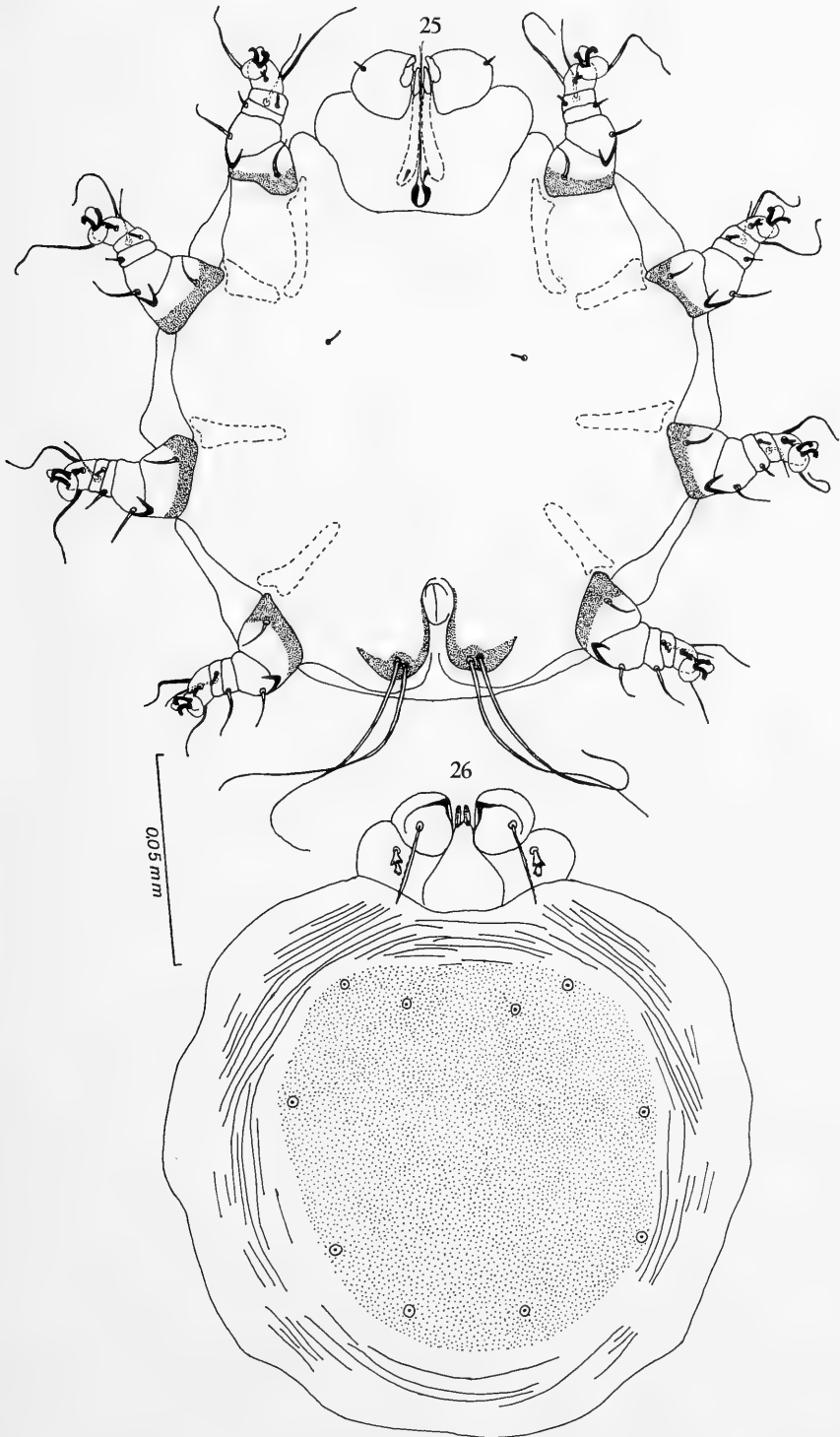


Fig. 25—26. *Psorergatoides artibei* sp. n. Female. 25, holotype ventrally and 26, dorsally

15—60  $\mu$ . Oval two-valved vulva between more sclerotized adanal lobes, which carry the pairs of terminal setae (60—70  $\mu$ ). Trochanteres with seta of 9  $\mu$  without ventral spur. Femora with ventro-posterior seta of same length (11  $\mu$ ) on all legs, and distinct ventro-posterior spur. Genua with posterior seta 15  $\mu$  on genu IV, 6—8  $\mu$  on genera I—III. Tibiae with a club-like ventral spine and dorso-medial seta of different length 20  $\mu$  on leg I, 12  $\mu$  on legs II—IV. Tarsi with two-pointed spine, up to 30  $\mu$  long dorsal setae, two-pointed claws and bilobed empodium. Tarsi I and II with bulbous median sclenidion and a smaller one within duplication of epidermis (Fig. 31—32). Dorsum (Fig. 26). Dorsal shield sclerotized and punctured. Length 110  $\mu$ , in paratypes  $\emptyset$  104  $\mu$  (94—121), width 99  $\mu$ , in paratypes  $\emptyset$  95  $\mu$  (81—101). Point-like anterior paramedian setae distinct behind level of first pair of lateral setae. Soft parts of dorsum weakly striated. Gnathosoma like in other species. Gnathosoma setae (Fig. 33) two-lobed, both lobes deeply incised, palptibiae setae 19  $\mu$  long saw-like, palptarsus (Fig. 28) with two strongly sclerotized claws and a blunt spine. Digitus fixus of chelicerae (Fig. 29) saw-like dentated with two stronger anterior spines.

Male (allotype): Length including gnathosoma 158  $\mu$ , in 8 paratypes measured  $\emptyset$  144  $\mu$  (127—161), width 119  $\mu$ , in paratypes  $\emptyset$  114  $\mu$  (99—122). Venter (Fig. 27). Like female, but with median transverse subterminal sclerite without terminal setae. Setae on tibia I (15  $\mu$ ) longer than that on tibia IV (9  $\mu$ ). Measurements in table II. Dorsum (Fig. 30). Genital opening oval, relatively far behind posterior border of dorsal shield, 4—5  $\mu$  long. There are two pairs of genital setae equally distant from each other (12  $\mu$ ). Penis pointed 30  $\mu$  (26—32), penis sheath 16—20  $\mu$ . Dorsal shield 102  $\mu$  long,  $\emptyset$  97  $\mu$  in paratype (90—110  $\mu$ ), and 88  $\mu$  wide, in paratype  $\emptyset$  83  $\mu$  (82—90). Gnathosoma like female.

#### Developmental stages:

Egg: Almost globular, average of 3 measurements 109  $\mu$  (101—116).

Larva: Length  $\emptyset$  of 3 specimens 120  $\mu$  (110—133), width  $\emptyset$  92  $\mu$  (87—113).

Protonymph: Length  $\emptyset$  of 3 specimens 135  $\mu$  (127—145), width 114  $\mu$  (107—122).

Deutonymph: Length  $\emptyset$  of 3 specimens 146  $\mu$  (143—148), width  $\emptyset$  121  $\mu$ .

Type host: *Artibeus lituratus fallax* (Peters, 1865).

Type locality: Paramaribo, Surinam, 7.XII.1969.

Pathology: Mites were found within epidermis of outside of ears, causing hyperkeratosis.

Deposition of types: Holotype and allotype in Leiden, coll. nr P 1226—7; paratypes Paris, coll. nr 55 J 4—5; London 1971/167; Hamburg, coll. nr A 31/71; Washington, Antwerpen, Cayenne 71.01, 02, 03, Columbus, Chicago, Paramaribo, Nijmegen.

#### 4. *Psorergatoides molossi* spec. nov.

Female (holotype): Length including gnathosoma 115  $\mu$ , in 20 paratypes measured  $\emptyset$  120  $\mu$  (115—124), width 96  $\mu$ , in paratypes  $\emptyset$  101  $\mu$  (92—117). Venter (Fig. 34). Cuticle soft. Epimerae I widely separated from epimerae II. Ventral setae 2—3  $\mu$ , lying 14  $\mu$  (12—16) apart. Vulva 8  $\mu$  between adanal lobes carrying pairs of terminal setae of 34  $\mu$  (32—40) length. Legs relatively short with complete but short setation. Trochanteres without ventral spur, femora with distinct small spur and only 2  $\mu$  long almost spine-like seta. Genua with spine-like seta (1—2  $\mu$ ). Tibiae with short (4  $\mu$ )

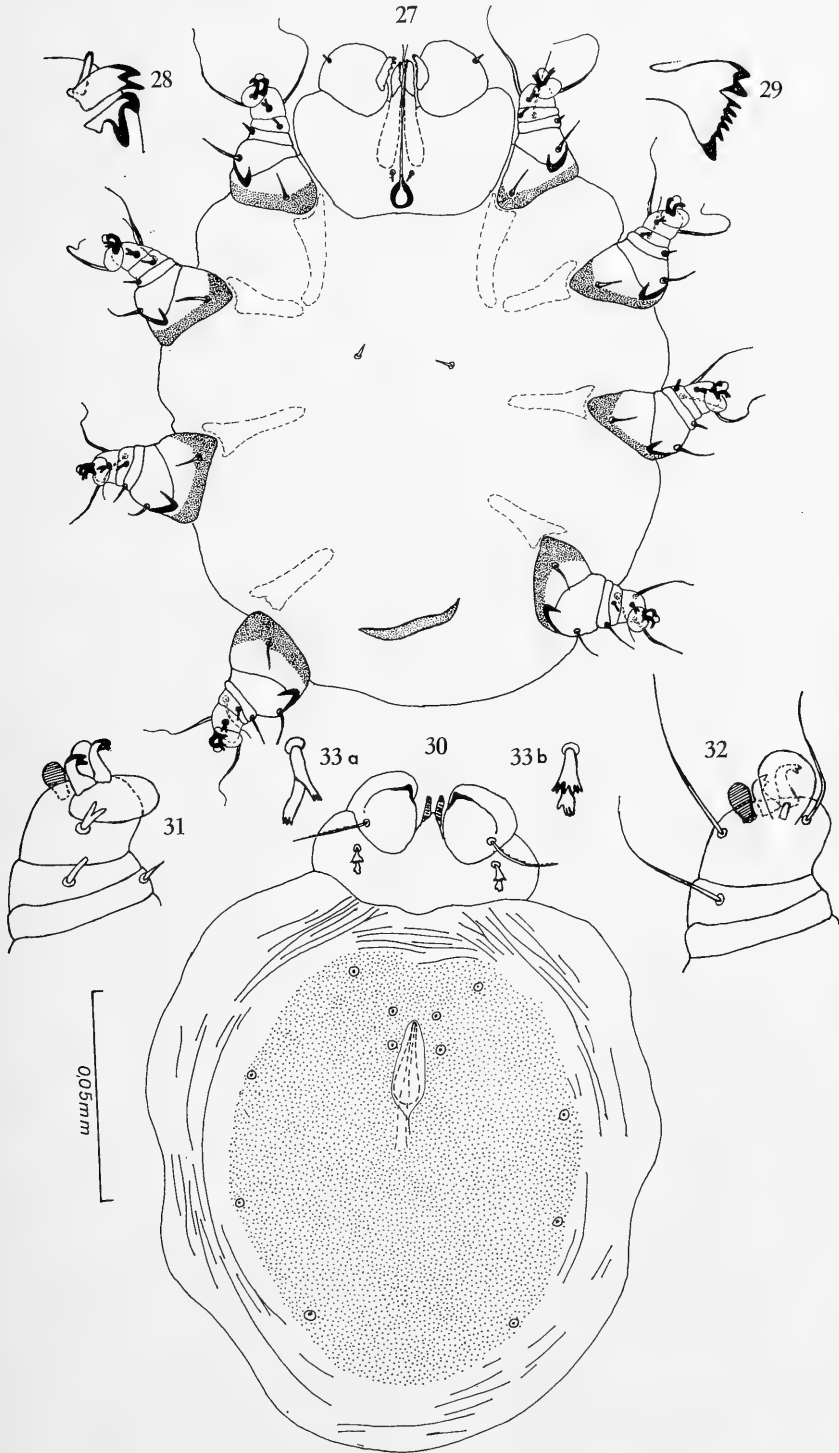


Fig. 27—33. *Psorergatoides artibeii* sp. n. Male. 27, allotype ventrally; 28, palptarsus of a squashed paratype; 29, chelicera of a squashed paratype in ventral view; 30, allotype dorsally; 31, leg I ventrally; 32, leg I dorsally; 33, a, gnathosoma seta in lateral view; 33, b, in dorsal view

dorsal seta and a club-like lateral spine. Tarsi with a two-pointed spine, short dorsal setae (Fig. 37, 38), a bilobed empodium and two simple claws. Tarsi I and II with two solenidia: median bulbous, lateral within duplication of epidermis. Dorsum (Fig. 35). Almost round sclerotized and punctured dorsal shield with encaved anterior border. Shield length  $81 \mu$ , in paratypes  $\varnothing 80 \mu$  (76—83), width  $78 \mu$ , average  $80 \mu$  (78—83). Five pairs of point-like setae. Soft parts of dorsum distinctly striated. Gnathosoma with furcate, deeply incised gnathosoma setae (Fig. 41). Palptibia with broad dorsal spur,  $14 \mu$  long saw-like posterior seta and point-like anterior seta. Palptarsus with two two-pointed claws and a blunt spine (Fig. 42). Digitus fixus of chelicerae (Fig. 40) saw-like with two larger anterior teeth.

Male (allotype): Length including gnathosoma  $108 \mu$ , in 20 paratypes measured  $\varnothing 101 \mu$  (92—117), width  $80 \mu$ , average  $91 \mu$  (80—105). Venter (Fig. 36). Like female, but without subterminal median protuberant tubercle or sclerite, without terminal setae. Dorsum (Fig. 39). Dorsal shield with longitudinal furrow, length  $73 \mu$ , in paratypes  $\varnothing 69 \mu$  (64—81), width  $69 \mu$  (62—69). Genital opening between squarely arranged pairs of genital setae, distance between anterior setae  $8 \mu$ , between posterior  $5 \mu$ . Penis of  $21 \mu$  (18—25), penis sheath  $11 \mu$  (10—15).

Developmental stages: like *P. glossophagae* but without femoral spur.

Egg: Almost globular, average of 7 specimens  $80 \mu$  (70—93).

Larva: Measurements of 10 specimens length  $\varnothing 101 \mu$  (89—110), width  $90 \mu$  (71—101).

Protonymph: Measurements of 5 specimens length  $\varnothing 99 \mu$  (96—104), width  $92 \mu$  (81—97).

Deutonymph: Measurements of 10 specimens, length  $\varnothing 117 \mu$  (106—132), width  $109 \mu$  (94—133).

Type host: *Molossus molossus* (Pallas, 1766).

Type locality: Lelydorp, Surinam, 11 hosts parasitized 30.XI.1969—13.II.1970.

Pathology: Mites were found within the epidermis of inner and outside of ears, on dorsal surface of wing membrane and tail membrane, and on feet and tail. They cause hyperkeratosis, thickening of wing membrane causing impossibility to fold parasitized parts.

Deposition of types: Holotype and allotype in Rijksmuseum van Natuurlijke Historie, Leiden, coll. nr P 1228—9. Paratypes ♂ and ♀. Paris, coll. nr 55 J 10—11; London, coll. nr 1971/150—1; Hamburg A 38/71; Washington, Antwerpen, Columbus, Chicago, Cayenne, 71.11, 12, 13, 14. Paramaribo, Nijmegen.

Specimens from *Molossus ater*: On three bats of the closely related species *Molossus ater* Geoffroy, 1805 from the place Lelydorp, mites were found, which morphologically cannot be separated from *P. molossi*. Measurements for comparison are given in table IV. We consider the mites from the two host species to be conspecific.

#### Comparison with related species

Instead of a key for determination we give measurements and characteristics, tabulated (Table I, II). Males of *P. nycteris* and *P. laviae* are unknown.



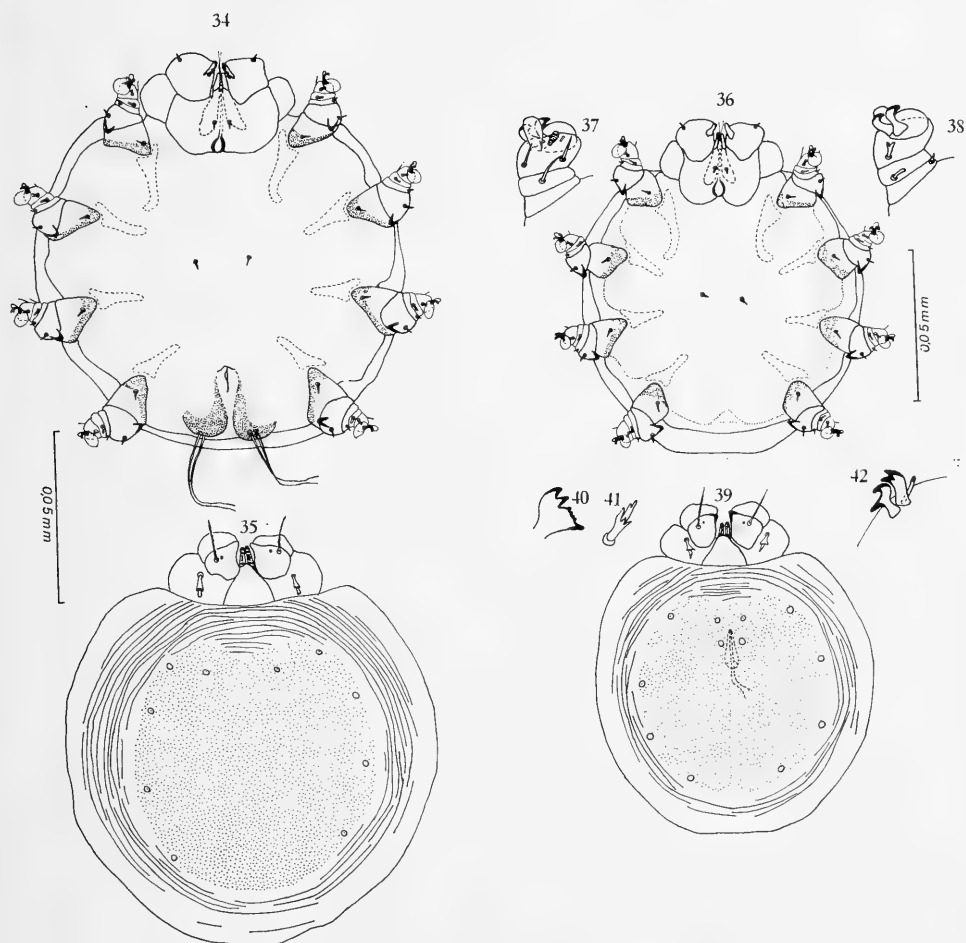


Fig. 34—35. *Psorergatoides molossi* sp. n. Female. 34, holotype ventrally; 35, dorsally. Fig. 36—42. *Psorergatoides molossi* sp. n. Male. 36, allotype ventrally; 37, leg I dorsally; 38, leg I ventrally; 39, allotype dorsally; 40, chelicera of a squashed paratype; 41, gnathosoma seta; 42, palptarsus of a squashed paratype

#### Skin reaction of the host produced by *Psorergatoides* spp.

Sections of parasitized areas in *Molossus molossus*, *Glossophaga soricina* and *Artibeus lituratus* show the same host-parasite-reactions in the epidermis. Therefore these reactions may be described together.

The mites are living between the stratum granulosum and the stratum corneum. The layers of the corneum may be parakerateous or hyperkerateous. At the place of active mites normal epidermal development is disturbed: the stratum germinativum is activated, showing more mitoses than usual, thus forming small rings around mites, which seem to be mostly immobile. The cells of the Malpighi layer often show sickle-shaped nuclei; in

these layers production of melanin is prevented in contradiction to non-parasitized regions. Beneath moulting specimens underlying epidermis forms a thick corneum layer, which seems to eliminate parasite in moulting. Newly hatched stages are able to pierce through thick layers. Hypertrophy of connective tissue is observed especially in the wing membrane, resulting in the impossibility to fold this membrane. Gravid females contain never more than one mature egg.

These reactions of host skin are similar to those in hosts of the *Psorergates dissimilis*-group (Lukoschus, 1967).

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TABLE I - Comparative data of *Psorergatoidea* species (measurements in microns)  
Females

<i>Psorergatoidea</i> spp.	xycteris	keri- voulae	indici- cola	hippo- sideros	loncho- rhina	molossi	glosso- phagae	rhino- lophi	larvae	embal- lonurae	artabei
Setae on femora I-III	2	2	1	1	1	1	1	1	1	1	1
Points on tarsal spine	2	2	1	1	2	2	2	2	2	2	2
Points on tarsal claw	1	1	2	1	1	1	1	1	1	1	2
Length setae											
genu IV	1-2	12	absent	1	1-2	2	2	absent	4	1-2	15
genu I-III	1-2	1-2	absent	1	1-2	2	2	absent	4	1-2	6-8
femora I-III	6	15-20	3	15-18	1-2	2	12	12-15	15	10	11
tarsi	9	20	4	10-15	5-10	4	16	12	30	12	30
palptibia	6	15	18	15-18	12	14	16	20	21	12	19
gnathosoma	4	3-4	6	5	2	6	5-6	3	4	4	6-8
terminais	25-30	75-80	5	45-60	20-30	32-40	20-25	45-60	50	8-10	60-70
Tibial spine	+	narrow	absent	+	narrow	+	+	narrow	+	+	+
Distance ventral setae	12	16	absent	12	9	12-16	15-20	15-18	15	absent	15-50
Body length $\phi$											
minimum	188	178	170	136	105	120	177	128	188	149	151
maximum	175	170	156	117	102	115	166	120	166	138	133
Body width $\phi$											
minimum	205	186	186	150	118	124	191	138	190	153	179
maximum	169	156	144	135	100	101	153	114	153	149	119
Dorsal shield length	160	148	136	108	80	92	143	110	140	135	108
Dorsal shield width	180	162	154	142	112	117	179	125	165	150	143
	135	130	112	84	88	80	118	79	120	107	104
	130	126	94	85	78	80	103	72	116	91	99

TABLE II - Comparative data of *Psorergatoides* species (measurements in microns)  
Males

<i>Psorergatoides</i> spp.	keri- voulæ	indici- cela	hippo- sideros	loncho- rhina	molossi	glosso- phagæ	rhino- lophi	emba- lonuræ	artibeï
Setae on femora I-III	2	1	1	1	1	1	1	1	1
Points on tarsal spine	2	1	1	2	2	2	2	2	2
Points on tarsal claw	1	2	1	1	1	1	1	1	2
Length setae									
genu IV	8-9	absent	absent	absent	1	2	absent	absent	15
genua I-III	1-2	absent	absent	absent	1	2	absent	absent	6-8
femora I-III	12-15	3	11	1-3	2	8	10	13	7
tarsi	15-20	3	7-10	7	3	15-18	11	5-10	23-30
palptibia	13	13	10	12	10-12	14	12	8	19
gnathosoma	4	6	4	4	5-6	6	3	3	8
terminals	absent	5-10	25-30	absent	absent	absent	60-70	15-20	absent
Distance ventral setae	18	absent	4-5	5	12	18	5	absent	15-35
genitals ant.	4-5	2-3	6-7	8-9	8	7-8	10-11	11	12
genitals post.	4-5	7	10-11	9-10	5	7-8	14-15	11	12
Length penis	52	34-51	42	29	18-25	19-29	26	50	26-32
penis sheath	22	18-22	14	14	10-15	13-16	12	22	16-20
Body length $\phi$									
minimum	185	154	100	99	101	169	99	111	144
maximum	186	143			92	156	96		127
		166			117	179	105		161
Body width $\phi$									
minimum	145	126	84	90	91	131	82	99	114
maximum	147	105			80	117	81		99
		140			105	140	86		122
Dorsal shield length	120	103	78	69	69	101	78	88	97
width	90	96	61	69	69	79	70	81	83

TABLE III - Comparative measurements of *Psorergatoides indicicola* specimens from two host species (in microns)

Specimens measured ex host Saccopteryx	20 ♀♀ canescens	15 ♀♀ bilineata	20 ♂♂ canescens	11 ♂♂ bilineata
Length $\phi$	170	178	154	152
minimum	156	161	143	127
maximum	186	188	166	165
Width $\phi$	144	140	126	119
minimum	136	124	105	100
maximum	154	161	140	128
Shield length $\phi$	112	129	103	111
width $\phi$	104	119	96	101
Terminal setae	5	5	7	5
Penis			43	41
Penis sheath			25	30

TABLE IV - Comparative measurements of *Psorergatoides molossi* specimens from two host species (in microns)

Specimens measured ex host Molossus	20 ♀♀ molossus	20 ♀♀ ater	20 ♂♂ molossus	5 ♂♂ ater
Length $\phi$	120	128	101	109
minimum	115	106	92	106
maximum	124	145	117	115
Width $\phi$	109	115	91	96
minimum	99	92	80	89
maximum	113	145	105	101
Dorsal shield				
length	80	81	69	71
width	80	82	65	66
Length terminal setae	37	30	-	-
Distance ventral setae	15	14	12	11-15
Penis length			11	18-25
Penis sheath			6	8-12

TABLE V — Host list of *Psorergatoides* spp.

Species	Host	Family and subfamily of the host	Locality
<i>P. nycteris</i> Fain, 1959a	<i>Nycteris</i> sp.	Nycteridae	Ruanda Urundi
	<i>Nycteris macrotis</i> Dobson	Nycteridae	Congo
<i>P. rhinolophi</i> Fain, 1959a	<i>Rhinolophus clivosus zuluensis</i> And.	Rhinolophidae	Congo
	<i>Rhinolophus hildebrandti</i> Peters	Rhinolophidae	Congo
	<i>Rhinolophus aethiops</i> Peters	Rhinolophidae	Angola
	<i>Rhinolophus ferrumequinum</i> (Schreber)	Rhinolophidae	Belgium, France
	<i>Rhinolophus hipposideros</i> (Bechstein)	Rhinolophidae	Belgium
	<i>Rhinolophus affinis</i> Horst.	Rhinolophidae	Birma
	<i>Rhinolophus euryale</i> Blasius	Rhinolophidae	Italy, Spain
	<i>Rhinolophus mehelyi</i> Matschie	Rhinolophidae	Italy
<i>P. hipposideros</i> Fain, 1959b	<i>Hipposideros abae</i> Allen	Hipposideridae	Congo
	<i>Hipposideros caffer centralis</i> And.	Hipposideridae	Congo
<i>P. emballonurae</i> Fain, 1959b	<i>Emballonura nigriscens</i> (Gray)	Emballonuridae	New Guinea
<i>P. indicicola</i> sp. n.	<i>Saccopteryx canescens</i> Thomas	Emballonuridae	Surinam
	<i>Saccopteryx bilineata</i> Temminck	Emballonuridae	Surinam
<i>P. lonchorhinae</i> Fain, 1959b	<i>Saccopteryx canina</i> Wied	Emballonuridae	Venezuela
	<i>Lonchorhina aurita</i> Tomes	Phyllostomidae, Phyllostominae	Venezuela
<i>P. glossophagae</i> sp. n.	<i>Glossophaga soricina</i> Pallas	Phyllostomidae, Glossophaginae	Surinam
<i>P. artibeii</i> sp. n.	<i>Artibeus literatus fallax</i> Peters	Phyllostomidae, Stenodermatinae	Surinam
<i>P. kerivoulae</i> Fain, 1959a	<i>Kerivoula cuprosa</i> Thomes	Vespertilionidae	Congo
	<i>Kerivoula barrisoni</i> Aellen	Vespertilionidae	Congo
	<i>Myotis muricola</i> Gray	Vespertilionidae	Borneo
	<i>Myotis bocagei</i> Peters	Vespertilionidae	Côte d'Ivoire
	<i>Plecotes auritus</i> (L.)	Vespertilionidae	Belgium
<i>P. laviae</i> Fain, 1959a	<i>Lavia frons</i> Geoff.	Megadermatidae	Ruanda Urundi
<i>P. molossi</i> sp. n.	<i>Molossus molossus</i> Pallas	Molossidae	Surinam
	<i>Molossus ater</i> Geoffrey	Molossidae	Surinam





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## INHOUD

- I. LANSBURY. — A review of the genus *Cercotmetus* Amyot & Serville, 1843 (Hemiptera-Heteroptera: Nepidae), p. 83—106, Figs. 1—91.



# A REVIEW OF THE GENUS *CERCOTMETUS* AMYOT & SERVILLE, 1843 (HEMIPTERA-HETEROPTERA: NEPIDAE)

by

I. LANSBURY

*Hope Department of Entomology, University Museum, Oxford, England*

## ABSTRACT

The genus is defined and a key to species presented. *Cercotmetus asiaticus* Amyot & Serville, *asiaticus* var. *longicollis* Montandon, *brevipes* Montandon, *robustus* Montandon, *dissidens* Montandon, *pilipes* (Dallas), *fumosus* Distant, *strangulatus* Montandon and *compositus* Montandon are redescribed and figured. *Cercotmetus formosanus* Sonan is made a synonym of *brevipes* and the position of *horni* Montandon is discussed. All the available distribution data are given, based on material examined by the author. No new species are described in this review.

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## INTRODUCTION

Ten species and one variety of *Cercotmetus* have been described making it the second largest Ranatrine genus. *Ranatra* F. with an almost cosmopolitan distribution is the largest with about 120 species. *Cercotmetus* has a limited distribution and appears to be confined to an area East of 70° longitude, the most northerly record is from Bhoutan and it is not found South or East of New Guinea \*). The largest number of species are found in the Viet Nam-Thailand region.

Lundblad (1933) reviewed the species found in Sumatra and Java, redescribing and figuring *C. asiaticus* Amyot & Serville, *brevipes* and *compositus* Montandon. Hafiz & Pradhan (1949) redescribed and figured *fumosus* Distant, recording it from India for the first time.

Amyot & Serville (1843) described *Cercotmetus* very briefly, including one species, *asiaticus* which becomes the type species. Dallas (1849) added *pilipes* and Montandon (1903) described *compositus*. Between 1909 and 1911 Montandon described another

\*) An immature specimen of *Cercotmetus* has since been discovered in the USNM Collections from Australia, Groote Eyland, collected June 5, 1948, R. R. Miller. It may be *dissidens* or a new species.

five species and a variety of *asiaticus*. Montandon's types of *strangulatus*, *brevipes*, *horni* and *asiaticus* var. *longicollis* have been lost, but as they may eventually be found I have not designated neotypes. I have been fortunate in finding specimens of *brevipes* and var. *longicollis* named by Montandon which enabled me to redescribe them fully. The types of *robustus* and *dissidens* are both extant and I have been able to study them. The type series of *compositus* is in the Paris Museum and was not available for study. Again however, I did find material named by Montandon in another Museum which enabled me to redescribe and figure the species. The unique type of *horni* is lost and I have not seen any specimens which could with certainty be attributed to this species. I have not been able to trace the whereabouts of the type series of *Cercotmetus formosanus* Sonan (1928), described from Formosa.

No new species are described in this review. All the distribution data given are based on material seen by myself, localities are spelt as on the original data labels, supplementary information is in square brackets. All illustrations are by the author.

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## BIOLOGY

Nothing is known about the biology of *Cercotmetus*. The strongly developed fringes of hairs on the middle and hind tibiae, very short fore legs and small robust respiratory siphon suggests an active predator more likely to be found in large lakes and running water, unlike its closest relative *Ranatra* which is most often found in stagnant conditions. Lundblad (1933) states that *C. asiaticus* was found in flowing water in Java and Sumatra, *brevipes* was found in Toba Lake, Sumatra. Hafiz & Pradhan (1949) found *fumosus* in the Tel River, Belgaon, Patna State.

The ovarian eggs of *Cercotmetus* are typically Ranatrine with two anterior respiratory horns (Fig. 1). Hinton (1962) distinguished the eggs of *Cercotmetus* from *Ranatra* by the length of the horns, those of *asiaticus* and *fumosus* being over 10 mm long, the

largest *Ranatra* horns then known being less than 8 mm long. Cobben (1968) illustrates a *Ranatra* species from West Africa which has horns clearly in excess of 8 mm. A specimen of *brevipes* from Sarawak contained eight ovarian eggs, the horn varying between 5—6 mm long. Ovarian eggs of *compositus* from Sumatra were found to be over 12 mm long.

#### TERMINOLOGY

To avoid lengthy descriptions several terms are used and defined as follows:

Interocular space = narrowest part of the vertex between the eyes.

Anterior collar = raised dorsal anterior margin of the prothorax.

Prothorax (pronotum) = distance dorsally from the anterior to posterior margin along the centre of the prothorax.

Transverse groove = division of the prothorax, always in the dorsal posterior half, only clearly visible laterally as a well defined sulcus.

Anterior lobe = distance dorsally from the anterior margin to the theoretical line of the transverse groove of the prothorax.

Posterior lobe = distance dorsally from the theoretical line of the transverse groove to the posterior margin of the prothorax.

Prothoracic pit = ventral depression at the distal end of the prothorax where it adjoins the mesosternum.

#### *Cercotmetus* Amyot & Serville, 1843

*Cercotmetus* Amyot & Serville, 1843: li & 441 (type species *asiaticus*). — Montandon, 1903: 107—108 (discussion & descript.). — Montandon, 1909: 63—65 (discussion & descript.). Lundblad, 1933: 45—51 (key to species & redescript.). — Hinton, 1961: 224—257 (physiol. ovarian egg). — Hinton, 1962: 65—68 (key to Nepid genera and some species using ovarian eggs).

Body subcylindrical and elongate with a posterior respiratory siphon which is about one fourth the length of the body.

Fore legs prehensile. Fore coxae elongate, always shorter than the femora. Middle and hind coxae small and rounded. Middle coxae always wider apart than hind coxae. Fore femora often irregularly annulated light and dark brown, shorter than the prothorax, with one tooth about midway along the ventral margin. Extending distally from the tooth a ventral sulcus fringed with short hairs. Fore tibiae and tarsus always shining and clearly marked compared with the femora. Fore tibiae about half as long as the femora, fore tarsus about one fourth the length of the tibiae, claws absent from fore legs. Middle and hind legs relatively long, greatly removed from the fore legs, tibiae with prominent fringes of long hairs. Middle femora always shorter than hind femora and middle tibiae always shorter than middle femora. All tarsi one-segmented.

Eyes large, outer margins reflexed downwards obscuring the ventral margin of the head. Clypeus very prominent, higher than the lora which are distinct from the inner margins of the eyes. Vertex variably raised above the eyes. The three-segmented antennae are not visible from above as they lie in ventral depressions between the eyes.

Prothorax dorsally divided into two lobes by a transverse groove which is only visible at lateral margins. Anterior lobe always much longer than the posterior lobe with two

short lateral sulci along antero-lateral margins Humeral width always greater than anterior width, humeral angles with short sulci. Posterior margin deeply concave.

Scutellum small and triangular, twice as long as broad. Clavus and corium coriaceous. Membrane with many small veins forming an irregular reticulate pattern. Tergites dark reddish brown and flat. Metasternum usually posteriorly emarginate. Sternites same colour as the elytra. First sternite not visible, second small and rounded between the hind coxae,

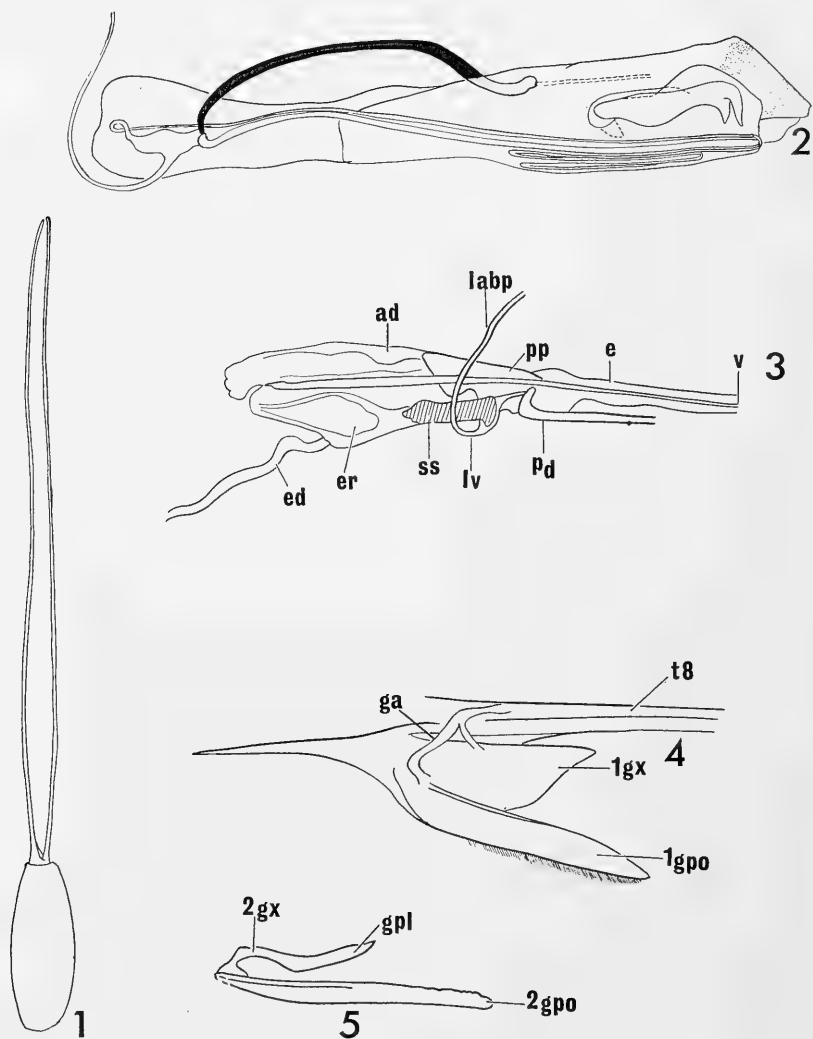


Fig. 1—5. 1, ovarian egg of *C. compositus* from Sumatra; 2, ♂ genital capsule of *asiaticus* from Java; 3, enlarged view of structures within anterior diverticulum of *compositus* from Sumatra; 4 and 5, diagrammatic view of ♀ genitalia of *compositus* from Sumatra, ad, anterior diverticulum; e, endosoma; ed, ejaculatory duct; er, ejaculatory reservoir; gpl, gonoplac; ga, gonangulum?; labp, lateral arms of the basal plate; lv, lamina ventralis; pd, posterior diverticulum; pp, phallosheath plates; ss, sclerotised strut; v, vesica; 1 gpo, 2 gpo, first and second gonapophysis; 1 gx, 2 gx, first and second gonocoxa; t8, paratergite 8



third-sixth longitudinally carinate, seventh variably developed as the operculum.

Male genitalia (Fig. 2 & 3) genital capsule 'U'-shaped, lateral margins sclerotised, dorsally enclosed by a membrane, ventrally the capsule is lightly sclerotised. Attached to the anterior end of the capsule is a large membranous anterior diverticulum within which part of the genitalia is enclosed (Fig. 2). Posteriorly the capsule is open allowing the anal cone and posterior diverticulum to protrude. Parameres symmetrical extending through clefts of the capsule.

Basal plates and bridge thin and lightly sclerotised, lateral arms of the basal plates long and lightly sclerotised extending well back into the anterior diverticulum. The lateral arms curve round the very small lightly sclerotised phallosomal plates uniting ventrally and joining a very short lamina ventralis. Attached to the other end of the lamina ventralis is a lightly sclerotised strut directed cephalad, the membranous ejaculatory reservoir is joined to the free end of the sclerotised strut. The ejaculatory duct enters the reservoir anterior of the lateral arms of the basal plate. The seminal duct enters the heavily sclerotised vesical rod which extends the entire length of the capsule (Fig. 3).

The posterior diverticulum is very long, thin and "V" shaped. The upper lateral margins are lightly sclerotised, the base more heavily so. Within the posterior diverticulum the vesical rod is enclosed in a membranous endosoma, ventrally the endosoma is joined to the anterior end of the posterior diverticulum, the dorsal margin is joined to the phallosomal plates.

Female genitalia (Fig. 4 & 5). Eighth paratergite elongate extending caudad and forming the respiratory siphon. First gonocoxa elongate, antero-dorsal margin produced cephalad as a long thin apodeme. First gonapophysis elongate, tapering caudad and sclerotised, dorsal edge of the first gonapophysis with rami extending about half way. Gonangulum? short and sclerotised, fused to paratergite nine?. Second gonapophysis very long, sclerotised and fused at the base. Second ramus extending along basal half of second gonapophysis and interlocking with first ramus. Second gonocoxa slender and curved, joined posteriorly by a lightly sclerotised bridge to the opposite second gonocoxa. Gonoplac sclerotised and elongate. Single median spermatheca present.

The genitalia of *Cercotmetus* are basically similar to those of *Ranatra*. I was unable to identify with certainty the gonangulum and ninth tergite of the first gonocoxa of the female genitalia as described by Scudder (1959).

#### SYSTEMATIC POSITION OF *Cercotmetus*

*Cercotmetus* clearly belongs to the *Ranatrinae* by having the parasternites concealed by the ventral laterotergites and eggs with two anterior respiratory horns. Lansbury (1972) has split the Oriental *Ranatra* into several species groups, *Cercotmetus* has many affinities with the *R. gracilis* Dallas group (*stali*, *distanti* and *spinifrons* Montandon and *parmata* Mayr) . . . short respiratory siphon, clypeus higher than lorum, vertex conspicuously raised or tuberculate, metasternum posteriorly emarginate, middle coxae wider apart than hind coxae and the ends of the hind femora do not reach the posterior margin of the sixth sternite . . .

This combination of similar features between all the species of one genus and about 20% of the species of a very similar genus in the same faunistic region may be due to convergence. The data available do not so far support the possibility that species of

*Cercotmetus* are found in the same type of habitats as species of the *gracilis* group of *Ranatra*.

*Cercotmetus* is easily distinguished from *Ranatra* by a number of characters viz., outer margin of eyes reflexed downwards obscuring ventral margin of head, fore femora always shorter than prothorax and not sharply constricted in region of ventral tooth, middle and hind tibiae with conspicuous fringes of long hairs, phallosome and ancillary structures not contained within the sclerotised genital capsule but in the large membranous anterior diverticulum and the ejaculatory duct entering reservoir anterior of lateral arms of the basal plate.

#### KEY TO THE SPECIES OF *Cercotmetus*

*Cercotmetus* is a very homogeneous genus. Lundblad (1933) split *Cercotmetus* into two groups dependent upon whether the mesosternum was longitudinally keeled or smooth; this character I have found to be a little unreliable, because it is likely to be associated with the development of flight muscles. Since males are so far unknown of *C. robustus*, *dissidens* and *fumosus*, non-sexual characters have been used in separating the species in the key. Colour is of no use in naming *Cercotmetus*, in general they are some shade of brown and often covered with a layer of debris which obscures most of the ground colour and external features. The male genitalia are completely hidden by the operculum. To examine the genitalia, it is necessary to relax and lever down the operculum and partially withdraw the capsule from within the abdomen.

- |       |                                                                                                                                            |                                   |
|-------|--------------------------------------------------------------------------------------------------------------------------------------------|-----------------------------------|
| 1     | Vertex raised between the eyes, but without a prominent tubercle (Fig. 23, 36) . . . . .                                                   | 2                                 |
| —     | Vertex with a prominent tubercle (Fig. 56, 61) . . . . .                                                                                   | 4                                 |
| 2 (1) | Not more than 42 mm long, middle femora clearly shorter than prothorax . . . . .                                                           | <i>brevipes</i> Montandon         |
| —     | More than 47 mm long, middle femora longer than the prothorax . . . . .                                                                    | 3                                 |
| 3 (2) | Eyes widely separated (Fig. 36), fore femoral tooth small (Fig. 40) . . . . .                                                              | <i>robustus</i> Montandon         |
| —     | Eyes larger (Fig. 43), fore femoral tooth larger (Fig. 48) . . . . .                                                                       | <i>dissidens</i> Montandon        |
| 4 (1) | Middle femora not more than one fifth longer than the prothorax . . . . .                                                                  | 5                                 |
| —     | Middle femora between one third and one half longer than the prothorax . . . . .                                                           | 6                                 |
| 5 (4) | Not more than 40 mm long . . . . .                                                                                                         | <i>pilipes</i> (Dallas)           |
| —     | At least 48 mm long . . . . .                                                                                                              | <i>fumosus</i> Distant            |
| 6 (4) | Mesosternum with a prominent keel (Fig. 15) . . . . .                                                                                      | <i>asiaticus</i> Amyot & Serville |
| —     | Mesosternum not keeled (Fig. 14) . . . . .                                                                                                 | 7                                 |
| 7 (6) | Respiratory siphon about twice as long as the operculum . . . . .                                                                          | <i>strangulatus</i> Montandon     |
| —     | Respiratory siphon about three times as long as the operculum . . . . .                                                                    | 8                                 |
| 8 (7) | Distal third of sixth tergite raised and often very hairy (Fig. 89, 90), middle and hind femora with long hairs distad ventrally . . . . . | <i>compositus</i> Montandon       |
| —     | Distal third of sixth tergite not unduly raised and never hairy (Fig. 12, 13), middle and hind femora bare distad ventrally . . . . .      | <i>asiaticus</i> Amyot & Serville |

## DESCRIPTION OF SPECIES

*Cercotmetus asiaticus* Amyot & Serville  
(Fig. 6—21)

*Cercotmetus asiaticus* Amyot & Serville, 1843: 441 (type species *asiaticus* by monotypy). — Montandon, 1903: 107—109 (descr. note, distrib.). — Montandon, 1909: 63—64 (discussion). — Montandon, 1911: 93 (comp. note). — Montandon, 1911A: 653 (discussion). — Montandon, 1913: 408 (comp. note). — Sonan, 1928: 379 (comp. note). — Lundblad, 1933: 44—48 (key, descr. figs and distrib.).

Males: 46—50 mm long, respiratory siphon 10—12 mm; females 49—53 mm long, respiratory siphon 11—16.5 mm.

Two forms of *asiaticus* have been found, the principal distinction being in the degree of dorso-ventral development of the posterior lobe of the prothorax and the length of the keel on the mesosternum. If the posterior lobe is slightly expanded dorso-ventrally, then the mesosternum is broader and more rounded and only carinate posteriorly between the middle coxae (Fig. 14 & 16). The antennae of this form (Fig. 19) do not differ significantly from the form with a reduced posterior lobe with a much longer keel on the

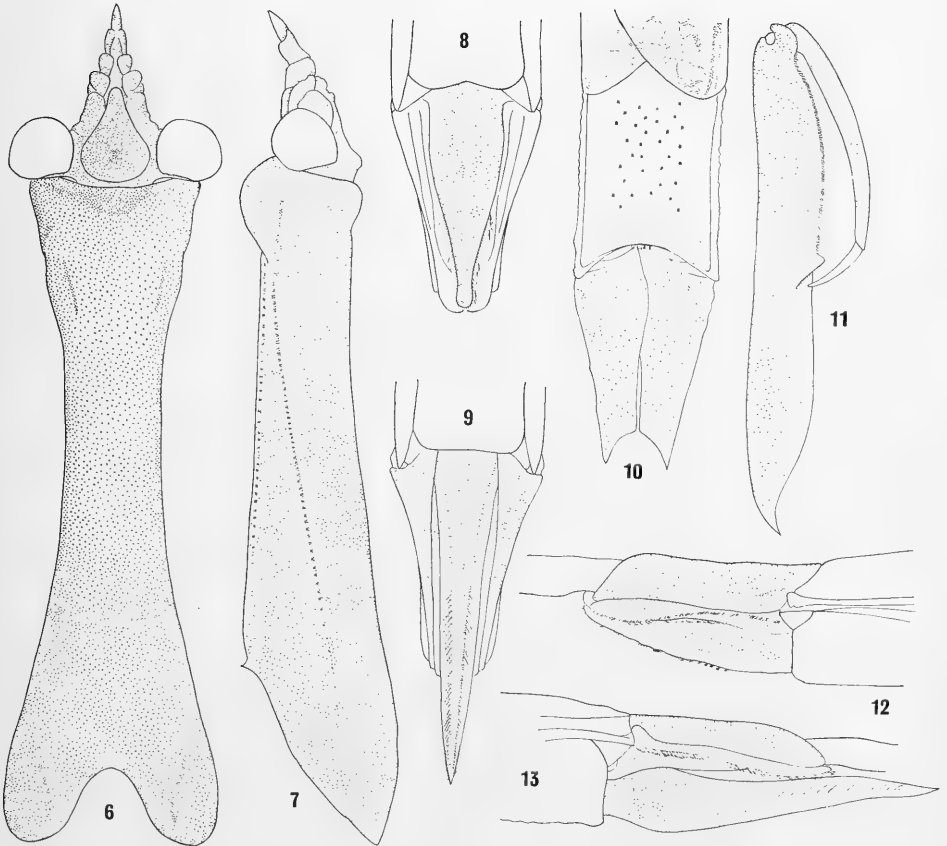


Fig. 6—13. *Cercotmetus asiaticus*, 6—8 and 10—12 ♂, 9 and 13 ♀ Java, 6, head and prothorax from above; 7, id. from the side; 8, 9, 12 and 13, operculum; 10, 6th tergite; 11, fore leg

mesosternum (Fig. 15, 17 & 18). The expanded posterior lobe and ancillary external changes may be associated with "flight" muscle development. A similar phenomenon has been found in several species of *Ranatra*. The expanded prothoracic form of *asiaticus* is very uncommon, of the fifty or so specimens studied, four males and one female have been found of this form.

Interocular space slightly greater than the width of an eye. Vertex tuberculate between the eyes (Fig. 7).

Prothorax elongate "hour-glass" shaped. Anterior collar raised. Anterior lobe between 2.5—2.9 times longer than the posterior lobe (Fig. 6).

Prothorax ventrally tricarinate, each keel with small irregular nodules along their apices. Central keel commencing from between the fore coxae, becoming rather indistinct towards the shallow prothoracic pit. Lateral keels not so conspicuous, becoming obsolescent posteriorly. The sides of the prothorax behind the eyes with short lateral keels, also with a row of nodules reaching the posterior lobe (Fig. 7).

Meso- and metasternum carinate (Fig. 15 and 17), occasionally the mesosternum is only carinate between the middle coxae, if so the posterior lobe of the prothorax slightly expanded (Fig. 16). Posterior margin of metasternum always emarginate. Middle coxae about 1.5 times wider apart than hind coxae (Fig. 14 and 15).

Membrane reaching less than half way along the sixth tergite (Fig. 10).

Fore coxae just over half as long as the prothorax. Fore leg (Fig. 11). Middle and hind femora slightly flattened. Middle femora much longer than prothorax and slightly shorter than hind femora which reach beyond the end of the membrane. Hind tibiae clearly shorter than middle and hind femora. Femora and tibiae sometimes annulated light and dark brown.

Male operculum boat shaped, tip almost spatulate (Fig. 8 and 12). Male genital capsule and paramere (Fig. 20 and 21). Female operculum very long (Fig. 9 and 13). Male respiratory siphon about 1.2—1.4 times longer than sixth sternite and over twice as long as the operculum, ♀ siphon over 1.5 times as long as the sixth sternite and less than twice as long as the operculum.

This species was described from Java. The type series almost certainly consisted of a ♂ and ♀. I have been unable to trace their present whereabouts. Montandon (1909) refers to an example labelled by Amyot in the Paris Museum "*Cercotmetus asiaticus*, Indes or. Mars 1836"; I have not been able to verify whether this specimen still exists.

This is the most common species and is easily recognised by the combination of tuberculate vertex and long middle femora, the ♀ is unmistakable because of the very long operculum (Fig. 9 and 13).

#### Distribution.

Java: 7 ♂ 5 ♀ Java, Soekaboemi E. le Moults (ML), 1 ♂ 2 ♀ Java, Preanger, N.O.I. Mt. Besser, May 1936 Coll. F.C. Drescher (ML), 1 ♂ Java, Preanger, N.O.I. Telaga Warna, Puntjak, 1480 m 30 March 1936 Coll. F. C. Drescher (ML), 2 ♀ Java, G. Tji-soeroe 1935—1936 E. le Moults (ML), 1 ♂ Java, Bodjong Kalong, Cheribon, E. le Moults (ML), 1 ♂ Borneo, Long Bloe-oe, Mahakkam 1898, Nov. Dr. Nieuwenhuis (ML), 2 ♀ West Java, Goenoeng Roesa, M.E. Walsh (NMB), 1 ♀ West Java, Djampang Wetan, M.E. Walsh (NMB), 1 ♂ Java, Tjibodas, Gil Kei-Gerlu Dend Exp. Dr. Fr. Motium (UZMC), 1 ♂ Java, Hj. Jensen 30 Sept. 1908 (UZMC), 1 ♂ 1 ♀ Batavia, December 1815 Mus. Westerm. (UZMC), 1 immature Java, Djombang July 1922, P.

Bouvien (UZMC), 1 ♀ Det. Montandon 1911, Java Occident. Mons Gede, 4000' August 1892 H. Fruhstorfer (DEI), 1 ♀ Det. Montandon 1911, Süd Java (DEI), 1 ♂ 1 ♀ Det. Montandon 1909, Java, Malang (MBUD), 1 ♀ Java, Xantus (MBUD), 1 ♂ Java, Malang (AMNH), 1 ♀ Java, alte Sammlung (KU), 1 ♂ Java, Malang (LAM).

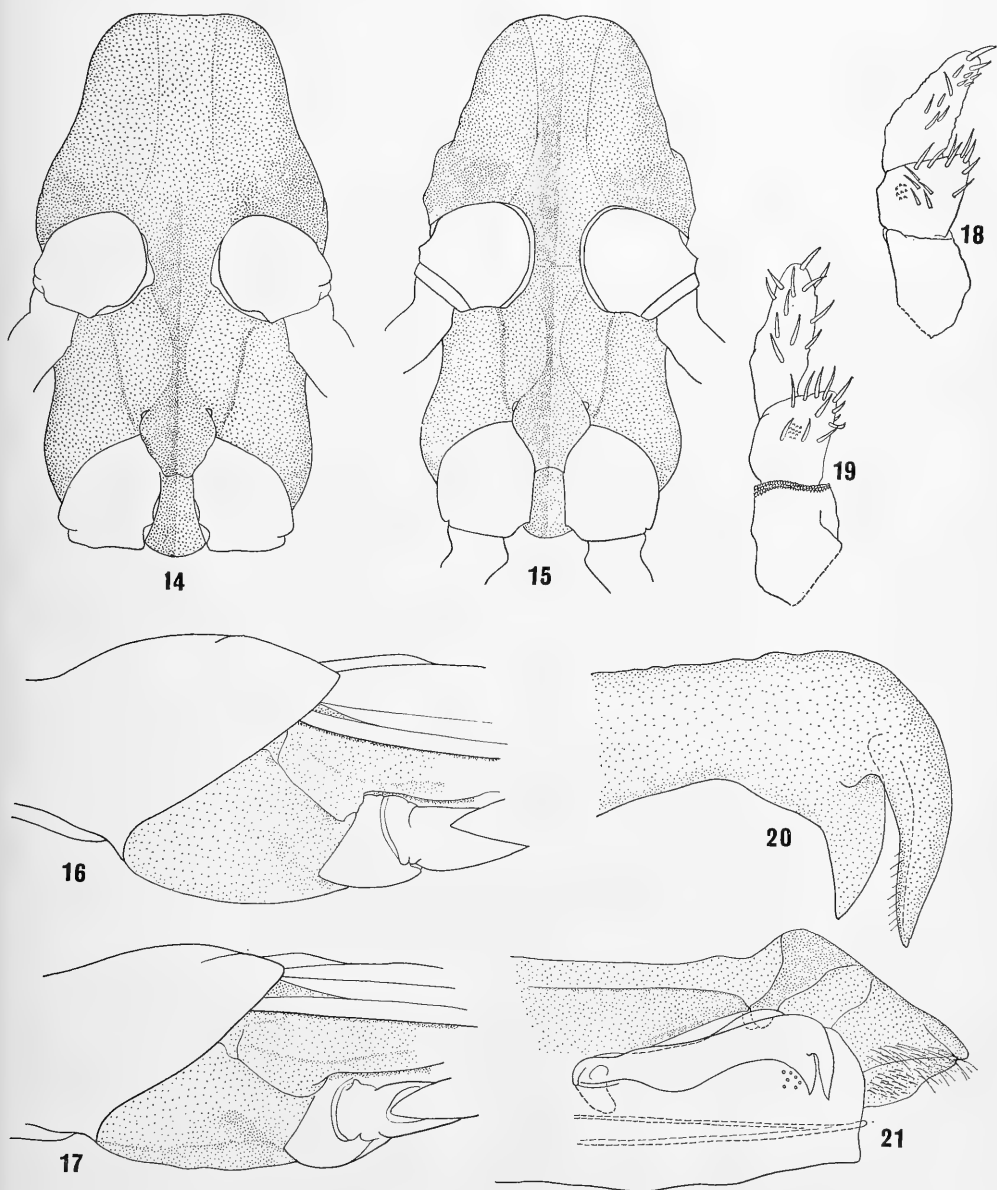


Fig. 14—21. *Cercotmetus asiaticus* ♂ from Java; 14 and 15, meso and metasternum; 16, side view of 14; 17, side view of 15; 18 and 19, antennae; 20, paramere; 21, end of the genital capsule

Sumatra: 1 ♀ Sumatra Medan Mjöberg (NRS), 1 ♀ Sumatra, Battack Coll. Schneider (NMB), 1 ♀ Sumatra, Silago April 1877 (ML).

Borneo: 1 ♂ 1 ♀ Borneo, Long Bloe-oe, Nov.—December 1898 Dr. Nieuwenhuis (ML), 1 ♂ Borneo, Long Bloe-oe, Mahakkam, Nov. 1898 Dr. Nieuwenhuis (ML), 2 ♀ Borneo, Long Bloe-oe, Mahakkam April 1899 Dr. Nieuwenhuis (ML), 1 ♀ Borneo, 3 April 1903 M. C. Piepers (ML), 1 ♂ 1 ♀ Borneo, Smitau J. v. Veldhuizen (ML), 1 ♀ Borneo, Mout.? Kenepat Geb. 1894 (ML), 1 ♂ Borneo, Brongebied Kajan riv. 1900 (ML), 1 ♀ Centr. Borneo, Koetei-Fl.-Quellgeb., Linnaea v. (ZMB), 2 ♀ Nord Borneo, Rolle v. (ZMB), 1 ♀ Sarawak, foot of Mt. Dulit, junction of Rivers Tinjar and Lejok 17 August 1932 B. M. Hobby & A. W. Moore (BM), 1 ♀ Sudost Borneo, Tandjong, Fitz Such 18 December 1894 (KU).

1 ♀ Ile de Sepandjang, Java Sea, E. le Moutl (ML).

Malaya: 1 ♀ Perak, Kwala Kangsar, B. Jachan vend 15 July 1900 (KU).

Siam: 1 ♂ Siam, Khao Sabap Chantaboon 1936 MacBeth (BM).

### *Cercotmetus asiaticus* var. *longicollis* Montandon

(Fig. 22)

*Cercotmetus asiaticus* var. *longicollis* Montandon, 1909: 64—65 (Borneo). — Montandon, 1911: 91 (obs. on elevation of *longicollis* to species level in descr. of *horni*). — Lundblad, 1933: 47, 50 (key).

Females: 52.5—54 mm long, respiratory siphon 11—12 mm.

This variety differs by having a much more elongate parallel sided prothorax. The anterior lobe is proportionately much longer than the posterior lobe and the eyes are much larger compared with the typical form.

Montandon (1909) stated that specimens of var. *longicollis* were in the Paris Museum and his own collection. I have not been able to trace any of this material. I have been fortunate in finding in the ZMA a ♀ named by Montandon.

#### Distribution.

Borneo: 1 ♀ Det. Montandon 1911, Borneo, Barabai Z.O. Afd. Geschenk A. Pool 1883 (ZMA), 1 ♀ Sarawak (AMNH).

Malaya: 1 ♀ Mt. Ophir [Malay Peninsula, Malacca, A. R. Wallace] (BM).

### *Cercotmetus brevipes* Montandon

(Fig. 23—35)

*Cercotmetus brevipes* Montandon, 1909: 65. — Montandon, 1911: 91 and 93 (obs.) — Sonan, 1928: 379 (comp. note). — Lundblad, 1933: 48—49 (Figs. descrip. and key).

*Cercotmetus formosanus* Sanan, 1928: 377—379, Figs. (Syn. nov.).

Males: 32—35 mm long, respiratory siphon 7—7.5 mm; females 38—41 mm long, respiratory siphon 7.5—8.9 mm.

Interocular space about 1.5 times or more the width of an eye. Tip of clypeus turned up (Fig. 24). Antennae (Fig. 27) large and spinose. Anterior collar not very prominent with an inconspicuous blunt projection behind the eyes. Anterior lobe about 2.5—2.9 times longer than posterior lobe and with a blunt ridge posteriorly, not so conspicuous in the ♀.

Prothorax ventrally tricarinate, central keel commencing from between the fore coxae becoming evenly rounded and raised posterior of the line of the transverse groove. Outer keels slightly shorter, becoming obsolescent about the line of the transverse groove.

Anterior lateral margins of the mesosternum with two small nodules. Mesosternum evenly rounded between the middle coxae. Metasternum bluntly carinate, posterior



Fig. 22. *Cercotmetus asiaticus* var *longicollis* ♀ from Borneo; head and prothorax from above

margin emarginate, sometimes the emargination is obscured by the deposition of debris. Middle coxae over two times wider apart than hind coxae (Fig. 25).

Fore coxae less than half as long as the prothorax. Fore leg (Fig. 26). Middle and hind legs ? and slender, annulated light and dark brown. Middle femora clearly shorter than the prothorax and about two thirds the length of the hind femora which almost reach the posterior margin of the fifth sternite. Membrane large, reaching about half way along the sixth tergite which is slightly expanded distally (Fig. 30 and 33).

Male operculum narrow and sharply carinate (Fig. 32 and 34). Male genital capsule and paramere (Fig. 28 and 29). Female operculum very narrow and sharply carinate

(Fig. 31 and 35). The respiratory siphon in both sexes is between 1.5—1.75 times longer than the sixth sternite and just over twice as long as the operculum.

Montandon (1909) described this species from a male in his own collection of unknown provenance and a female from Sumatra in Kirkaldy's collection, both these specimens have proved untraceable. In the DEI Collections I found a male and female named by Montandon which has enabled me to fix this species. Sonan (1928) described *C. formosanus* from Formosa, Jitsugetsu-tan Lake 13 September 1928, R. Takahashi, the type series consisting of one male and three young nymphs. The figure and description leave

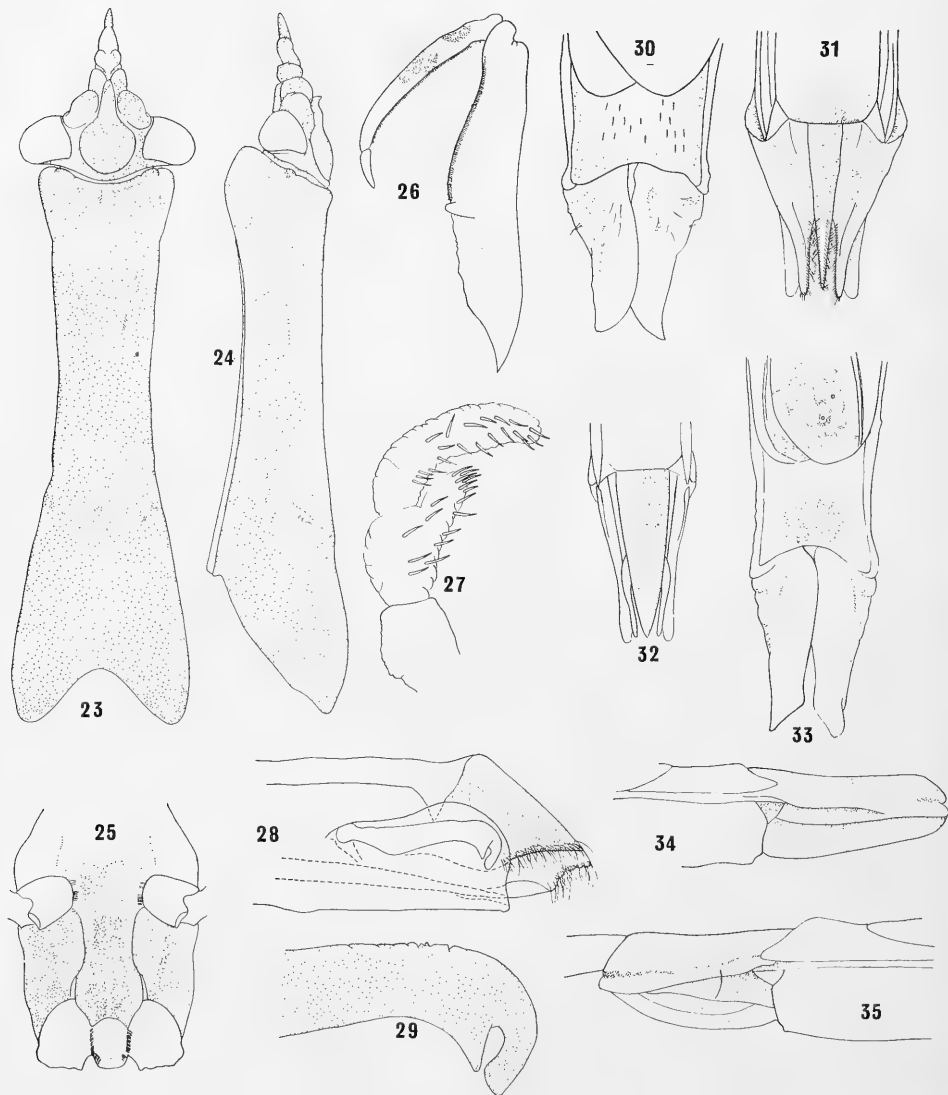


Fig. 23—35. *Cercotmetus brevipes*, 23—29 and 32—34 ♂ from Sarawak, 30 ♀ from Annam and 31 and 35 ♀ from Thailand. 23, head and prothorax from above; 24, id. from the side; 25, metasternum; 26, fore leg; 27, antennae; 28, end of genital capsule; 29, paramere; 30 and 33, 6th tergite; 31, 32, 34 and 35, operculum



no doubt that *formosanus* is a synonym of *brevipes*. Despite extensive enquiries, I have not been able to find Sonan's specimens.

Distribution.

Sumatra: 1 ♀ Sumatra, August 1916; Soengei gloegoen? Beekje met zandige leem op terras van Bohorok bij Bohorok, Boven Langkol S.O. leg J. E. A. den Doop (ZMA), 1 ♀ N.O. Sumatra, Tandjong Morawa Serdang, B. Hagen (ML).

Java: 1 ♀ Java, Muller (ML).

Sarawak: 2 ♂ 1 ♀ Sarawak, Ban 6 December, J. M. Bryan (BM).

India: 1 ♂ Bengal (UZMC), 1 ♂ E. Bengal, Rajshai 1—6 February 1907, N. Annandale (BM).

Thailand: 1 ♀ 3 immature Thailand, Ban Dan Ngui Amphur Kabinburi, Parjinburi Prov. 2—5. December 1965 Kol. Mongkolpanya (AMNH).

Viet Nam: 1 ♀ Det. Montandon 1911, Annam, Phuc Son, November—December H. Rolle (DEI), 1 ♂ Rep. Viet Nam, 1 mi. N. Quang Tri, 9 June 1970, A. R. Gillogly (OUM), 1 ♀ as before 15 June 1970 (OUM).

Philippines: 1 ♂ Clark Air Force Base, 13 December 1970, W. R. Reisen (Pol. Coll.).

China: 1 ♂ S. China, Fukien Shaowu' Shui-PeiKai, 5 June 1941, T. C. Maa (BISH).

1 ♂ Telaga Pabila (ML).

1 ♂ Det. Montandon 1911, no data (DEI).

Lundblad (1933) recorded *brevipes* from Sumatra, Tobasee and commented on the male from Annam in the DEI.

*Cercotmetus brevipes* is easily separated from other species of the group by the shape of the fore femora (Fig. 26) and very short legs, especially the middle femora.

***Cercotmetus robustus* Montandon**

(Fig. 36—42)

*Cercotmetus robustus* Montandon, 1911: 92—92. — Montandon, 1911A: 652—653 (Obs. and comp. with *dissidens*). — Montandon, 1913: 407 (comp. notes). — Lundblad, 1933: 50 (key).

Female 50 mm long, respiratory siphon 7.25 mm.

Interocular space about twice the width of an eye, posterior part of the vertex raised (Fig. 37). Vertex with a conspicuous circlet of hairs. Antennae (Fig. 39) small, second segment spinose, third sparsely so. Anterior collar broadly rounded, not very prominent with a slight "step" more or less in line with the upper margin of the eyes (Fig. 36). Prothoracic sulci prominent, posterior lobe slightly striate and about half as long as the anterior lobe.

Prothorax ventrally tricarinate, central keel commencing from between the fore coxae and reaching the prothoracic pit which has a vestigial median carina. Lateral keels shorter, not so prominent with irregular nodules, becoming obsolescent at the line of the transverse groove.

Anterior margin of the mesosternum slightly depressed, carinate between the middle coxae which are twice as wide apart as the hind coxae. Metasternum carinate, posteriorly emarginate (Fig. 41).

Fore coxa slightly less than half as long as the prothorax. Fore leg (Fig. 40). Middle and hind legs slightly flattened, femora expanded distally. Middle femora slightly longer than prothorax. Hind tibiae much longer than middle tibiae and almost as long as the hind femora which almost reach the anterior margin of the sixth sternite. Membrane small, reaching less than half way along the sixth tergite (Fig. 38).

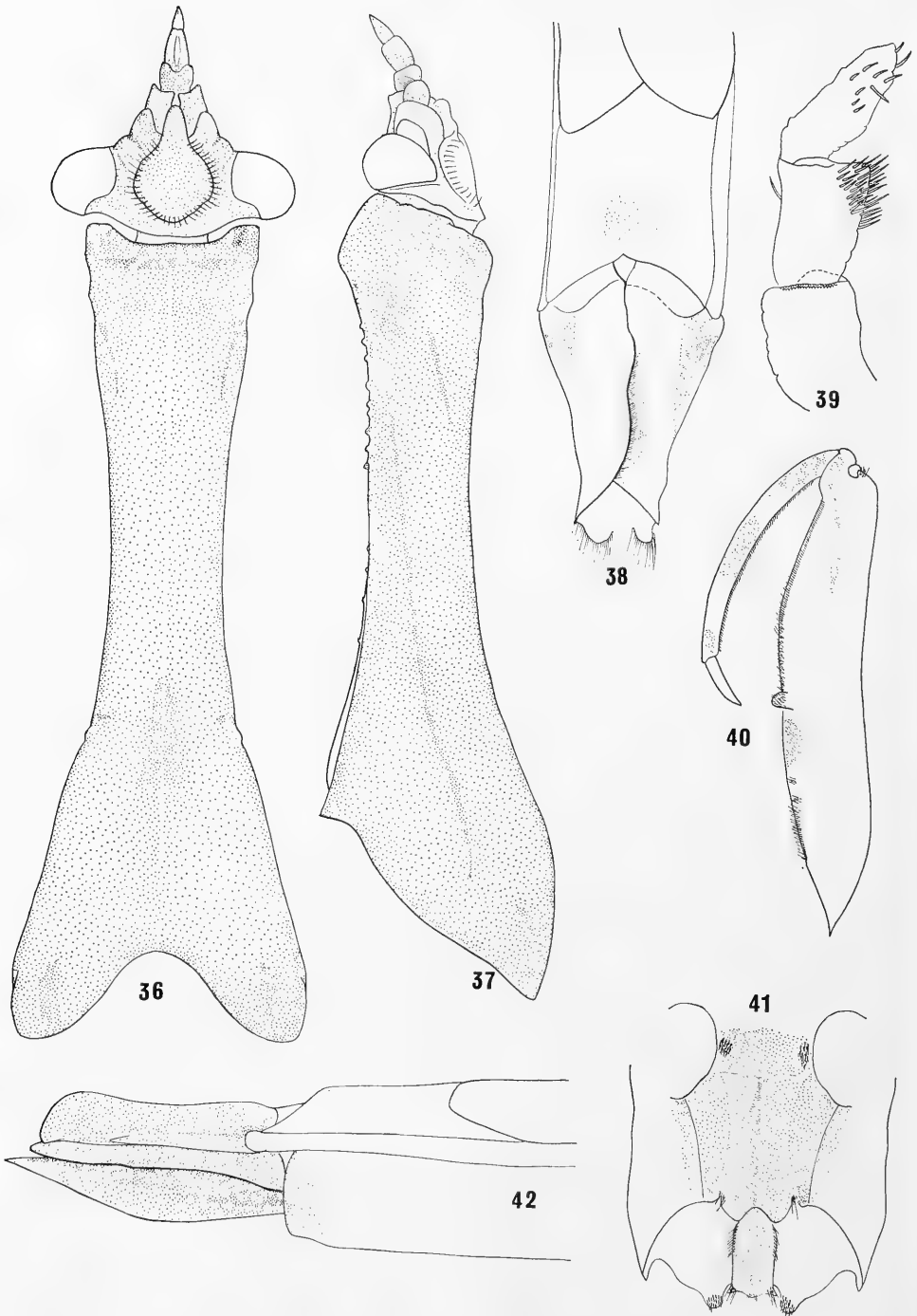


Fig. 36—42. *Cercotmetus robustus* holotype ♀; 36, head and prothorax from above; 37, id. from the side; 38, 6th tergite; 39, antennae; 40, fore leg; 41, metasternum; 42, operculum

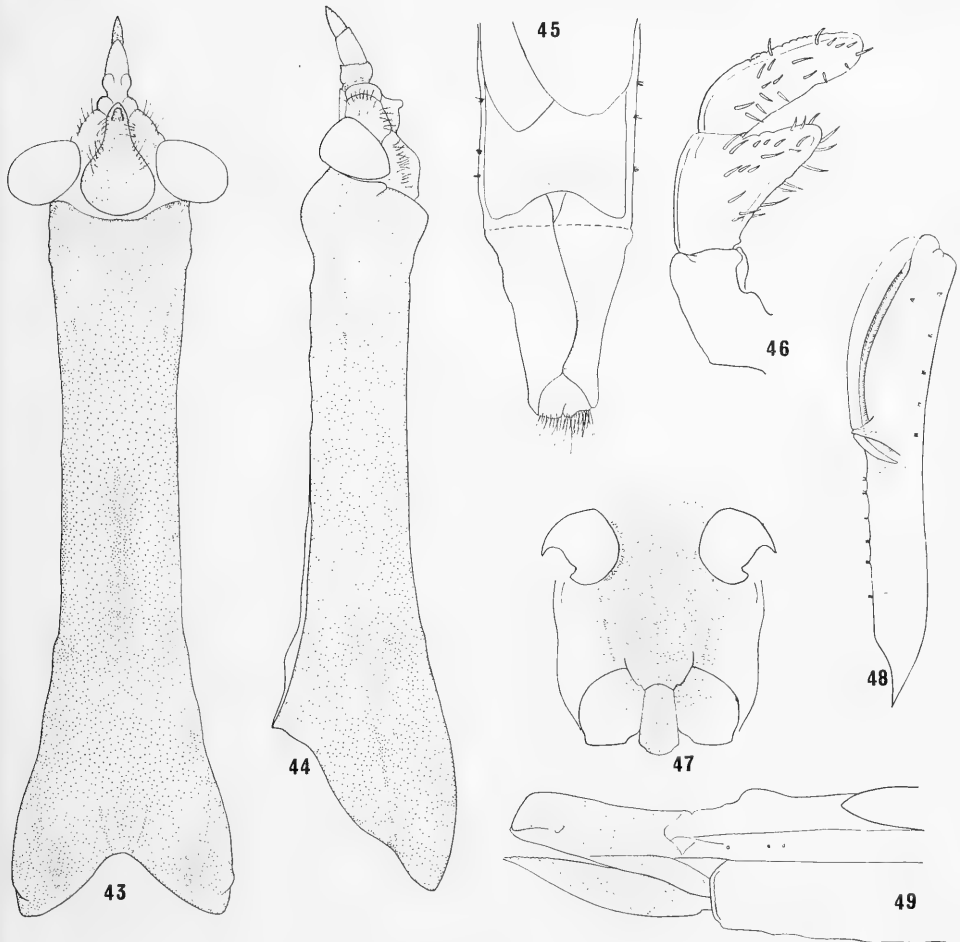


Fig. 43—49. *Cercotmetus dissidens* holotype ♀; 43, head and prothorax from above; 44, ibid from the side; 45, 6th tergite; 46, antennae; 47, metasternum; 48, fore leg; 49, operculum

Operculum long and carinate (Fig. 42). Respiratory siphon slightly longer than the sixth sternite and one third longer than the operculum.

Holotype ♀ Celebes, Gegend um den Posso See, February 1895, Sarasin (DEI).

This species is very distinctive, the circlet of hairs on the vertex, large size and small eyes are diagnostic. This species is only known by the holotype on which the description and figures are based.

### *Cercotmetus dissidens* Montandon

(Fig. 43—49)

*Cercotmetus dissidens* Montandon, 1911A: 652—654. — Montandon, 1913: 407—408 (repeat of 1911A). — Lundblad, 1933: 50 (key).

Females: 45—51.5 mm long, respiratory siphon 7.5—9 mm.

Interocular space clearly greater than the width of an eye which are very large. Vertex

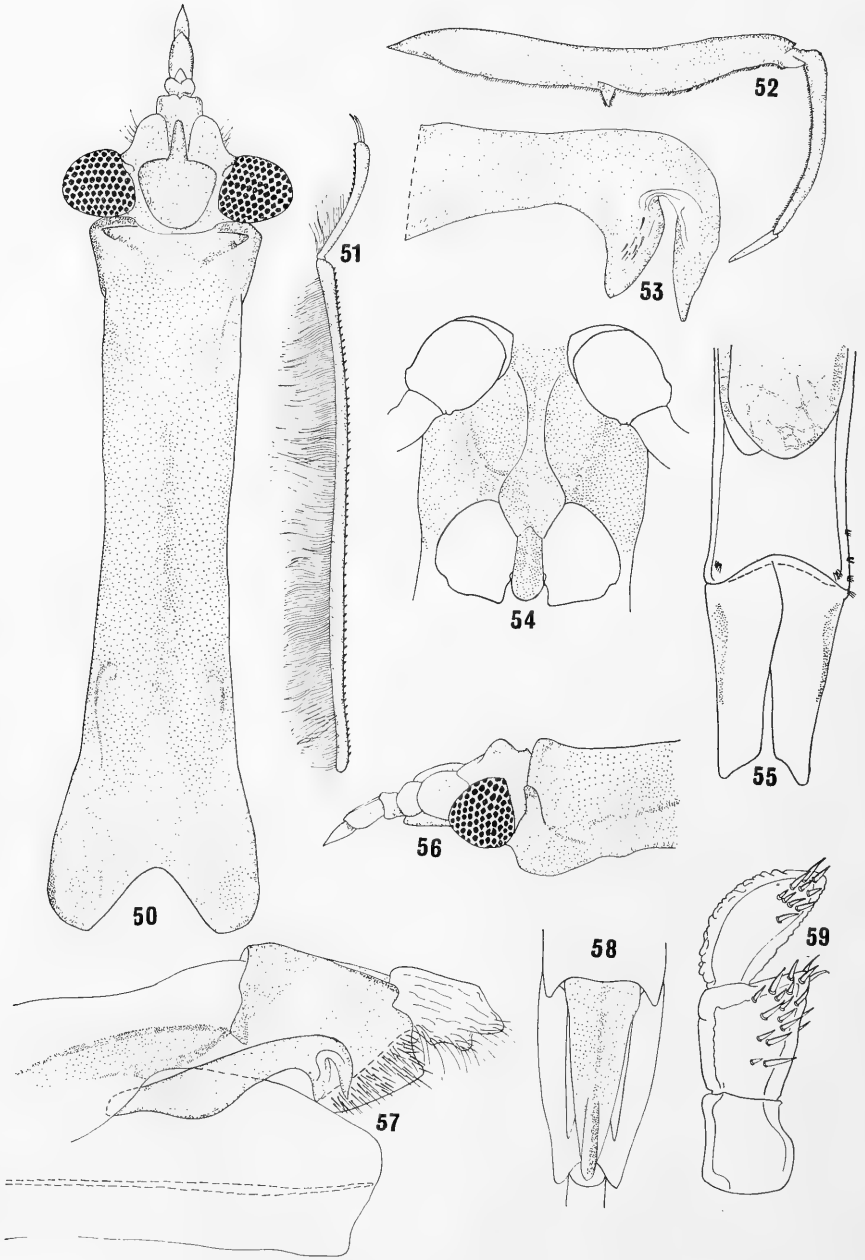


Fig. 50—59. *Cercotmetus pilipes* holotype ♂; 50, head and prothorax from above; 51, middle tibia; 52, fore leg; 53, paramere; 54, metasternum; 55, 6th tergite; 56, head and part of prothorax from the side; 57, end of genital capsule; 58, operculum; 59, antennae

and clypeus very hairy. Clypeus with a prominent nodule anteriorly (Fig. 44). Antennae (Fig. 46) large, second and third segments with sparse spines. Anterior collar broadly raised with a pair of small tubercles behind the eyes (Fig. 44). Prothoracic sulci prominent. Posterior half of anterior lobe bluntly carinate. Posterior lobe about half as long as anterior lobe (Fig. 43).

Prothorax ventrally with a central keel which becomes obsolescent about half way along the anterior lobe, posteriorly prothorax raised. Lateral margins with small irregular nodules.

Mesosternum broadly rounded, slight ridges between the middle coxae which are much wider apart than the hind coxae. Metasternum carinate, posterior margin emarginate (Fig. 47).

Fore coxa slightly less than half as long as the prothorax. Fore leg elongate (Fig. 48). Middle and hind legs slightly flattened, middle femora clearly longer than the prothorax and shorter than hind tibiae which are as long as the hind femora. Apices of the hind femora almost reaching the posterior margin of the fifth sternite and over half way along the large membrane (Fig. 45). All legs including fore coxae with very small clumps of irregularly spaced setae.

Operculum narrow (Fig. 49). Respiratory siphon slightly longer than sixth sternite and just over twice as long as the operculum.

Holotype ♀ Nieuw Guinea, Sabang, 10 July 1907 Lorentz (ZMA).

In addition to the type I have seen the following material: — New Guinea: 1 ♀ Neth. Ind.-American New Guinea Exped. Araucaria Camp, 800 m, 8 March 1939 L. J. Toxopeus (ML), 1 ♀ Neth. Ind.-American New Guinea Exped. Bernhard Camp B, 100 m, 3 April 1939 L. J. Toxopeus (ML), 1 ♀ as before, 10 April 1939 L. J. Toxopeus (ML), 1 ♀ Neth. New Guinea, Exp. Manang a. d. Digoel 10 m, 12 September 1959 (ML).

*C. dissidens* has certain affinities with *robustus*, but can be distinguished by its large eyes, short ventral prothoracic keel and much larger antennae. The operculum of *robustus* (Fig. 42) is much longer than that of *dissidens* (Fig. 49).

### *Cercotmetus pilipes* (Dallas)

*Ranatra* (*Cercotmetus*) *pilipes* Dallas, 1850: 9—10, pl. 2, f. 6. — *Cercotmetus pilipes*, Montandon 1903: 110 (note on *pilipes*). — Distant, 1906: 23—24 (precis of Dallas, 1850). — Montandon, 1909: 63 (comp. note). — Montandon, 1911: 93 (comp. note). — Sonan, 1928: 379 (comp. note). — Lundblad, 1933: 50 (key). — Hafiz & Pradhan, 1949: 362 (discussion).

Male: 38 mm long, respiratory siphon 10 mm.

Greatest width of an eye less than the interocular space. Vertex with a prominent tubercle (Fig. 56). Antennae (Fig. 59) with stout sparse spines. Anterior collar with distinct tubercles behind the eyes (Fig. 56). Anterior lobe posteriorly carinate, slightly more than twice as long as the posterior lobe which is carinate anteriorly.

Prothorax ventrally tricarinate, central keel commencing posterior of the fore coxae, terminating anterior of the prothoracic pit, lateral keels becoming obsolescent at the line of the transverse groove.

Mesosternum rounded with a pair of nodules on anterior lateral margins, slightly ridged between the middle coxae which are wider apart than the hind coxae. Metasternum carinate, posteriorly emarginate (Fig. 54).

Fore coxa just over half as long as the prothorax. Middle and hind legs flattened, tibiae with very prominent fringes of hairs (Fig. 51). Middle femora slightly longer than prothorax. Hind tibiae longer than middle tibiae, but clearly shorter than hind femora. Apices of hind femora reaching about one third beyond anterior margin of the sixth sternite, but not reaching the end of the large membrane which extends over half way along the sixth tergite (Fig. 55).

Operculum constricted distally (Fig. 58). Male genitalia (Fig. 53 and 57). Respiratory siphon twice as long as the sixth sternite and three times as long as the operculum.

Holotype ♂ Bhoutan (OUM). The type was discovered amongst the foreign Nepidae with *Ranatra gracilis* Dallas which was described in the same paper. Originally these specimens were in the collection of the Honourable East India Company and were acquired by the Hope Department, Oxford in about 1860—1861.

This species appears to be rather uncommon and may be separated from the remainder by its small size, tuberculate vertex, dense fringes of hairs on the middle and hind tibiae and posteriorly carinate mesosternum.

### *Cercotmetus fumosus* Distant

(Fig. 60—67)

*Cercotmetus fumosus* Distant, 1904: 278. — Distant, 1906: 23, f. 15 (redescript.). — Montandon, 1909: 64—65 (comp. with *asiaticus* var *longicollis* and *brevipes*). — Montandon, 1911: 93 (comp. with *robustus*). — Montandon, 1911A: 650 (comp. with *strangulatus*). — Sonan, 1928: 379 (comp. note). — Lundblad, 1933: 50 (key). — Hafiz & Pradhan, 1949: 361—363 (redescript. and first record for India).

Females: 47.9—51 mm long, respiratory siphon 9.5 mm.

Interocular space slightly exceeding the width of an eye, occasionally eye width greater than interocular space. Vertex tuberculate (Fig. 61). Antennae (Fig. 65 and 66) large and spinose, third segment with a prominent nodule on reserve, hidden) side. Anterior collar slightly raised with blunt nodules behind the eyes. Anterior lobe twice as long as posterior lobe (Fig. 60).

Prothorax ventrally tricarinate, marginal keels reaching the line of the transverse groove becoming obsolescent posteriorly. Central keel extending from between fore coxae to prothoracic pit, rather poorly defined posterior of the line of the transverse groove.

Anterior margin of the mesosternum with a pair of small nodules, slightly ridged between the middle coxae which are about twice as wide apart as the hind coxae. Metasternum bluntly carinate, posterior margin emarginate (Fig. 64).

Fore coxa slightly less than half as long as the prothorax. Fore leg (Fig. 62) the sulcate area of the femora is distinctly flattened. Middle and hind femora slightly flattened. Middle femora slightly longer than the prothorax and clearly shorter than the hind femora which reach about one third beyond the anterior margin of the sixth sternite and between half and two thirds of the way along the membrane. Hind tibiae slightly longer than middle femora and almost as long as the hind femora.

Distant (1904) states that the corium was "with some amount of brownish ochraceous pubescence" this is not noticeable on the type now. Membrane large reaching well over half way along the sixth tergite (Fig. 63).

Operculum narrow and carinate (Fig. 67). Respiratory siphon about two and a half times longer than the operculum and one fourth longer than the sixth sternite. The

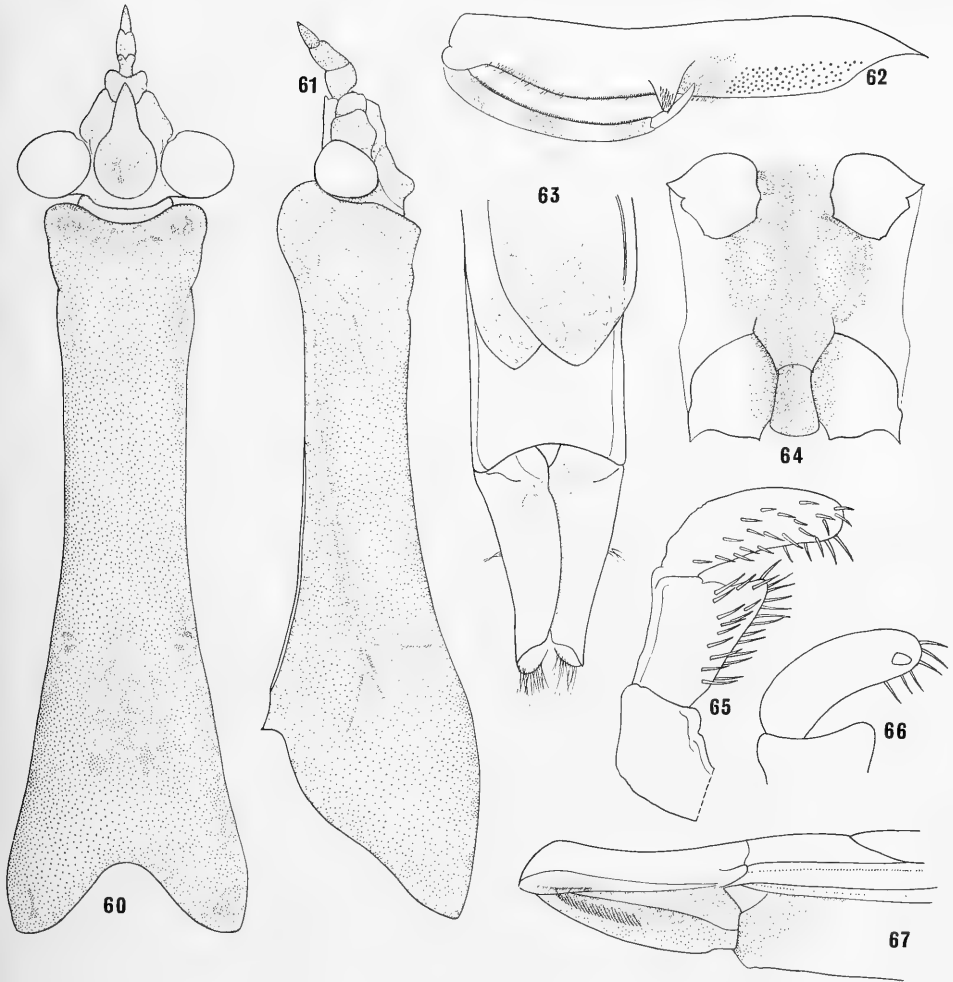


Fig. 60—67. *Cercotmetus fumosus* holotype ♀; 60, head and prothorax from above; 61, id. from the side; 62, fore leg; 63, 6th tergite; 64, metasternum; 65, antennae; 66, detail of reverse of 3rd antennal segment; 67, operculum

siphon of the type was missing when it was first described.

Holotype ♀ Ceylon, Green Coll. (BM).

In addition to the type I have seen material from the following areas of Ceylon: 1 ♀ Ceylon, Anuradhapura, 19—21 December 1910 A. Luther (ZMH), 1 ♀ Ceylon, Det. Montandon, 1910 as *compositus* (MBUD), 1 ♀ Ceylon, Ambanganga near Parakrama Samudra. Anicut Angamedalla Pelonnaruwa, C. H. Fernando (CNM), 1 ♀ Ceylon, Magalla Wema near Nikaweratiya, 18 March 1962 C. H. Fernando (CNM).

See *strangulatus* for comments on this species.

### *Cercotmetus strangulatus* Montandon

(Fig. 68—79)

*Cercotmetus strangulatus* Montandon, 1911A: 650—651. — Lundblad, 1933: 50 (key). — Hafiz & Pradhan, 1949: 362 (discussion):

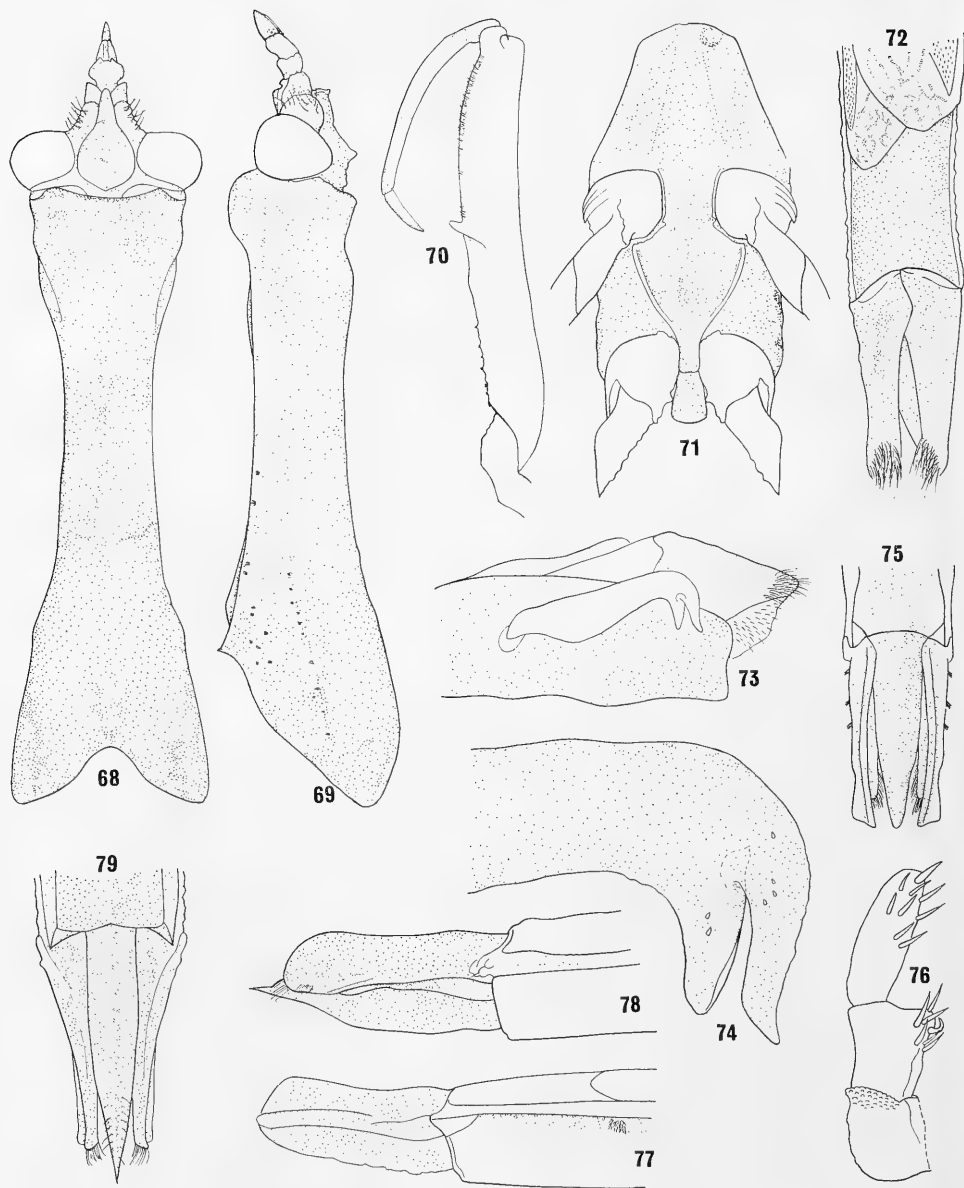


Fig. 68—79. *Cercotmetus strangulatus*, 68—77 ♂ from Knuckles, Ceylon, 78 and 79 ♀ from Ceylon. 68, head and prothorax from above; 69, id. from the side; 70, fore leg; 71, meso and metasternum; 72, 6th tergite; 73, end of genital capsule; 74, paramere; 75 and 77—79, operculum; 76, antennae

Males: 40—42 mm long, respiratory siphon 9.5—10 mm; females: 45—47 mm long, respiratory siphon 10—11 mm.

Eye width equal to or greater than the interocular space. Vertex tuberculate, tip of clypeus nodulate (Fig. 69). Antennae (Fig. 76) small, second and third segments with



several stout spines. Anterior collar prominent. Anterior lobe slightly less than twice as long as the posterior lobe and carinate posteriorly (Fig. 68). Lateral margins of the prothorax posterior of the eyes with short blunt ridges, posterior of these a diagonal ridge extending onto the posterior lobe (Fig. 69).

Prothorax ventrally tricarinate, central keel extending from posterior margins of the fore coxae to prothoracic pit. Lateral keels minutely nodulate not reaching beyond the line of the transverse groove.

Mesosternum nodulate anteriorly, depressed between the middle coxae which are about twice as wide apart as the hind coxae. Metasternum carinate, posteriorly appearing rounded although it is in fact slightly emarginate (Fig. 71).

Fore coxa about half as long as the prothorax. Fore leg (Fig. 70), sulcate area of femora slightly flattened. Middle and hind femora also flattened with their apices slightly enlarged. Male middle femora just over one fourth longer than the prothorax, female middle femora slightly longer 100: 30—35. Hind tibiae slightly longer than middle femora and almost as long as the hind femora. Apices of the male hind femora as long as or just surpassing the end of the large membrane (Fig. 72) and about half way along the sixth sternite, apices of female hind femora not quite reaching the end of the membrane.

Male operculum carinate, long and narrow, tip slightly narrowed (Fig. 75), central ridge of operculum crenulate (Fig. 77). Female operculum carinate, long and narrow (Fig. 78) extending well beyond the end of the connexivum (Fig. 79). Male genitalia (Fig. 73 and 74). Male respiratory siphon about three times as long as the operculum and twice as long as the sixth sternite, female siphon just over twice as long as the operculum and two thirds longer than the sixth sternite.

This species was described from Ceylon, Kandy and the female type was in Montandon's own collection; unfortunately I have not been able to discover its present whereabouts.

#### Distribution.

Ceylon: 2 ♀ Ceylon (BM), 1 ♀ Ceylon, Colombo 11 December 1910 A. Luther (ZMH), 1 ♀ Ceylon, Hobburunne (NMB), 2 ♂ 1 ♀ Ceylon, Central Province, Knuckles 15—24 August 1965 (CNM), 1 ♀ Ceylon, Homadala Estate, Udugama, Southern Province, from the edge of a stream 15 March 1965 P.B. Karuneratne (CNM).

This species is most likely to be confused with *fumosus*, female *strangulatus* can be easily recognised by the much longer operculum (Fig. 78) compared with *fumosus* (Fig. 67).

### *Cercotmetus compositus* Montandon

(Fig. 80—91)

*Cercotmetus compositus* Montandon, 1903: 109—110. — Montandon, 1909: 63—64 (discussion). — Montandon, 1911: 91—93 (comp. with *horni* and *robustus*) — Montandon, 1911A: 651 (comp. with *strangulatus*). — Paiva in Annandale, 1917: 80—81 (Descript. & figs.). — Lundblad, 1933: 50—51 (key, discussion & figs).

Males: 48—53 mm long, respiratory siphon 13—15.5 mm; females: 50—60 mm long, respiratory siphon 13.5—16 mm.

Interocular space variable, usually slightly less than the width of an eye, occasionally more, anterior inner margins of eyes sharply concave (Fig. 80). Vertex tuberculate (Fig.

81). Antennae (Fig. 84) large with stout spines. Anterior collar variable never very prominent. Anterior lobe over twice as long as the posterior lobe, sometimes nearly three times as long. Occasionally the distal fourth of the anterior lobe and proximal third of the posterior lobe slightly carinate.

Prothorax ventrally tricarinate, lateral keels reaching the line of the transverse groove. Central keel extending from the posterior margin of the fore coxae to distal fourth of the prothorax, becoming more rounded and raised distally.

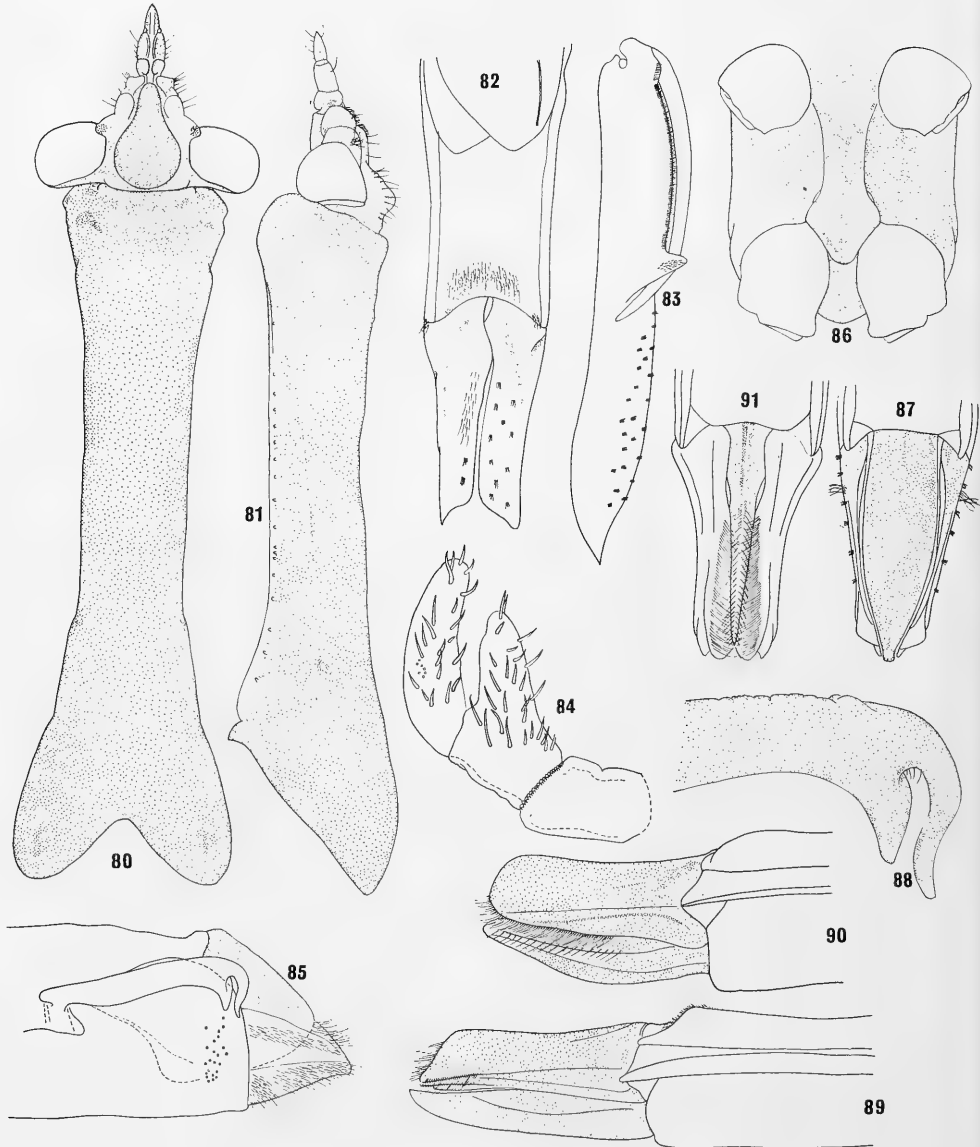


Fig. 80—91. *Cercotmetus compositus*, 80—89 ♂ and 90 and 91 ♀ from Sumatra. 80, head and prothorax above; 81, id. from the side; 82, 6th tergite; 83, fore leg; 84, antennae; 85, end of genital capsule; 86, metasternum; 88, paramere; 87 and 89—91, operculum

Mesosternum anteriorly slightly raised, not carinate but depressed anterior of the middle coxae which are about twice as wide apart as the hind coxae. Metasternum carinate (Fig. 86). The posterior margin of the metasternum is rather variable, about half the material studied had the posterior margin rounded (Fig. 86) the remainder were emarginate, two specimens had distinctly "lop-sided" emarginations. This variation occurred in both sexes from all the localities studied.

Fore coxa always more than half as long as the prothorax. Fore leg (Fig. 83) sulcate area distinctly flattened, middle and hind femora also flattened, distally enlarged and with a conspicuous fringe of hairs along distal ventral margins. Middle femora about one third longer than prothorax. Middle and hind tibiae fringed with very long hairs, proximal apices of middle tibiae bare and nearly as long as the middle femora. Hind tibiae about the same length as the middle femora and slightly shorter than the hind femora which reach about half way along the sixth sternite and the end of the membrane. Distal margin of the corium with short golden hairs. Sixth tergite raised and pilose (Fig. 89 and 90).

Male operculum "boat-shaped" broad and carinate (Fig. 87) slightly longer than the connexivum (Fig. 89). Female operculum very narrow and sharply carinate (Fig. 90 and 91). Male genitalia (Fig. 84 and 85). Respiratory siphon length three times or more that of the operculum and always more than twice as long as the sixth sternite, female siphon similar but slightly less than twice as long as the sixth sternite.

Montandon (1903) described *compositus* from a series of specimens (Laos, Hormand 1876; Bangkok, Mahe; Balasore) in the Paris Museum. Lundblad (1933) figured the parameres of a male from Laos and Balasore showing that two forms of *compositus* were apparently present in Montandon's type series. Unfortunately, I have not been able to see any of the material in the Paris Museum and have had to rely upon material named by Montandon from other Museums. My figures are based on a series from Sumatra, the parameres agree extremely well with Lundblad's figure based on the male from Laos in the Paris Museum.

#### Distribution.

Siam: 2 ♂ 4 ♀ Lower Siam, Trong W. L. Abbott (of this series 1 ♂ 1 ♀ Det. Montandon 1909 as *compositus*; 1 ♂ 2 ♀ Det. Montandon 1909 as *asiaticus* var *longicollis* and 1 ♀ Det. Montandon 1909 as *asiaticus* (USNM), 1 ♀ Siam, Sikuki River, Ban Ban, November 1923 Hugh Smith (USNM).

Viet Nam: 1 ♂ 1 ♀ Annam, Phuc Son, November—December, H. Rolle, H. Fruhstorfer, Det. Montandon 1911 as *compositus* (DEI), 2 ♂ Rep. Viet Nam 1 mile north of Quang Tri, 23 June 1970, taken alongside sides of stream just returned to normal level after flooding, A. R. Gillogly (Pol. Coll.), 1 ♂ 3 ♀ Cochin China, October 1923 (ML).

Sumatra: 4 ♂ 4 ♀ N.O. Sumatra, Tandjong (ML).

This species is easily recognised by its very large size, raised sixth tergite and the long hairs on the middle and hind femora disto-ventrally.

Paiva in Annandale (1917) recorded *compositus* from Cambodia with details as follows: "Two specimens. One from a small pool or ditch at the edge of the lake, Tale Sap, Patalung, 13.i.16, another from Koh Si Hah, Tale Sap, Singora Province". The figure of the hind leg showing the prominent distad ventral patch of hairs on the femora confirms the identity of these two specimens with the present concept of *compositus*.

SPECIES NOT SEEN  
**Cercotmetus horni** Montandon

*Cercotmetus horni* Montandon, 1911: 91—92. — Lundblad, 1933: 50 (key).

Female 42.5 mm long, respiratory siphon 9 mm.

According to Montandon (1911) *horni* may be distinguished from the other species by the following characters:

Large subglobose eyes, interocular space slightly wider than the width of an eye. Vertex not tuberculate. Prothorax "hour-glass" shaped. Membrane small like *asiaticus*. Mesosternum posteriorly slightly carinate.

It was described from New Guinea and dedicated to Dr. W. Horn of the Entomological Museum, Berlin. I have not been able to locate the unique type.

This species is very similar to *dissidens* and in my key comes out at the same couplet. Montandon must have described *dissidens* very shortly after *horni* since both were published in 1911. In his description of *dissidens* he does not refer to *horni*, comparing the former with *robustus* and *asiaticus*. I feel there is a possibility that *horni* and *dissidens* may be the same species.

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## INHOUD

K. KUMANSKI. — Die Unterfamilie Drusinae (Trichoptera) in Bulgarien, p. 107—121,  
Abb. 1—27.





# DIE UNTERFAMILIE DRUSINAE (TRICHOPTERA) IN BULGARIEN

von

KRASSIMIR KUMANSKI

*Sofia, Bulgarien*

## EINLEITUNG

Bis jetzt wurden auf dem Territorium Bulgariens, desgleichen auch auf der ganzen Balkanhalbinsel von der Unterfam. Drusinae nur die Gattungen *Drusus* Steph. und *Ecclisopteryx* Kol. festgestellt. Der grösste Teil der Arten gehört zu der ersten Gattung, in welcher zusammen mit den im europäischen Raum weitverbreiteten Arten auch viele Formen mit kleinem Areal (Endemiten) vorkommen. Nach Schmid (1956) ist letzteres ein Resultat der postglazialen Arealzerstückelung der kälteliebenden Ausgangsformen. Die in den Hochgebirgsregionen isolierten Populationen evoluierten in vielen Fällen auf selbständigem Wege.

Im Verlauf unserer Untersuchungen über die bulgarischen Drusinae ergab sich die Möglichkeit, parallel mit der Beschreibung einiger unbekannter Formen (*D. bureschi* sp.n., *D. romanicus meridionalis* ssp.n., *D. discophorus balcanicus* ssp.n., ♀ von *D. botoșaneanui* Kum.) und mit der Ergänzung unserer Kenntnisse einiger der bekannten Arten, eine kurze zoogeographische Analyse der Gruppe vorzunehmen, die im Schlußteil vorliegender Übersicht gegeben ist.

Die Verwirklichung der Arbeit in dieser Form wurde dank des mir von Herrn Dr. L. Botoșăneanu, Bukarest, überlassenen Vergleichsmaterials von ♂ der *D. romanicus* Murg. & Bots. und *D. tenellus* Klap. ermöglicht. Ich will ihm hier meinen herzlichsten Dank aussprechen. Dank gebührt auch meinem Kollegen Al. Popov, der die ersten Exemplare von *D. bureschi* sp.n. sammelte und mir übergab.

## SYSTEMTISCH-TAXONOMISCHER TEIL

*Drusus* Stephens

Gruppe *discolor*

*Drusus discolor* Rambur

Das mir zur Verfügung stehende massenhafte Material und die in der Literatur enthaltenen Angaben bezüglich der Morphologie des Imago, machen keinen übereinstimmenden Eindruck. Es handelt sich um die Beschreibung und die Abbildungen des Weibchens dieser Art bei Schmid (1956), die sich ziemlich stark von denen bei McLachlan (1876) unterscheiden, wie auch von der von Ulmer (1909) gegebenen Beschreibung. So schreibt McLachlan (p. 168—169):

„... In the ♀ the 9th dorsal segment is very narrow. Tubular piece above forming

two lanceolate acute hairy valves with a deep triangular excision between them; the sides broadly triangular; apex forming a deep cavity; on each side, below the tubular piece there is a very small oval appendage. Vulvar scale with broad triangular side lobes, and a longer slender middle lobe . . .”,

während wir bei Schmid bei der Umschreibung der Genitalia des Weibchens von *D. discolor* (p. 21), lesen:

„ . . . Pièce tubulaire large, mais extrêmement courte; le Xe segment est composé de deux lobes très largement séparés. La partie ventrale du IXe segment est plus longue que la pièce tubulaire et légèrement concave sur ses côtés. Les lobes latéraux de l'écaille vulvaire sont un peu plus longs que le lobe central et disposés en un demi-cercle régulier . . .”

Ob es sich hier nicht um das Weibchen einer anderen Art handelt?

Unsere Materialien entsprechen ziemlich gut der Originalbeschreibung und zur Unterstützung dieser Behauptung lege ich die Abbildungen der ♀ Genitalia (von einem Exemplar aus dem Pirin-Gebirge) bei. Offenkundig sind in unserem Falle die dorsalen Loben des X. Segments nicht so breit als tief separiert (Abb. 1) und im Profil (Abb. 2) sind sie betont länger als die subanale Platte („partie ventrale du IXe segment“); die Umriss der Subgenitalplatte (Abb. 3) sind ihrer Form nach von einem Halbkreise weit entfernt.

Diese Art ist bei uns aus den Rila- und Pirinmassiven bekannt; vor nicht langer Zeit stellte ich sie auch in den Balkan-Gebirgen fest, am Bach bei der Berghütte „Raj“, 1600 m Höhe, 10.VI.1970, 1 ♂.

#### Gruppe *muelleri*

#### *Drusus romanicus meridionalis* ssp.n.

Kumanski (1969) und Szczesny (1970) erwähnen die nicht völlige Ähnlichkeit zwischen den bulgarischen Exemplaren und den rumänischen der Originalbeschreibung der Art (Murgoči & Botoșăneanu, 1954). Nach einem eingehenden Vergleich der bulgarischen Materialien mit 2 ♂ Exemplaren aus Rumänien (leg. und det. L. Botoșăneanu) kam ich zur Überzeugung, daß es sich tatsächlich um zwei Unterarten handelt, die sich in ihrem Habitus und der Morphologie der Genitalien unterscheiden.

Die Unterscheidungsmerkmale der neuen Unterart bestehen in der helleren, rauchgelben allgemeinen Zeichnung des Körpers und in folgenden Eigenheiten der Genitalorgane:

App. superiores (Abb. 4a—c) bei den ♂ bemerkenswert kürzer als bei der Nominatform (Abb. 4d, e). App. intermediales im Profil mit schwächer individualisiertem oberen (freien) Teil; derselbe erhebt sich bei *romanicus romanicus* in seinem Vorderende unter einem geraden Winkel. Letzterwähntes ist nicht nur bei den Vergleichsexemplaren gut sichtbar, sondern auch bei der von Schmid gegebenen Zeichnung (1956, Pl. II, Abb. 4a), während die Abbildungen bei Murgoči & Botoșăneanu (1954) den unsrigen ähnlich sind. Innumrisse der App. inferiores (Abb. 5a) ebenfalls von denen der Nominatform (Abb. 5b) verschieden. Titillatoren einfach, nur mit einem einfachen subapikalen Dorn (Abb. 6).

Genitalia des ♀ im allgemeinen denen von *discolor* (Abb. 1—3) näherstehend als den für *romanicus romanicus* gegebenen Zeichnungen (Murgoči & Botoșăneanu, 1954, p. 971, Fig. 15—17). X. Segment mit tiefem, scharfem dorsalem Aus-

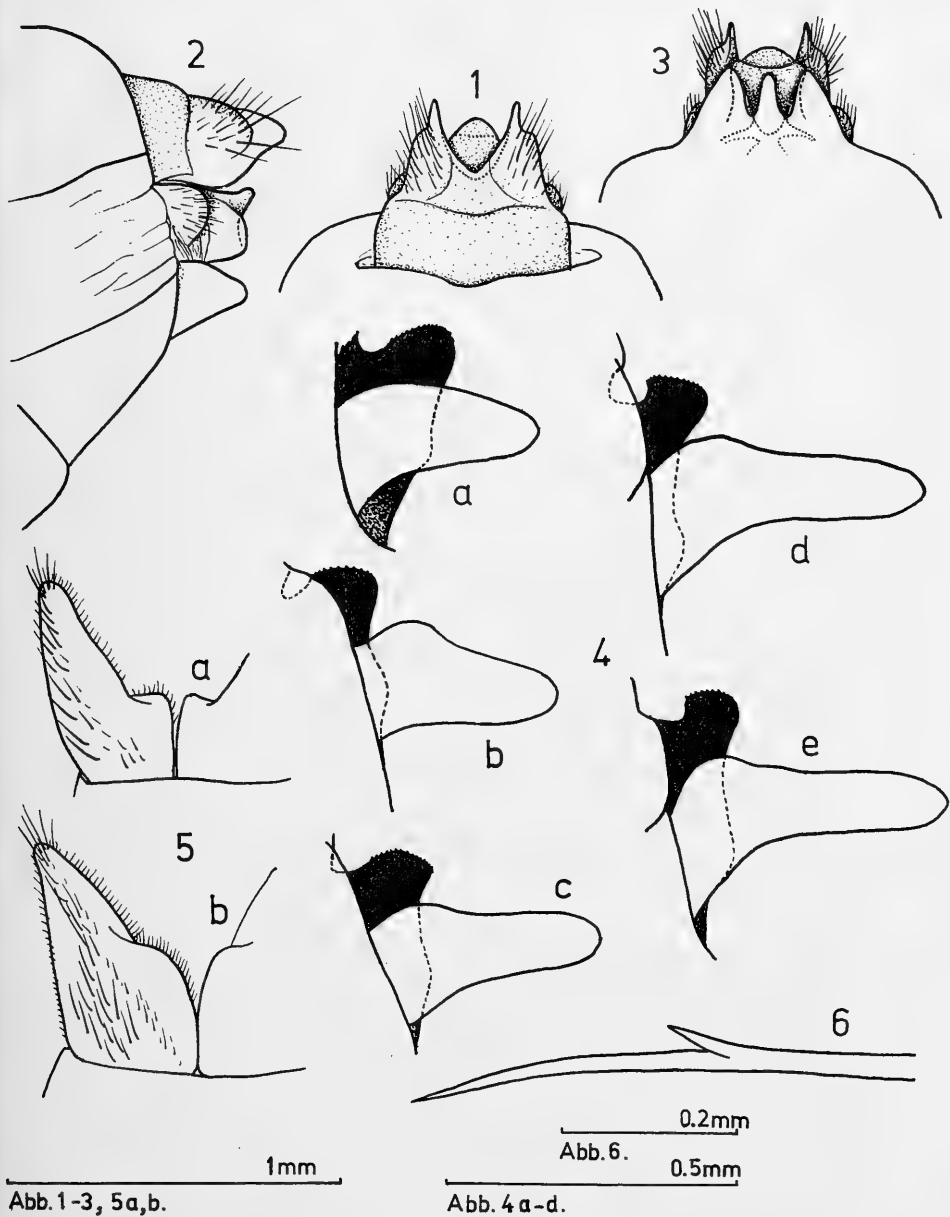


Abb. 1—3. *Drusus discolor* Ramb., Genitalia des ♀: 1, von oben gesehen; 2, Lateralansicht; 3, von unten gesehen. Abb. 4—6. *Drusus romanicus* Murg. & Bots., ♂: 4a-c, Ap. superior und Ap. intermedialis (Lateralansicht) des *Drusus romanicus meridionalis* ssp. n. (a, Exemplar vom Rila-Geb., b und c, vom Pirin-Geb.); 4d, e, dasselbe von *Drusus romanicus romanicus* Murg. & Bots. (d, Exemplar vom Banater-Geb., e, vom Fagarasch-Geb.); 5, App. inferiores (Fragment) von: a, *D. r. meridionalis* ssp. n.; b, *D. r. romanicus* Murg. & Bots.; 6, *D. r. meridionalis* ssp. n., Titillator

schnitt, der die dreieckigen freien lateralen Loben (Abb. 7) abtrennt. Letztere mit flacher Außenoberfläche, ohne die für *discolor* charakteristischen lateralen Erhebungen. Im Profil (Abb. 8) X. Segment groß, dreieckig. Subgenitalplatte (Abb. 9) verkürzt, mit dicken lateralen Loben, die nur gerundet enden, ohne sich der Spitze zu einzuengen; Medialteil zweimal länger als breit, fast so lang wie die lateralen Loben.

Das Material der neuen Unterart ist aus dem Pirin-Gebirge, Bänderischki-Zirkus, Bergbach unterhalb der Muratowi-Seen (2200 m Höhe), 21.IX.1967, 1 ♂ und 3 ♀ und aus der Umgebung der Berghütte „Demjanitza“ (1900 m Höhe), 1.VIII.1970, 1 ♂, wie auch aus dem Rila-Gebirge, Bergbach in dem Malöwitza-Zirkus, 9—12.VIII.1969, 2 ♂ (leg. M. Kownacka) und oberhalb der Hütte „Sawratschitza“ (etwa 2200 m Höhe), 10.VIII.1968, 2 ♂ (leg. Dr. I. Buresch).

#### Gruppe *mixtus*

#### *Drusus biguttatus* Pictet

Weit verbreitet in Mitteleuropa. Sein zweimaliges Auffinden von uns bestätigt die ursprüngliche Publikation der Art aus Bulgarien (Schmid, 1955, p. 119), Rila-Gebirge (Schmid, in lit.).

Neue Fundstätten: Pirin-Gebirge, Berghütte „Demjanitza“, 1—3.VIII.1970, 1 ♂ und 1 ♀ und Berghütte „Wichren“ (2060 m Höhe), die gleichen Daten, 1 ♂.

#### Gruppe *annulatus*

#### *Drusus annulatus* Stephens

Diese gewöhnliche mitteleuropäische Art wird für Bulgarien nur von Navás (1929) erwähnt. Vermutlich wurde diese Art mit *D. botosaneanui* verwechselt, aber wegen der Unmöglichkeit einer Nachprüfung des alten Materials muß sie unter gewisser Reserve im Verzeichnis der bulgarischen Köcherfliegen stehen bleiben.

#### *Drusus botosaneanui* Kumanski

Noch bei der kürzlich vorgenommenen Beschreibung der Art wurde ihre Verwandtschaft mit *D. tenellus* (Klap.) hervorgehoben. Vor nicht langer Zeit hatte ich die Möglichkeit das ♂ Exemplar zu betrachten, nach welchem *D. tenellus* von Klapálek (1913) aus Bulgarien erwähnt wurde. Dieses Exemplar erwies sich als zu *D. botosaneanui* gehörig. Ein abermaliger Vergleich der Typus-Serie mit der Beschreibung von *tenellus* (Klapálek, 1898) und mit dem Text und den Figuren von Schmid (1956, pp. 61—62, Pl. X, Fig. 2; Pl. XIII, Fig. 1 und Pl. XV, Fig. 1a und 2a), wie auch besonders mit 2 ♂ *D. tenellus* aus Rumänien, Apuseni-Massiv (leg. und det. L. Botoşăneanu) zerstreute jeden Zweifel in bezug auf die Tatsache, dass die bisherigen Mitteilungen über *tenellus* aus unserem Lande sich in Wirklichkeit auf *botosaneanui* beziehen.

Die Ähnlichkeit sowie auch die Unterschiede zwischen den beiden Arten werden auch bei den bis jetzt unbekanntem Weibchen von *botosaneanui* illustriert, deren Charakteristik folgt:

Färbung und Grösse wie bei den ♂.

Genitalia ♀: IX. und X. Segment völlig miteinander verschmolzen; Hinterrand des letzteren (Abb. 10) mit tiefem und scharfem medialem Ausschnitt, der die spitzen

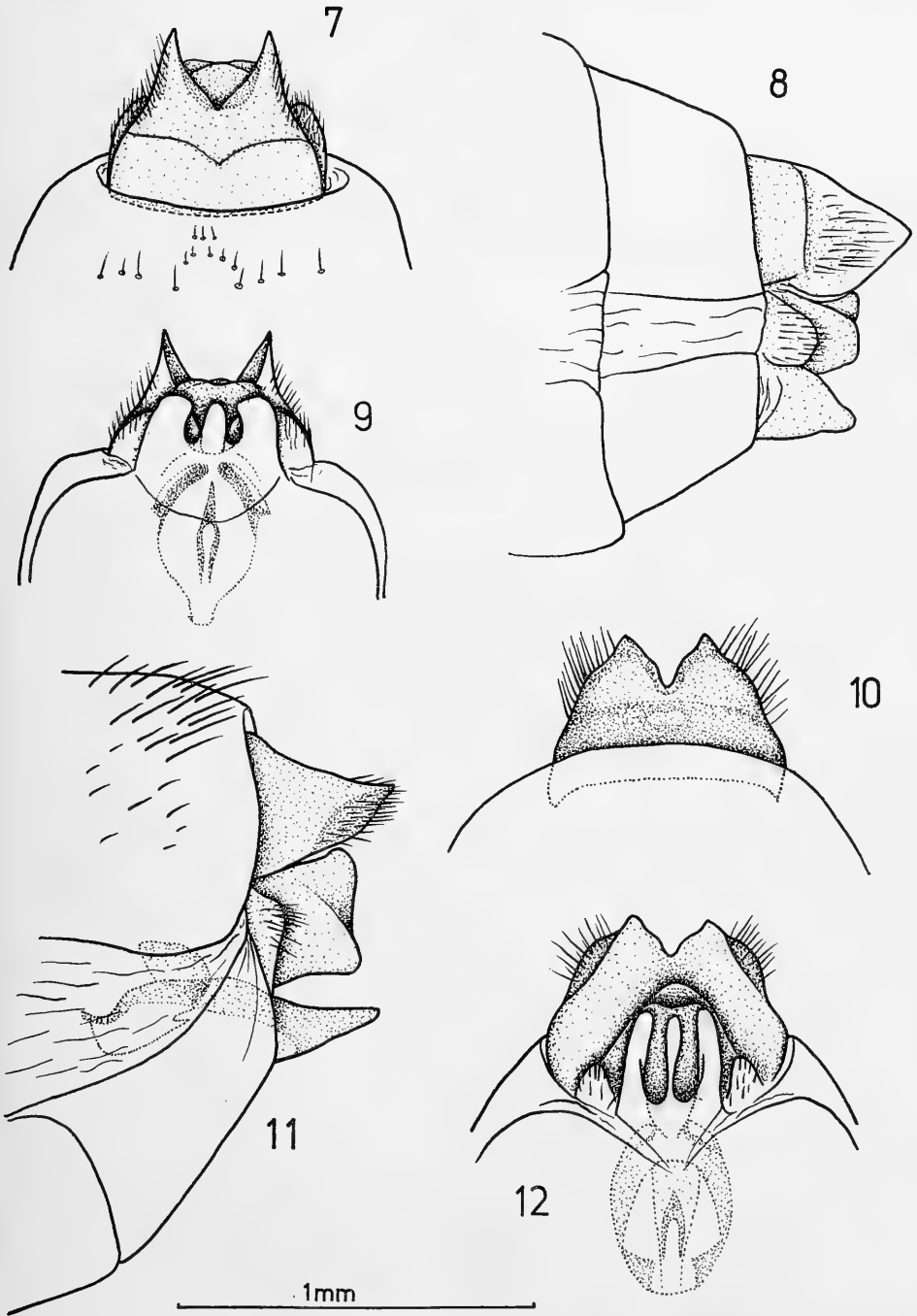


Abb. 7—9. *Drusus romanicus meridionalis* ssp. n., Genitalia des ♀: 7, von oben gesehen; 8, Lateralansicht; 9, von unten gesehen. Abb. 10—12. *Drusus botosaneanui* Kum., Genitalia des ♀: 10, von oben gesehen; 11, Lateralansicht; 12, von unten gesehen

dreieckigen lateralen Loben trennt. Letztere fein, ihrem schwach hervorgehobenen ventralen Teil zu behaart. Subanale Platte an ihrer Basis (horizontal sowie auch im Profil) sehr breit (Abb. 11), mit gerundetem oberem distalem Rand. Untere laterale Loben des IX. Segments schwach abstehend, mit breiter Basis. Subgenitalplatte verlängert, verhältnismäßig dünn im Profil (Abb. 11), ihr medialer Teil dünn, verlängert-schlägelförmig, fast die Länge der lateralen erreichend (Abb. 12).

Das ♀ von *D. botosaneanui* ähnelt einerseits dem ♀ von *tenellus*, von welchem es nach ihren stark entwickelten Loben des X. Segments und nach den Umrissen des dieselben trennenden Ausschnitts unterschieden werden kann; letzterer ist bei *tenellus* viel flacher und breit. Andererseits ist die Ähnlichkeit auch mit dem ♀ von *annulatus* ziemlich groß; bei letzterem erreicht jedoch der mediale Teil der vulvaren Platte kaum die Mitte der lateralen.

Diese Beschreibung wurde nach massenhaftem Material vorgenommen, das während des Monats Juli 1970 im Rhodopengebirge, längs des Baches bei der Berghütte „Smoljanski-Seen“ (1560 m Höhe) gesammelt wurde.

#### Gruppe *discophorus*

#### *Drusus discophorus discophorus* Radovanović

Nach der Auffindung von *Drusus discophorus* Rad. in den Balkengebirgen (Kumanski, 1971), wurde eine große Serie der gleichen Tiere im selben Gebiete gesammelt. Beim Überprüfen dieses Materials wurden einige Unterschiede zwischen den Individuen der Populationen aus den Balkengebirgen und aus dem Rila- und Pirin-Gebirge festgestellt. Die geographische Isoliertheit der beiden Populationen und die morphologischen Unterschiede zwischen ihnen dienten als Kriterium bei der Trennung von *D. discophorus* in zwei Unterarten.

Das Männchen der Nominatform ist durch seine Originalbeschreibung (Radovanović, 1942) und besonders durch die Arbeiten von Schmid (1956) und Botoşăneanu & Sýkora (1963) gut bekannt. Jedoch sind die Angaben über das ♀, die wir nur in der Beschreibung finden nicht genügend, besonders wegen der raschen Steigerung des Artenbestandes der Gattung *Drusus* mit nahestehenden neuen Formen. Aus diesem Grunde gebe ich vor der Beschreibung der neuen Unterart einige ergänzende Angaben über *D. discophorus discophorus*, die sowohl als unterscheidende Diagnose der Unterart dienen, als auch für ein allgemeines Erkennen der dieser Unterart zugehörigen Weibchen.

Gesamtzeichnung dunkel, aber in Alkohol aufbewahrte Exemplare sind ohne schwarze Einzelheiten. Die insgesamt untersuchten 21 ♂ und 8 ♀ von verschiedenen Hochgebirgsfundorten aus dem Rila- und Pirin-Gebirge zeigen in der Grösse keine Unterschiede; sie sind im allgemeinen kleiner als die neue Unterart. Flügel mit dicken und dunklen Adern. Länge des Vorderflügels zwischen 7.9 und 9.1 mm.

Bei den ♂ beläuft sich die Breite der spinulösen Zone des VIII. Tergiten auf 0.60—0.63 mm. Eines der charakteristischsten Merkmale dieser Unterart sind die vorstehenden Teile der App. intermediales. Diese sind im allgemeinen größer und derber; der Abstand zwischen ihren Spitzen bewegt sich zwischen 0.35 und 0.40 mm, durchschnittlich ist er 0.37 mm.

Beim ♀ ist die mediale Vertiefung des Hinterrandes des X. Segments sehr flach und mit stark verkürzten Seiten. Die freien behaarten Teile des X. Segments entsprechend schwach individualisiert und am besten bei Betrachtung im Profil sichtbar. Subanalplatte

massiv; ventrale Anhänge des IX. Segments verlängert. Subgenitalplatte mit einem sehr kurzen medialen Teil.

*Drusus discophorus balcanicus* ssp. n.

Kopf und Basalglieder der Antennen ziemlich dunkel, rötlichbraun; Palpen, Antennen, Thorax und Beine etwas heller, gelbbraun. Beine verlängert; das Verhältnis zwischen der Länge von Femur, Tibia und Metatarsus wie 8.0 : 7.0 : 3.7.

Tergite und Sternite des Abdomens rauchfarben-bräunlich. Flügel am hellsten, gelb, mit verhältnismäßig dünnen Adern.

♂ und ♀ ungefähr gleich gross, im allgemeinen größer als die Nominalunterart; Länge des Vorderflügels 10.6—12.3 mm.

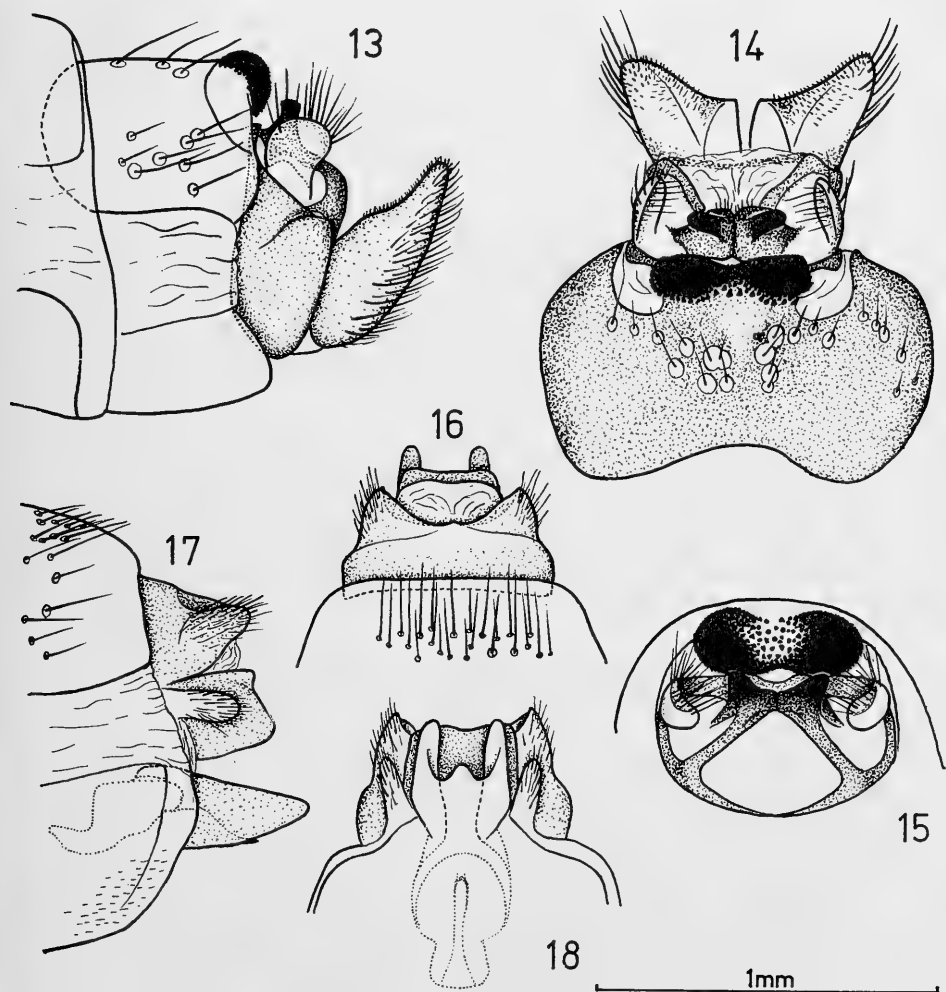


Abb. 13—18. *Drusus discophorus balcanicus* ssp. n. 13—15, Genitalia des ♂: 13, Lateralansicht; 14, von oben gesehen; 15, von hinten gesehen (Fragment); 16—18, Genitalia des ♀: 16, von oben gesehen; 17, Lateralansicht; 18, von unten gesehen

**Genitalia** ♂: in allgemeinen Linien nach dem Bau von *D. discophorus discophorus* konstruiert. VIII. Tergit dunkler als die übrigen; die charakteristische Vertiefung an ihrem Medialteil vorhanden. Spinulose Zone sehr kompakt; Dornen dicht, im Medialbezirk zerstreuter; Außenumrisse, der Dorsalseite zu, mit flacher medialer Vertiefung, dank derer die seitlichen Bezirke schwach hervorstehen. Die Breite der Zone variiert zwischen 0.47 und 0.60 mm; im Durchschnitt ist sie 0.53 mm. Die freien Teile der App. intermediales zarter als die der anderen Unterart. Letztere sind im Profil erkennbar (Abb. 13) und noch besser bei einer Betrachtung von oben (Abb. 14) und en face (Abb. 15) zu sehen. Der Abstand zwischen den Spitzen der App. intermediales ist kleiner als bei der Nominatunterart und beläuft sich fast ohne Abweichungen auf 0.33 mm. App. superiores und App. inferiores ohne Unterschiede von der Nominatform.

**Genitalia** ♀ auf Abb. 16—18; praktisch denen von *D. discophorus discophorus* gänzlich nahe.

Die Fundorte der neuen subspecies befinden sich in dem Zentral-Balkengebirge: Berg-hütte „Täža“ (1500 m Höhe), 17.V.1968, 3 ♂ und 1 ♀; Bach bei der Berghütte „Raj“, 1 ♀ und subalpiner Bach (1900—2000 m Höhe), rechter Zufluß des Baches Täža, 10.VI.1971, massenhaft anzutreffen (insgesamt 43 ♂ und 10 ♀ gesammelt).

#### *Drusus bureschi* sp. n.

Helle Insekten, fast gänzlich bräunlichgelb. Dunkler, fast braunfarbig ist nur das Basalglied der Antennen, die metatarsalen Glieder und die Dorsalseite des Abdomens. Maxillartaster verhältnismäßig lang; Basalglied dicker und ungefähr halb so lang wie das folgende; drittes Glied am dünnsten und ein wenig länger als das zweite. Beine verlängert. Vordertibia sehr lang, 6/7 von der Länge des Femurs erreichend und fast zweimal so lang wie der Protarsus (Abb. 19).

Spornzahl 1, 3, 3. Kein Grössenunterschied zwischen den Geschlechtern; Körperlänge (ohne Kopf) 7.8—9.4 mm, Vorderflügel 11.0—12.8 mm. Geäder ohne Besonderheiten.

**Genitalia** ♂: In seinem Distalteil zeigt das VIII. Tergit eine weitläufige spinulose Zone; ihre Breite bewegt sich zwischen 0.65 und 0.75 mm, durchschnittlich 0.73 mm. Bei Ober- und Hinteransicht (Abb. 20 und 21) ist die unregelmäßige Verteilung der Dörnchen zu sehen: im Medialteil sind sie ziemlich spärlich und die schwach hervortretenden Seitenbezirke sind dicht bedeckt. In seinem Medialteil bildet das Tergit die für *discophorus* charakteristische Vertiefung. In seiner unteren Hälfte ist das IX. Segment mäßig lang, im Dorsalteil stark eingeengt und bis zu einem schmalen Chitinstreifen reduziert, der unter der Unterhülle des VIII. Tergit versteckt ist. App. superiores gut entwickelt, im Profil oval (Abb. 22). Sie sind rückwärts und teilweise nach oben gerichtet, gleichlaufend, mit leicht konkaver medialer Oberfläche. App. intermediales mit charakteristischer Form, die am besten bei Betrachtung von oben und von hinten erfaßt werden kann. Sie stellen zwei schwarze, stark chitinisierte und ziemlich dicke Auswüchse dar, die quer gelagert (Abb. 20) und im Profil nach hinten und oben gerichtet sind. Deren freie Teile sind in ihrem distolateralen Teil am größten; ihre Ober-ränder fein gezähnt, mit je einer schwachen Erhebung vor den oberen Ecken; der Abstand zwischen letzteren beträgt 0.56—0.60 mm. Basalbezirke der App. intermediales gross, dicht genähert, aber nicht mit einander verschmolzen. X. Segment verhältnismäßig massiv, ventral geschlossen; seine Lateralecken stark verdickt, im Profil zwischen den oberen und unteren Anhängen hervorspringend. Perianalfeld, vom inneren Rand des



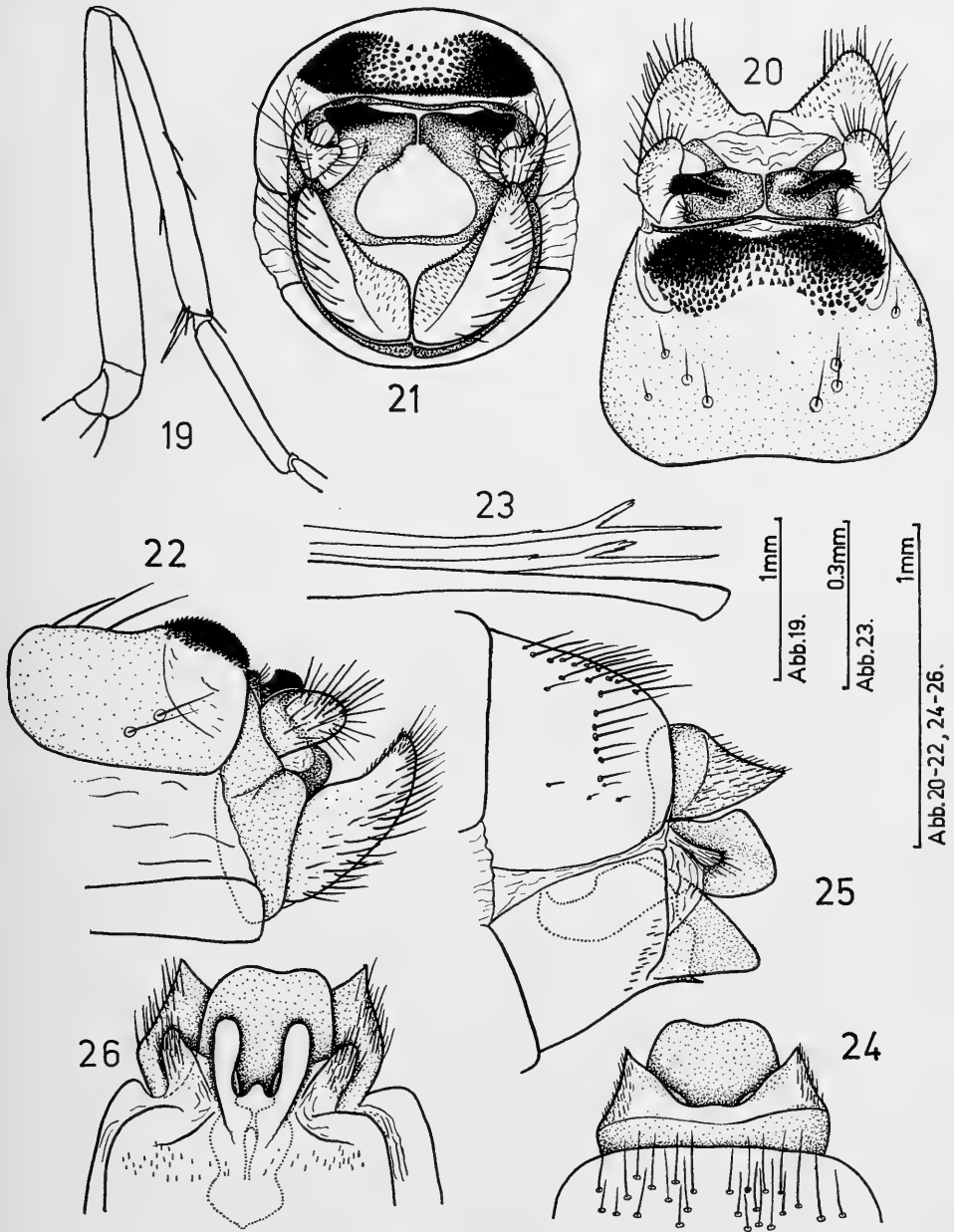


Abb. 19—26. *Drusus bureschi* sp. n. 19, Vorderbein des ♂; 20—23, Genitalia des ♂: 20, von oben gesehen; 21, von hinten gesehen; 22, Lateralansicht; 23, Penialapparat. 24—26, Genitalia des ♀: 24, von oben gesehen; 25, Lateralansicht; 26, von unten gesehen

X. Segments umrissen, mit breiter birnförmiger Basis. App. inferiores denjenigen von *discophorus* ähnlich — ziemlich groß, mit zugespitztem und nach oben gerichtetem distalem Teil (Abb. 22). Penialapparat (Abb. 23) ohne Abweichungen vom allgemeinen Schema der Gattung: Phallus mit schwach erweitertem distalem Teil; Titilatoren fast seine Länge erreichend, mit sehr dünnen, nadelförmig zugespitzten Enden und mit je einem Dörnchen in ihrem Distaldrittel.

Genitalia ♀: IX. und X. Segment völlig verschmolzen, dorsal ziemlich breit. Letzteres mit zwei gut formierten, von allen Seiten dreieckigen Loben, kurz und verhältnismäßig dicht behaart durch einen breiten und ziemlich tiefen Ausschnitt getrennt (Abb. 24). Der ventrale Teil des IX. Segments stellt eine breite und dicke, stark chitinierte subanale Platte dar, im Profil schräg abgeschnitten (Abb. 25). An ihrer Basis sind lateral die stark behaarten seitlichen Anhänge gelagert; sie sind gerundet, im Profil sehr schmal, mit einem langen freien Teil. Seitliche Loben der Subgenitalplatte lang, oval, im Profil dreieckig, mit einem breiten Basalteil. Medialteil sehr kurz (Abb. 26).

Material und Fundorte: Östliche Balkangebirge, a) Eleno-Twärdischki-Paß (1000 m Höhe), 25.V.1969, 1 ♂ (leg. Al. Popov); b) Längs eines kleinen Bergbaches, 4 km östlich vom Paß und c) Bei einem ungestümen Bergbach, am Beginn des Twärdischka-Baches (eines Zuflusses der Tundža), ungefähr 10 km östlich vom Paß, 12.VI.1971, insgesamt 3 ♂ und 4 ♀; d) Balkangebirge bei der Stadt Sliwen, Örtlichkeit Karandilja, 21.V.1969, 1 ♂ (leg. Al. Popov).

Als Typusexemplar bezeichnete ich ein ♂ vom Fundort c). Dasselbe sowie auch die übrigen Exemplare sind in Alkohol in der Sammlung des Zoologischen Instituts mit Museum bei der Bulgarischen Akademie der Wissenschaften aufbewahrt.

Die Art wurde unserem hervorragenden Zoologen, dem Akademienmitglied Dr. Iwan Buresch gewidmet.

Diskussion. Nach vielen ihrer Merkmale steht die neue Art *D. discophorus* ziemlich nahe; letztere galt als eine in dem Rahmen der Gattung isolierte Art (Schmid, 1956). Die Auffindung ihrer Unterart *balcanicus* in den Balkangebirgen sowie auch das Antreffen von *D. bureschi* erlaubt die Vereinigung der drei Taxa in eine neue Gruppe — die Gruppe von *discophorus*. Die Zusammengehörigkeit dieser Gruppe beruht bei den ♂ auf der Vertiefung der dorsalen Oberfläche des VIII. Tergiten, dem gleichen Aussehen der App. inferiores und dem gemeinsamen Schema des X. Segments mit App. intermediales und bei den ♀ auf der allgemeinen Ähnlichkeit der Genitalstrukturen.

Die Eigenheiten, die *D. bureschi* individualisieren, sind folgende: eine breite zona spinulata am VIII. Tergit; die eigenartige Form und die weit entfernten Spitzen der App. intermediales bei den ♂ und die zugespitzten seitlichen Teile des X. Segments bei den ♀.

In nachfolgender Tabelle sind die unterschiedlichen Merkmale der Vertreter aus der neuen Gruppe *discophorus* aufgeführt:

Arten	<i>D. d. discophorus</i> Rad.	<i>D. d. balcanicus</i> ssp.n.	<i>D. bureschi</i> sp.n.
Merkmale			
1. Geäder und Länge der Vorderflügel (mm)	derb und dick geädert 8.4 (7.9—9.1)	Geäder feiner 11.7 (10.6—12.5)	Geäder feiner 12.2 (11.0—12.8)
2. Genitalia ♂:			
a) Breite der Z. spinulata (mm)	0.62 (0.60—0.63)	0.53 (0.47—0.60)	0.73 (0.65—0.75)
b) Form der App. intermed.	massiv	dünnere	in der Form von Querplatten
c. Abstand zwischen den Spitzen der App. intermed. (mm)	0.37 (0.35—0.40)	0.33	0.58 (0.56—0.60)
3. Genitalia ♀:			
Loben d. X segm.	klein, im Profil gerundet-dreieckig	gerundet-dreieckig	groß und spitz
4. Lokalitäten	Jugoslawien; SW-Bulgarien: Rila, Pirin-Geb.	Bulgarien: Zentral-Balkan-Geb.	Bulgarien: Ost-Balkangeb.
5. Höhenbesiedlung (m)	1900—2500	1500—2000	950—1200

### *Ecclisopteryx* Kolenati

#### *Ecclisopteryx guttulata dalearlica* Kolenati

Die Art wurde für Bulgarien aus dem Rila-, Pirin- und Rhodopen-Gebirge erwähnt. In der Folge fand ich sie vielmals an verschiedenen Fundorten in diesen Gebirgen, desgleichen auch in den Balkangebirgen (Bach Tscherni Osäm oberhalb des Trojan-Klosters, 22.VII.1969, 1 ♂).

Die Flugperiode umfaßt das Juniende bis zur ersten Augushälfte, mit einem Maximum während des Monats Juli. Die Fundorte dieser Art befinden sich bei uns zwischen 1800 und 900 m Höhe.

Die Spornzahl beträgt bei den bulgarischen Exemplaren (♂ und ♀) beständig 1, 2, 3 (nach Schmid, 1956, p. 76: 1, 2, 2).

#### *Ecclisopteryx madida* McLachlan

Die einzige und unsichere Erwähnung (mit?) der zweiten Art dieser Gattung (Navás, 1929, p. 142) aus dem Rila-Gebirge betrachte ich als nicht genügend um ihr bleiben in der bulgarischen Köcherfliegen-Liste zu rechtfertigen, hauptsächlich wegen der Unmöglichkeit einer Revision des Materials. (Ein ähnlicher Fall ist auch *D. annulatus*).

#### BESTIMMUNGSTABELLEN DER GATTUNG *Drusus* AUS BULGARIEN

##### Männchen

1. Spornzahl 1, 2, 2 . . . . . *biguttatus* Pict.  
— Spornzahl 1, 2, 3 . . . . . *botosaneanui* Kum.

- Spornzahl 1, 3, 3 (selten 0, 3, 3) . . . . . 2
2. App. superiores im Profil schmal verlängert und biegsam, mit kürzerem ansteigendem Basal- und langem horizontalem Distalteil . . . *romanicus meridionalis* ssp. n.
- App. superiores ohne Umbiegung, viel kürzer . . . . . 3
3. Spinulose Zone des VIII. Tergit dorsal gerundet-dreieckig, mit drei hervorspringenden Bezirken — einen subapikalen und zwei lateralen apikalen . . . *discolor* Ramb.
- Spinulose Zone des VIII. Tergit mit zwei schwach hervorspringenden lateralen Bezirken; Dörnchen zwischen diesen spärlicher . . . . . 4
4. App. superiores überall oval-hervortretend, sehr klein; (in Bulgarien fraglich) . . . . . *annulatus* Steph.
- App. superiores  $\pm$  abgeflacht, mit konkaver Innen- und konvexer Außenseite . . . 5
5. App. intermediales dorsal in der Form von dünnen Querplatten, weit auseinander gespreizt (0.56—0.60 mm); spinulose Zone des VIII. Tergite breit (0.65—0.75 mm) . . . . . *buceschi* sp. n.
- App. intermediales derber, spinulose Zone schmaler . . . . . 6
6. App. intermediales massiv, dick; Abstand zwischen ihren Spitzen 0.35—0.40 mm; spinulose Zone 0.60—0.63 mm breit; Flügel mit groben Adern, Vorderflügel 7.9—9.1 mm lang (Rila- und Pirin-Gebirge) . . . . . *discophorus discophorus* Rad.
- App. intermediales dünner, Abstand zwischen ihren Spitzen 0.33 mm; spinulose Zone kompakt (0.47—0.60 mm); Geäder verhältnismäßig zarter; Vorderflügelänge 10.6—11.5 mm (Balkangebirge) . . . . . *discophorus balcanicus* ssp. n.

## Weibchen

1. Spornzahl 1, 2, 2 . . . . . *biguttatus* Pict.
- Spornzahl 1, 2, 3 . . . . . *botosaneanui* Kum.
- Spornzahl 1, 3, 3 . . . . . 2
2. Abdomenende (X. Segment) dorsal mit einem tiefen, scharfeckigen Ausschnitt, der die dreieckigen distalen Teile des Segments trennt; Medialteil der subgenitalen Platte mindestens bis zur Mitte der lateralen . . . . . 3
- Distalteile des X. Segments kleiner, dorsal durch einen breiten und flachen Ausschnitt getrennt; Medialteil der subgenitalen Platte sehr kurz, kaum angedeutet . . . 5
3. Medialteil der subgenitalen Platte bis zur Mitte der seitlichen (in Bulgarien fraglich) . . . . . *annulatus* Steph.
- Medialteil fast so lang wie die seitlichen . . . . . 4
4. Distalteile des X. Segments mit deutlichen Erhebungen an ihrer Außenseite, was sowohl von oben als auch ventral zu sehen ist; Lateralteile der subgenitalen Platte mit gerundet-zugespitzten Enden . . . . . *discolor* Ramb.
- Außenseiten glatt; laterale Teile am Ende nicht zugespitzt, nur breit gerundet . . . . . *romanicus meridionalis* ssp. n.
5. Distale Teile im Profil mit scharfen Spitzen . . . . . *buceschi* sp. n.
- Distale Teile mit gerundeten Spitzen (im Profil) . . . . . 6
6. Vorderflügelänge bis 9 mm; Geäder dick und derb (Rila- und Pirin-Gebirge) . . . . . *discophorus discophorus* Rad.
- Größere Tiere, Vorderflügelänge 10.8—12.1 mm; Geäder verhältnismäßig feiner (Balkangebirge) . . . . . *discophorus balcanicus* ssp. n.

## ZOOGEOGRAPHISCHE NOTIZEN

Die Analyse des Artenbestandes der Unterfamilie Drusinae in Bulgarien zeigt, daß die Fauna dieser Gruppe von zwei Komponenten zusammengestellt ist. Der erste schließt die weitverbreiteten europäischen Formen ein, die mit Sicherheit aus Bulgarien festgestellt wurden: *Drusus discolor*, *biguttatus* und *Ecclisopteryx guttulata dalecarlica*. Die südöstliche Verbreitungsgrenze dieser Arten zieht durch das Territorium Bulgariens. Unabhängig davon sind *D. discolor* und *E. g. dalecarlica* ziemlich massenhaft und weitverbreitet bei uns und nur bei *D. biguttatus* — eine der am seltensten anzutreffenden Arten — wird eine für die Peripherie des Areals natürliche Lichtung der Populationsdichte beobachtet.

Das zweite Element ist aus den Formen gebildet, die nur einzelne Bezirke vom Territorium der Balkanhalbinsel besiedeln. An erster Stelle steht hier die massenhaft vorkommende Art *D. botosaneanui*, welche alle hohen bulgarischen und aller Wahrscheinlichkeit nach auch einige ostjugoslawische Gebirge besiedelt. Besonders vermerkt muß die Art *D. discophorus* werden, die mit ihrer Nominalunterart in den Gebirgen Bosniens, Mazedoniens und Südwestbulgariens (Rila und Pirin) anzutreffen ist, und mit der Unterart *balcanicus* in der nordöstlichen Gegend ihres Areals (Balkangebirge). Der neuentdeckte *D. bureschi* ist aller Wahrscheinlichkeit nach ein Endemit aus dem Ost-Balkan. Er ist mit *D. discophorus* nahe verwandt und zusammen mit den zwei Unterarten des letzteren das Resultat einer Artenbildung von einer gemeinsamen Urform unter den Bedingungen der geographischen Isolierung.

Die Verbindung zwischen den Balkan-Gebirgsmassiven und den Karpaten wird im Westen von *D. tenellus* demonstriert (Montenegro, Bosnien, Mazedonien — Karpaten) und im Osten von *D. romanicus*. Von der letzterwähnten Art treffen wir in den Karpaten die Nominalunterart *romanicus romanicus* an und im Rila- und Pirin-Gebirge die Unterart *romanicus meridionalis*.

Wie schon im Anfang erwähnt, werden lokale Formen der Gattung *Drusus* in Hülle und Fülle angetroffen, was zu einer genauen Feststellung der artenbildenden Zentren beiträgt. Besonders reich an solchen Arten ist das Territorium der Balkanhalbinsel. Hier müssen auch die unlängst aus Bosnien beschriebenen drei neuen *Drusus*-Arten (Marinković-Gospodnetić, 1971) erwähnt werden, die wahrscheinlich Endemiten sind. Mit ihnen erreicht die Zahl der Balkanarten die Ziffer 17, von denen 13 nur von der Balkanhalbinsel bekannt sind (Abb. 27). Diese große Anzahl legt dar, daß gleichzeitig mit dem Hauptzentrum der Verbreitung — den Alpen — die Gebirge der Balkanhalbinsel, ähnlich den Karpaten (Botosăneanu, 1962), ein sekundäres, aber nach seinem Maßstabe bedeutendes artenbildendes Zentrum darstellen.

Obenerwähntes gilt im höchsten Grade für das ausgedehnte Gebiet der Dinarischen Alpen, das von 7 \* endemischen Formen besiedelt wird (58 % von allen balkanischen *Drusus*-Endemiten); in den Balkangebirgen sowie auch im Rhodopengebirgssystem sind je 2 solcher Formen zu vermerken und *D. discophorus discophorus* ist für die Dinarischen Alpen und das Rhodopensystem gemeinsam.

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\* Die jetzige Erforschungsstufe der Gebirge auf der Balkanhalbinsel berechtigt uns zur realen Annahme, daß die Anzahl der endemischen Formen durch künftige Untersuchungen noch erhöht werden wird; am aussichtsreichsten verbleiben in dieser Beziehung die zahlreichen einzelnen Gebirge vom System der Dinariden, die sich in Jugoslawien, Albanien und Griechenland befinden.

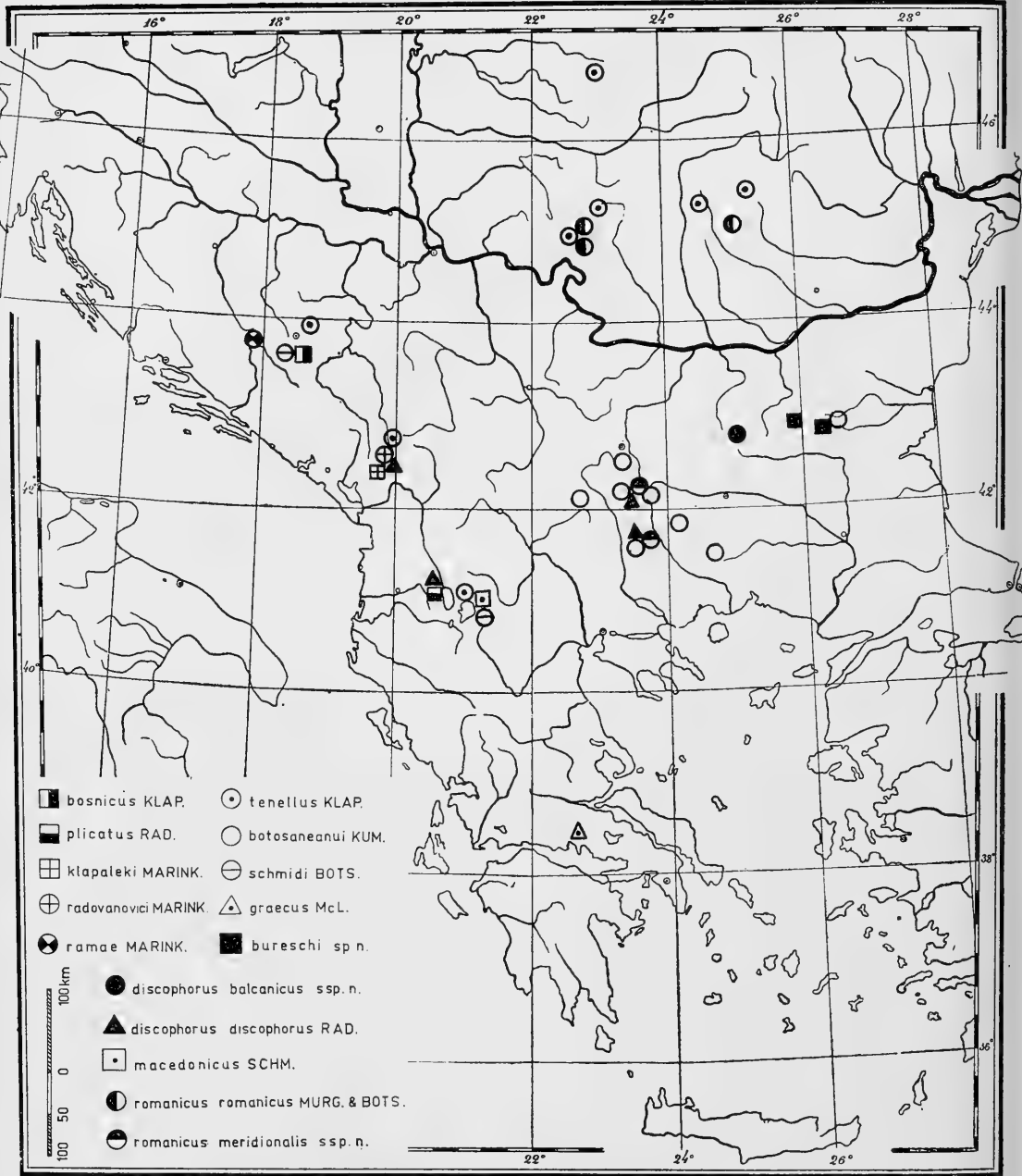


Abb. 27. Verbreitungskarte der endemischen *Drusus*-Arten der Balkanhalbinsel (einschließlich *Drusus tenellus* Klap. und *Drusus romanicus romanicus* Murg. & Bots.)

Die Wahrscheinlichkeit, daß die erwähnten Arten „jung“ sind (Neoendemiten) wird überzeugend durch das Fehlen von kraß morphologisch isolierten Formen unterstützt; fast in allen Fällen sind die Arten nicht stark voneinander verschieden und in zwei der Fälle erreichte die Absonderung nur das Unterart-Niveau.

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## INHOUD

J. P. VAN LITH. — Psenini from Nepal (Hymenoptera, Sphecidae), p. 123—143, Figs. 1—41.



## PSENINI FROM NEPAL (HYMENOPTERA, SPHECIDAE)

by

J. P. VAN LITH

Rotterdam

### ABSTRACT

The Psenini collected by the Canadian Nepal Expedition in 1967 are discussed. The following new forms are described and illustrated: *Psen nitidus himalayensis* (♀); *Psen lobicornis* (♂); *Psenulus orinus* (♀♂); *Psenulus chillcotti* (♀♂); *Psenulus godavariensis* (♂); and *Psenulus birganjensis* (♂). Of *Psen rufoannulatus* Cameron and *Psen rufiventris* Cameron the males are described for the first time.

Through the kind mediation of Dr. Carl M. Yoshimoto I had the opportunity to study the Psenini collected by the Canadian Nepal Expedition of the Entomology Research Institute, Ottawa. The material belongs to the Canadian National Collection in Ottawa; a few duplicates are in the author's collection.

So far only *Psenulus bicinctus* Turner (1912) and *Psen nepalensis* Van Lith (1968) were recorded from Nepal, collected by the Bishop Museum, Honolulu (Van Lith, 1972) and by the East Nepal Expedition 1961-1962 of the British Museum (Natural History), respectively. The fresh material consists of 12 species and one subspecies, of which five species and the subspecies are new; *Psenulus bicinctus* was not represented on this occasion.

Most of the material was collected in Malaise traps. Dr. W. R. M. Mason, the hymenopterist of the expedition, kindly supplied me with most of the notes on the collecting localities and the habitat of the Psenini; a few data originate from G. W. Byers (1971).

- a. Adhabhar, near Simra, 600 ft, and
- b. Lothar, near Birganj, 450 ft; Simra and Birganj are in the lowlands of the Terai (S Nepal), grazed sal forest (*Shorea robusta*, a large gregarious tree) typical of the region. Fourteen specimens were collected here in August and September.
- c. Godavari, a village about ten miles SE of Kathmandu. The greater part of the material, viz. 25 specimens, were collected here at an altitude of 5000 and 6000 ft, in July and August, one male of *Psen rufoannulatus* in mid April.
- d. Pulchauki, 8000 ft, a mountain about ten miles SE of Kathmandu. *Psen rufiventris* was collected here early July.
- e. Patibhanjyang, near Kathmandu, a mountain district of steep pastures and terrace cultivation, a little above the limit of rice cultivation. A second male of *Psen rufoannulatus* was taken here at an altitude of 6000—7500 ft, in July, along the trails through the mountain pastures.
- f. Bhurumche, about 20 miles N of Kathmandu at an altitude of approximately 9000 ft, the last Sherpa village on the road to Gosainkund. The surroundings are cut over forest of the evergreen oak *Quercus semicarpifolia*. There is much secondary *Rhododendron* forest and many clearings are used for pasture. *Psen lobicornis* was collected here early in July.

g. The localities of the Malaise traps in which the five specimens of *Psenulus orinus* were found in May, are only given in latitude and longitude degrees. However, Dr. Mason, in his letter of May 30, 1972, gives interesting information on the peculiarities of the sites of these traps, viz. trap no. 5, 10,100 ft, 27°57' N, 84°59' E, SW of Kathmandu; trap no. 6, 10,500 ft, 28°00' N, 85°00' E and trap no. 7, 9900 ft, same latitude and longitude, NW of Kathmandu, as follows: "Malaise trap no. 5 was placed in a comparatively wet gorge (it was the dry season) occupied by a small stream flowing over shale bedrock. The exposure was north and the forest consisted of *Tsuga*, *Abies*, *Acer*, *Corylus*, *Rhododendron* and dwarf bamboo. Traps no. 6 and no. 7 were set near together on a steep slope with northern exposure. The forest on north facing slopes is quite different from that on slopes facing in the other three directions. Although it was dry season the ground was very wet and consisted of a tangled and slippery mass of roots and vines, very difficult to walk in. The forest consisted mostly of *Rhododendron* with a few *Abies* still remaining. It would undoubtedly have been a pure *Abies* forest but for the logging activities of the local people. At the lower trap, no. 7, there were in addition many deciduous trees, such as *Quercus*, *Acer*, *Prunus* and *Daphne* as well as *Tsuga*, dwarf bamboo and numerous vines, mostly *Clematis*. I am told that these steep north facing slopes hold the snow in winter because the lower altitude of the sun does not strike them and melt the snow as it does on other exposures. Because of the superior moisture holding ability of the north slopes and also because they do not burn readily in the dry season the insect fauna seems to be much richer."

No other Psenini were collected in these three traps, but this may be due to the early time of the year.

Together with a female of *Psen rufoannulatus* from Kathmandu, 4400 ft, a total of 48 specimens is reached, a very satisfactory result. In this paper I have also included the allotype of *Psen rufiventris*, from Simla, which is in the British Museum collection and a female of *Psenulus chillcotti*, of the B.M. Nepal Expedition, 1954.

My thanks are due to the authorities of the Canadian National Collection, to Dr. W. R. M. Mason, who kindly authorized me to publish his notes on the habitats, and to Dr. Carl M. Yoshimoto, both of the Entomology Research Institute, Ottawa. I am also much obliged to the authorities and staff of the British Museum (Natural History), London, and of the Oxford University Museum, who enabled me to compare the material with types in their collections.

### ***Psen (Psen) nepalensis* Van Lith**

Van Lith, 1968: 103—104, ♀ (E Nepal).

New record from Nepal: 1 ♀, Kathmandu, Godavari, 5000 ft, 15 July, 1967.

This specimen has been compared with the holotype, collected in 1961 by the B.M. Nepal Expedition. Thorns on hind tibiae somewhat brownish, whitish in the type. Punctuation of scutum in both specimens dense and deep, punctures often in rows, interstices between rows often larger than diameter of punctures. Punctures on frons much deeper than in *P. emarginatus* Van Lith from Java, to which form it is closely related.

Long hairs on hind margins of tergites rather fine, much worn in some places.

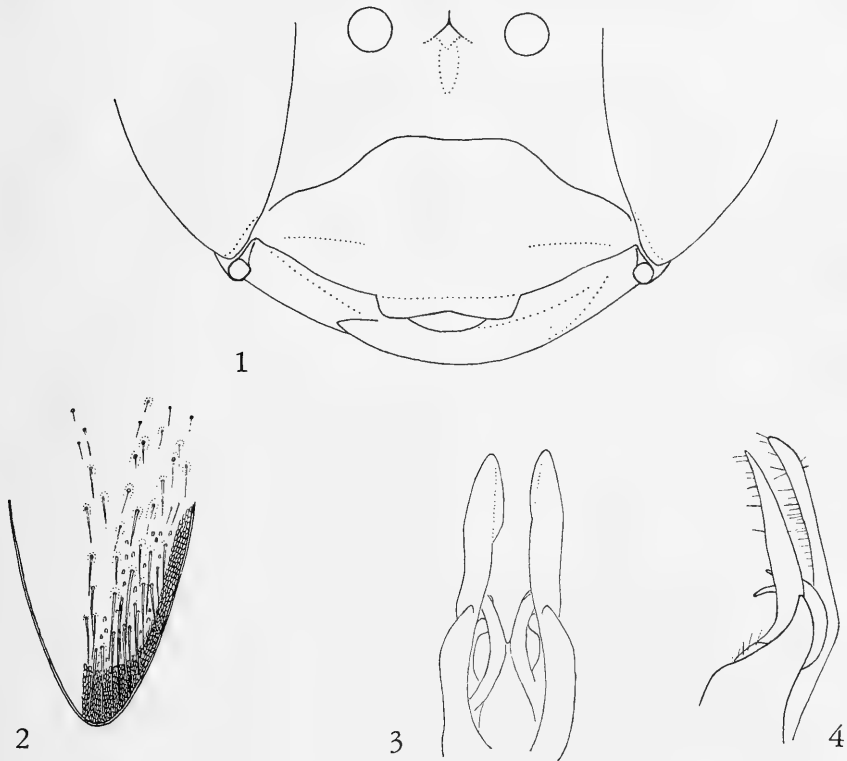


Fig. 1—4. *Psen rufoannulatus* Cameron. 1, face, ♀; 2, pygidial area, ♀; 3, ♂ genitalia, dorsal aspect; 4, the same, lateral aspect

### ***Psen (Psen) rufoannulatus* Cameron**

Cameron, 1907: 90, ♀ (N India: Simla).

Van Lith, 1965: 58—60.

This species was known only from the holotype from Simla. Fortunately the Canadian Expedition collected not only two females, but also two males.

Female. — Gaster slightly redder than in holotype: first two gastral tergites completely dark red, moreover base of third tergite laterally, ventral plate of petiole, second sternite and basal half of third sternite red. Fore basitarsi brown, following four segments yellowish-brown, mid tarsi completely, and apices of hind tarsal segments, yellowish-brown.

Vertex and scutum finely punctate, interstices mostly a few times larger than punctures. Second recurrent vein of fore wings ending in third submarginal cell, almost interstitial. Petiole about six or seven times as long as wide in the middle, rounded below, dorsally flattened, lateral carinae indistinct.

Face (Fig. 1) with silvery appressed pubescence and long erect white hairs. Petiole with usual outstanding lateral hairs. Tergites and sternites with dense short whitish pubescence; also with longer hairs, densest on apical part. Tergites 2—5 just before the

bare hind margin with fringe of long fine white hairs, from both sides directed inwards and their tips slightly curved. Pygidial area with long, backwards-directed, whitish bristles (Fig. 2).

Length, 10.5 mm.

Male. — Darker than female, only first tergite, two lateral spots on second tergite, ventral plate of petiole and second sternite laterally dark red. Mid tarsi brown.

Antennal segments 5—12 with broad oval tyloidea, distinctly concave on segments 6—10. Second recurrent vein of fore wings interstitial. Genitalia light brown, volsellae dark brown; stipites long and narrow, on inner side with small and narrow squamae (Fig. 3 and 4).

Pubescence of gastral segments as in female, apical margins of third and fourth sternites medianly with tuft of long yellowish-white hairs.

Length, 8—8.5 mm.

Nepal: 1 ♀, Kathmandu, 4400 ft, 28 April, 1967; 1 ♀, Kathmandu: Godavari, 5000 ft, 23 July, 1967; 1 ♂, Kathmandu: Godavari, 5000 ft, 15 April, 1967; 1 ♂, Kathmandu: Patibhanjyang, 6000—7500 ft, pastures, 3 July, 1967.

The fringes of long hairs on the posterior margins of the tergites are not conspicuous, but in both sexes distinctly present. Moreover the tyloidea of the male antennae resemble those of *P. dzimm* Tsuneki and *P. pilosus* Van Lith. Therefore I now consider *P. rufoannulatus* as belonging to the group of *P. emarginatus*.

#### ***Psen (Psen) nitidus himalayensis* subsp. nov.**

Two females, recorded below, differ from the nominate subspecies by the paler antennae and legs.

Tip of scape of antennae, pedicel and underside of the whole flagellum yellowish-brown. Dorsal side of flagellum dark brown, but apex of last segment somewhat paler.

Fore tibiae yellowish-brown, on outer side slightly infuscated. Basal third of hind tibiae yellowish-brown. Tarsi pale yellowish.

In *P. nitidus* from Java the underside of the flagellum is only slightly paler than the upper side and the tibiae are distinctly darker.

Nepal: 1 ♀ (holotype), near Simra, Adhabhar, 600 ft, 23—28 Aug., 1967, Malaise trap No. 22; 1 ♀ (paratype), near Birganj, Lothar, 450 ft, 5—12 Sept., 1967.

#### ***Psen (Psen) rufiventris* Cameron**

Cameron, 1890: 267—268, ♀ (*Psen rufiventris*; India, Madras).

Van Lith, 1965: 34—35 (*Psen (Psen) rufiventris*).

First description of male. — Head and thorax black with some metallic reflection; anterior margin of clypeus brownish, labrum yellowish-red, mandibles yellowish-red with dark red tips, palpi pale yellow. Scape of antennae reddish, upper side more brownish, flagellum dark brown above, yellowish-brown beneath. Pronotal tubercles, tegulae and veins of wings dark brown. Legs including trochanters reddish, fore side of fore tarsi dark brown, fore and mid femora slightly darkened above and below, hind femora and tibiae brownish above, hind tarsi except apices of segments darker brown. Tibial spurs of fore and hind legs yellowish-white.

Petiole and tergites 1—4 dark brown, base of second tergite laterally with pale red



spot, margin of fourth tergite reddish-brown, sides and apical margin of fifth tergite reddish, sixth and seventh tergites pale red. Ventral plate of petiole and second sternite reddish, following two sternites reddish-brown with paler margin, fifth and sixth sternites yellowish-red.

Clypeus swollen, with median depression on lower half. Anterior margin with wide emargination (Fig. 5). Frons swollen, head in frontal aspect as long as broad, postocellar area not distinctly raised. Frons superficially punctate, vertex almost smooth. Fine frontal carina, ending between antennae in a shining tooth. Genae and tempora smooth and shining. Mandibles normal. Scape of antennae thick, about twice as long as broad, more than one and a half times as broad as third segment. Third segment in frontal aspect about two and three quarters times as long as broad at apex, fourth segment about twice, following segments about one and a half times as long as broad at apex, last segment about twice as long as broad at base. Segments 5—6 convex below, following segments with slightly concave basal half and convex apical half. Segments 4—12 with distinct oval tyloidea, nearly as long as segments, sculpture little different from remainder of segment, tyloides on last segment indistinct.

Scutum with fine punctures, interspaces often larger than diameter of punctures, punctation medianly on apical half sparse. Scutellum and metanotum convex, with a few punctures. Propodeum with distinct horizontal and vertical part. Enclosed area long, with oblique longitudinal carinae, horizontal part behind enclosed area smooth. Back of propodeum with narrow median longitudinal groove and coarse reticulate carination except an almost unsculptured heart-shaped area, bordered by a high carina and with a few transverse carinae, on its upper half. Fore part of sides of propodeum smooth, apical half finely reticulate, sides and back separated by a fine curved carina. Mesopleura, metapleura and hypo-epimeral area smooth and shining. Anterior plate of mesepisternum indistinctly punctate. Anterior oblique suture narrow, widened upper part with a few fine transverse carinae. Epicnemial area smooth and shining, ventro-laterally curved forward, lateral epicnemial carina and precoxal carina extraordinarily high, forming a lobe when viewed from behind and, in frontal view, an extension of the epicnemial area. Subpleural signa indistinctly connected with precoxal carinae and hind margin of mesosternum, within this area fine superficial punctures and along the median carina a few long, irregular longitudinal carinae. No acetabular carina, only some fine transverse striae. Metasternum deeply emarginate posteriorly and with two high, oblique, lateral carinae.

First recurrent vein of fore wings ending in second, second recurrent vein ending well in third submarginal cell. Fore femora triangular, broadest part almost half the length of femora, fore basitarsus slightly bent, smooth and nearly bare, longer than following four segments together. Fore tibiae, mid femora and mid tibiae thick, mid basitarsus somewhat curved and at least as long as following four segments. Hind trochanters angular beneath, hind femora and tibiae very long and slender, hind basitarsus about as long as following three segments together. Mid tibiae without usual long apical spurs.

Petiole cylindrical and slender, with small depression dorsally at apex, more than twice as long as first tergite, about ten times as long as wide in the middle. First two gastral tergites smooth and almost impunctate, third tergite smooth, with distinct punctures on basal half, following tergites finely reticulate, sparsely punctate, margins impunctate.

Ventral plate of petiole and second sternite smooth, following sternites very finely aciculate; basal half of fourth sternite, which may be partly hidden, very smooth and shining. This smooth part bordered posteriorly by a narrow area which does not reach the lateral margins and is covered with extremely fine punctures, each bearing a fine short hair. Apical spine long.

Face below antennae with silvery and appressed short pubescence, but also with unusually dense pubescence of long, whitish, erect hairs with ends curved downwards. Frons with short, inconspicuous, pubescence, tempora and genae with short appressed silvery pubescence and a few long hairs, vertex with long brownish hairs. Scutum with short brownish pubescence, scutellum and metanotum with long erect brown hairs, mesosternum with dense short whitish pubescence, propodeum with long white hairs, petiole with relatively short and fine latero-ventral erect hairs, gaster very sparsely pubescent. Last gastral tergites before hind margin with a few long stiff hairs. Ventral side of gaster sparsely pubescent, only third sternite medianly at apex with tuft of long, dark brown, bent hairs, following sternites with a few stiff long hairs before apical margin, seventh sternite with dense and short pubescence. Upper two-thirds of back of hind femora bare.

Genitalia (Fig. 6, 7 and 8) large, pale yellowish-brown, including volsellae; stipites thin and easily crumpled.

Length, 11.5 mm.

North India: 1 ♂ (allotype), Simla, 30 August, 1918, Brunetti Coll., B.M. 1927—184 (BM).

Nepal: 1 ♂, Kathmandu, Pulchauki, 8000 ft, 21 July, 1967, Canadian Nepal Expedition (CNC).

This male differs from that from Simla only in the gaster being somewhat more reddish. The second tergite is red with brownish hind margin, the third brown with a broad reddish hind margin, the fourth tergite reddish with a small brown spot on base, the fifth tergite reddish with only a slightly darkened small basal spot, the following segments are completely reddish.

This peculiar form differs from other *Psen* by the raised clypeus in both sexes, the shape of the legs and the strongly developed epicnemial and precoxal carinae in the male. I could compare this material with the single female (holotype) of *Psen rufiventris*, in the collection of the Oxford University Museum. Although there are some differences, the male having higher epicnemial and precoxal carinae and the head, in frontal view, being higher (female Fig. 9), there is little doubt that the material is conspecific. More specimens of both sexes from the three localities, Madras, Simla and Kathmandu, would be very welcome.

### *Psen (Psen) simlensis* Van Lith

Van Lith, 1968: 119—120, ♀ (N India).

Nepal: 4 ♀, Kathmandu, Godavari, 6000 ft, 14—17 July and 7—17 Aug., 1967.

These females are identical with the type from Simla. All have the extreme apex of the pygidial area reddish, which was not mentioned in the original description. *P. simlensis* belongs to the group of *P. orientalis* Cameron, which has many representatives distributed over a large area, including palaeartic East Asia.

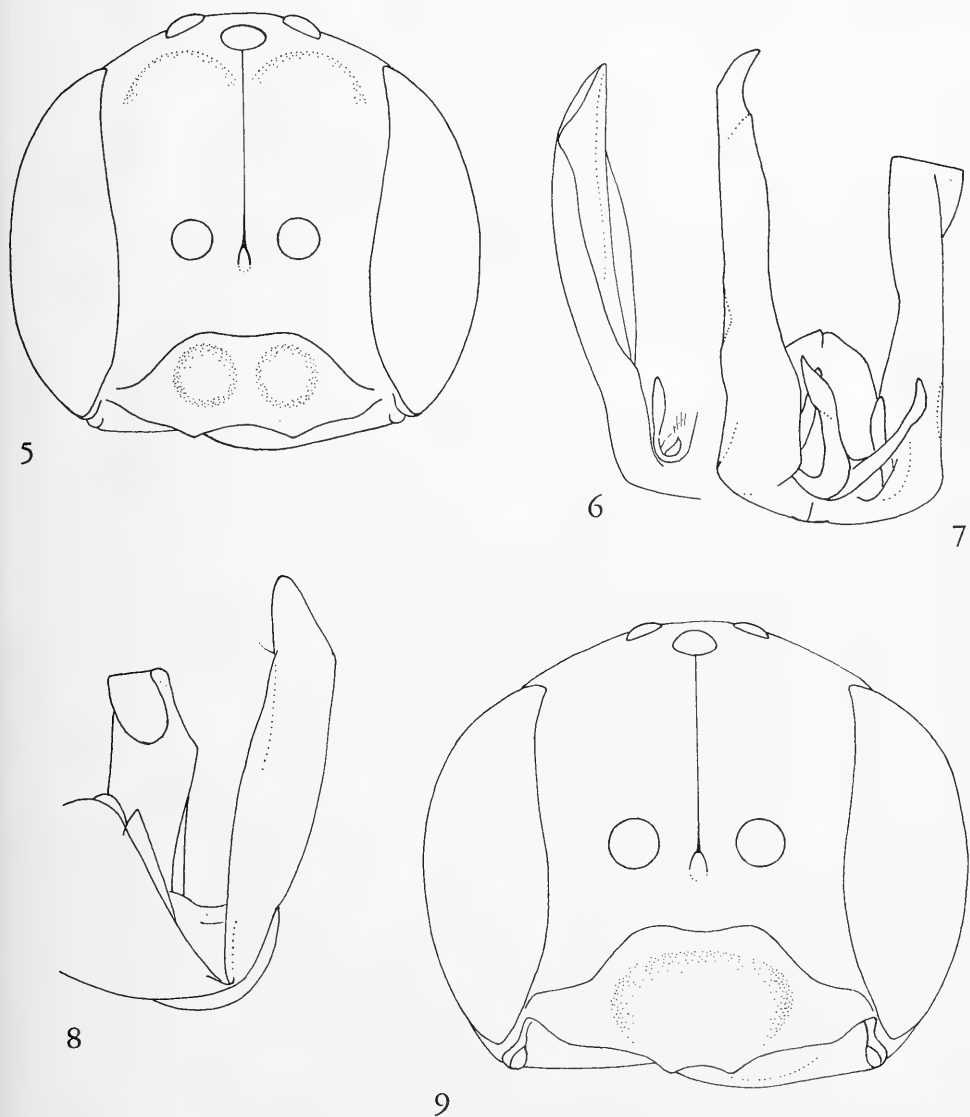


Fig. 5—9. *Psen rufiventris* Cameron, ♂ from Nepal, ♀, holotype, from Madras. 5, face, ♂; 6, right part of ♂ genitalia, latero-dorsal aspect; 7, ♂ genitalia, dorsal aspect; 8, the same, ventral aspect; 9, face, ♀

***Psen (Psen) lobicornis* spec. nov.**

Male. — Black, head and thorax with somewhat leaden gloss; tips of mandibles, palpi and tarsal claws brown. Apical spurs of tibiae light brown, apical spine brown.

Protruding median part of clypeal margin smooth and shining, broad triangularly emarginate (Fig. 10), disk of clypeus superficially punctate. Fine frontal carina, ending in a short and raised angular carina between antennae (Fig. 10). Frons with fine and

dense punctation, near oculi almost smooth, vertex also with fine punctation, densest around ocelli, where punctures often are placed in rows. Tempora and genae smooth and shining. Antennae (Fig. 11) long, scape large, about two and a half times as thick as third antennal segment at base (Fig. 10), third segment about three times as long as broadest part (in frontal aspect, when convexity is best visible), fourth segment about twice as long as broad in the middle, following segments gradually shorter, twelfth segment hardly convex, less than twice as long as broad in the middle, last segment about three times as long as broad at base. Segments 3—13 with distinct tyloidea, on third segment small, near apex, on segments 4—11 large, elliptic and medianly much raised so that these segments are strongly convex below, on segments 12—13 much narrower.

Scutum with fine but deep punctures, interspaces once or twice diameter of punctures, puncturation denser on posterior margin. Scutellum and metanotum less densely punctate. Enclosed area of propodeum about equitriangular, with eight longitudinal carinae; horizontal part of propodeum behind this area smooth, back of propodeum with strong, irregular carination, sides of propodeum with a few weaker carinae. Epicnemial areas, mesopleura including hypo-epimeral areas, and metapleura smooth and shining, very finely punctate; mesosternum with fine widespread punctures and median longitudinal carina with a few short, strong, transverse carinae. Anterior oblique suture foveolate, widened upper part with a few transverse carinae. Legs normal, slender, hind tibiae with a few short thorns on outer side. First recurrent vein of fore wings ending well in second submarginal cell, second recurrent vein ending in third submarginal cell near second cell.

Petiole longer than twice first tergite, at least eight times as long as wide in the middle, dorsally slightly rounded, apically with small deep pit, sides slightly depressed with two unsharp longitudinal carinae, ventrally rounded. Gaster shining, extremely finely punctate, apical spine long.

Face below antennae with appressed silvery pubescence and long erect whitish hairs, outer side of mandibles with long greyish hairs, frons with greyish-brown pubescence, long near oculi and on vertex. Thorax with appressed short and erect long pubescence, greyish-brown on scutum, more whitish below. Underside of fore and mid femora and back of hind femora with long whitish hairs, inner side of hind femora bare. Petiole with usual long and outstanding, pale, hairs. Pubescence of gaster short, brown, sparse, before apical margin of sternites a few long stiff hairs. Third and fourth gastral sternites with median tuft of long brown hairs.

Genitalia dark brown, long and slender, with rather long, transparent, inner squamae, apices of stipites with long brown hairs, bent at their apex (Fig. 12 and 13).

Length, 9 mm.

Female unknown.

Nepal: 1 ♂ (holotype), Bhurumche, near Kathmandu, 8500—9500 ft, oak forest, 1 July, 1967.

*P. lobicornis* belongs to the group of *P. orientalis* Cameron and is characterized by the strongly convex underside of the tyloidea. Probably it is closely related to *P. fuscinervis* (Cameron), which has linear tyloidea. The male of *P. simlensis* is still unknown, but its female has a more cylindrical petiole, an almost smooth vertex and finer punctate scutum.

***Psenulus orinus* spec. nov.**

Female. — Black; palpi dark brown, tibial spurs paler brown. Veins of wings black.

Clypeus slightly convex, densely but superficially punctate, margin medianly with about semi-circular emargination between two strong triangular teeth. Face (Fig. 14) above clypeus also with dense superficial punctures, centrally between clypeus and transverse carina, a shallow oval depression. Fine frontal carina, between antennae ovally broadened and excavate (Fig. 15), ending below antennae in a rectangular transverse carina (reversed V). Frons on both sides of carina slightly convex, very densely finely punctate, vertex shining, sparsely finely punctate. Occipital carina normally ending in hypostomal carina. Apex of mandibles bidentate. Antennae gradually thickening towards apex, third segment about three times, fourth and fifth segments about twice, segments 7—9 about one and a half, segments 10—11 about one and a third times as long as broad at apex, twelfth segment slightly more than twice as long as broad at base.

Scutum finely, distinctly, punctate, interstices often a few times diameter of punctures. Scutellum and metanotum sparsely, indistinctly, punctate. Enclosed area of propodeum rather narrow, pentagonal median part with indistinct median carina. Back of propodeum almost smooth, only very fine hair-bearing punctures and with deep median longitudinal groove. Propodeum latero-dorsally with broad foveolate groove, apex with some irregular carinae; posterior half of sides with indistinct carination. Epicnemial areas, mesopleura, metapleura and mesosternum almost smooth, shining. First recurrent vein of forewings interstitial, second recurrent vein ending just in third submarginal cell, upper side of second submarginal cell about two-fifths of bottom of cell. Legs normal.

Petiole (Fig. 16) long, about as long as first two gastral tergites and somewhat longer than half the length of the thorax, almost cylindrical, sides with a row of superficial large punctures, dorsally at base with lateral sharp carina, medianly a deep longitudinal groove, which is broad basally, tapers towards apex and ends in a triangular pit. Gaster shining, very finely sparsely punctate, last tergites and all sternites finely alutaceous, second sternite with indistinct triangular depression at base. Pygidial area elongate-triangular, narrowed towards apex, lateral carinae distinct (Fig. 17).

Face with short silvery pubescence, hardly appressed and therefore not concealing sculpture of clypeus, and with long whitish hairs intermixed. Head, thorax and legs whitish-pubescent, densely on mesosternum. Petiole with usual long, outstanding, whitish hairs. Pubescence of gaster brown, dense and short on posterior margins of fourth and fifth sternites, sixth sternite with dense backwards-directed golden-brown pubescence.

Length, 7.5 mm.

Male. — Resembling female. Carina between antennae less broadened (Fig. 19), transverse carina longer, bilobed, laterally bent upwards to outer side of antennal sclerites, anterior margin of clypeus more triangularly emarginate, teeth smaller (Fig. 18). Antennae longer, third segment about two and a half times, segments 4—12 slightly more than twice as long as broad at apex, last segment about two and a half times as long as broad at base. Segments 3—11 with long, oblique, narrow carina-like tyloidea, on twelfth segment reduced to a very short carina or point.

Petiole somewhat longer (Fig. 20), with distinct keel also ventrolaterally at base, sides slightly depressed. First recurrent vein of fore wings variable, in three males interstitial, in one male distinctly ending in first submarginal cell and in one male ending well in second submarginal cell. Apex of seventh gastral sternite: Fig. 23.

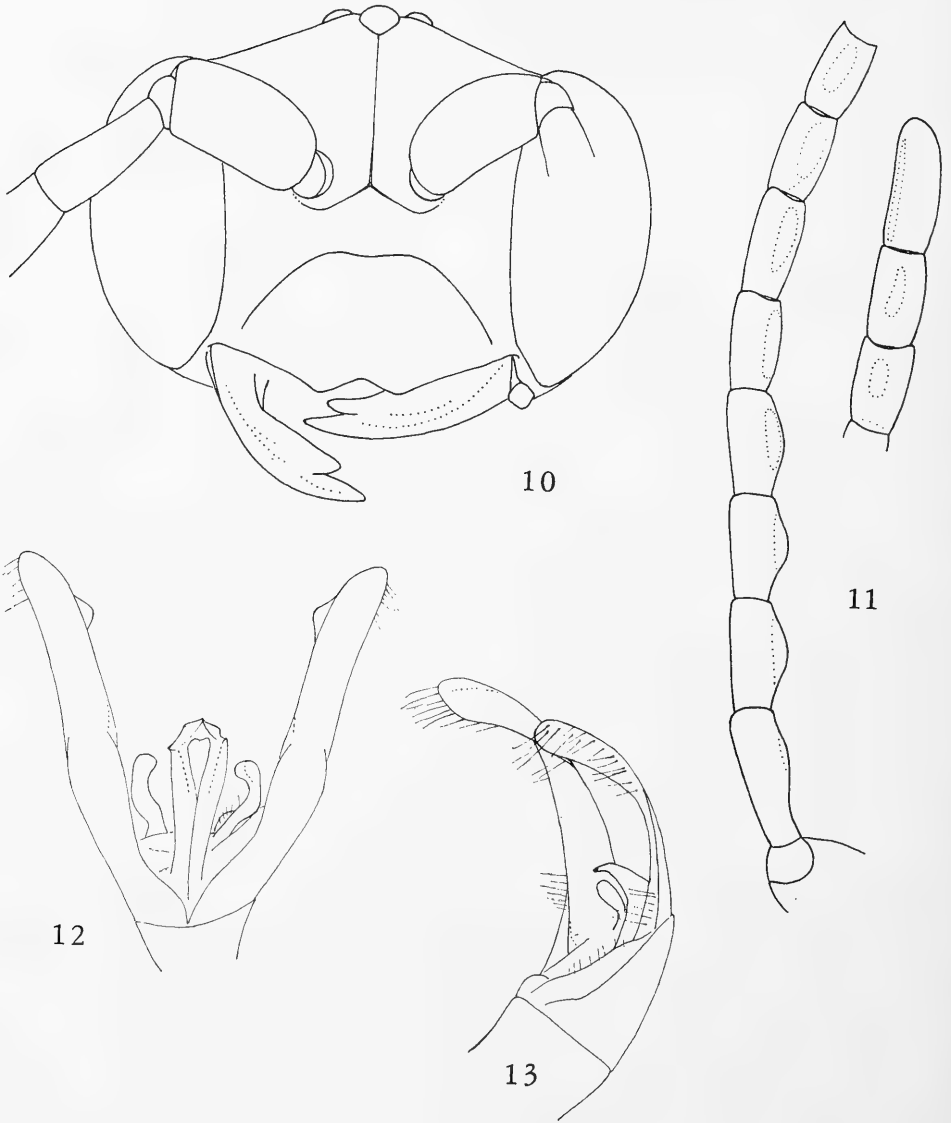


Fig. 10—13. *Psen lobicornis* sp. nov., ♂, holotype. 10, face; 11, antenna; 12, genitalia, dorsal aspect; 13, the same, lateral aspect

Genitalia pale straw-yellow, stipites with small semi-circular inner emargination and distinct inner tooth (Fig. 21 and 22).

Length, 7 mm.

Nepal: 1 ♀ (holotype), 28°00' N, 85°00' E, Malaise trap 7, 9900 ft, 21—27 May, 1967, 2 ♂ (allotype and paratype), 27°57' N, 84°59' E, Malaise trap 5, 10,100 ft, 26—31 May, 1967, 2 ♂ (paratypes), 28°00' N, 85°00' E, Malaise trap 6, 10,500 ft, 4—12 May and 21 May 1967.

*Psen montanus* Cameron (1907) is very similar and certainly closely related. It has also distinct clypeal teeth, a transverse carina below the antennae, a triangular pygidial area and its face is little pubescent. However, its palpi are pale brown, the antennal segments are much shorter and the punctation of the scutum is more dispersed. This species will be discussed in a separate paper. Its name is preoccupied by *Psen montanus* Ach. Costa, 1868, of which the type seems to be lost but which according to the description might be identical with *Psenulus atretus* Pz. (cf. de Beaumont, 1937: 87).

### *Psenulus quadridentatus* Van Lith

Van Lith, 1962: 37—38, ♀ and ♂ (Malaya).

Van Lith, 1972: 162, ♀ (Vietnam).

Nepal: 4 ♀, 17—25 July, 1967 and 4 ♂, 17—22 July, 30 July and 7—13 Aug., 1967, Kathmandu, Godavari, 6000 ft, in Malaise traps.

In the females, as in the holotype from Malaya, the pronotum is dorsally somewhat reddish transparent, covered with rather dense whitish pubescence.

Pronotum in males darker, but not fully black. Underside of antennal segments 1—5 yellowish-brown, following segments partly darkened, especially segments 8—10. Although the tyloidea of the antennae are little raised, they are, when examined under the right angle, well visible and not really indistinct, as I stated in the original description. On segments 4—6 they are large, reddish-brown and oval, on the seventh segment much smaller, reduced to a point on the eighth segment, and hardly visible on the ninth segment. Sometimes there is also a small shining point on the third segment. Segments 5—12 distinctly rounded below.

Genitalia (Fig. 24 and 25) pale straw-yellow, including volsellae. Apical spine dark brown. Apex of seventh gastral sternite: Fig. 26.

### *Psenulus chillcotti* spec. nov.

Female. — Head and thorax black; labrum and median part of mandibles reddish, palpi pale straw-yellow. Upper side of antennae dark brown, underside of scape and pedicel, and base and apex of flagellum more or less orange-red; in one female complete underside of flagellum orange-red. Posterior margin of pronotal tubercles more or less brownish, tegulae brownish. Fore and mid tibiae and tarsi yellowish, fore and mid femora, except upper side of apex largely dark brown, trochanters dark brown. Hind tibiae, femora and trochanters reddish, femora dorsally sometimes brownish darkened; hind tarsi, except extreme apices of segments, dark brown. Veins of wings dark brown. Gaster, including petiole, yellowish-red.

Protruding median part of clypeal margin with two large, shining, triangular teeth (Fig. 27), distance between teeth about one seventh of total distance there between eyes. Disk of clypeus opaque, very finely and densely punctate, also rest of face below transverse carina. Fine frontal carina, raised and broadened between antennae (Fig. 28), ending in an angular, short, transverse carina below antennae. Frons and vertex shining, frons densely but superficially punctate, vertex with fine scattered punctures, a few larger punctures between posterior ocelli. Antennae short, gradually thickening towards apex, third segment about twice as long as broad, following segments gradually shorter, segments 8—11 shorter than broad, last segment more than one and a half times as long as broad at base. Mandibles normally bidentate at apex.

Scutum with irregular punctation, very fine and dense between median scutal lines, on rest of scutum very fine, mixed with much larger punctures; scutum centrally more shining, with interstices a few times diameter of punctures; posterior margin with short longitudinal striae. Prescutal sutures about three quarters of length of scutum but superficial. Scutellum and metanotum scarcely and finely punctate. Enclosed area of propodeum with about twenty short oblique carinae, area between median carinae pentagonal, upper part of back of propodeum smooth and shining, lower four-fifths minutely punctate. Median longitudinal groove narrow, upper part widened and with a few transverse carinae, between back and sides of propodeum a broad, curved, foveolate groove; posterior half of sides of propodeum with fine irregular striae, anterior half smooth. Epicnemial areas, anterior plate of mesepisternum, mesopleura and mesosternum shining, only with minute hair-bearing punctures. Metapleura smooth and shining. Anterior oblique suture narrow, foveolate, widened upper part with a few transverse carinae. Legs normal, slender. First recurrent vein of fore wings ending just in second submarginal cell, second recurrent vein in third submarginal cell, distance from second cell about one fifth of length of bottom of cell. Petiole about as long as hind femora, at apex nearly twice as broad as at base (Fig. 29), almost cylindrical, dorsally more flattened with a small depression at apex, sides on apical half densely punctate. Tergites very finely punctate, apical margins smooth, sternites somewhat stronger punctate. Pygidial area distinct, small and narrow, finely punctate, lateral carinae almost parallel (Fig. 30).

Face with appressed silvery pubescence and also with many long erect silvery hairs, head and thorax with whitish pubescence, on mesosternum dense and short and also with long, whitish, hairs, epicnemial areas below with round patch of appressed and dense, yellowish-silvery pubescence. Fore and mid femora below with long whitish hairs. Gaster with short yellowish pubescence, margin of fourth and fifth gastral sternites with dense, short, white pubescence, sixth sternite with dense, backwards directed, golden pubescence.

Length, 8 mm.

Male. — Resembling female. Dorsal side of fore and mid femora almost completely yellowish-red, mid tibiae slightly darkened. Hind legs, including trochanters, reddish-brown, tarsi brown. Underside of antennae orange-red, in one male segments 6—9 more or less brownish.

Transverse carina below antennae longer, laterally bent upwards to reach outer sclerites of antennae. Antennae moniliform, segments 3—12 about one and a half times as long as broad in the middle, last segment slightly more than twice as long as broad at base. Segments 3—7 with narrow tyloidea, broadened towards apex, segments 8—11 with gradually shorter, elongate-oval, tyloidea, on twelfth segment reduced to a small point.

Upper half of back of propodeum as in female, lower half with transverse irregular carinae; posterior half of sides of propodeum with coarse, irregular, reticulate carination. Genitalia brownish-yellow (Fig. 32 and 33). Apex of seventh sternite: Fig. 31.

Length, 7—8 mm.

Nepal: 1 ♀ (holotype), 6000 ft, 23—25 July, 1967, 1 ♂ (allotype), 6000 ft, 27—30 July, 1967, Kathmandu, Godavari. Paratypes, all from the same locality: 3 ♀, 6000 ft, 19—20, 23—26 and 27—30 July, 1967; 2 ♀, 5000 ft, 27—30 July, 1967; 2 ♂, 6000 ft, 17—20 July, 1967. All, 2 ♀ excepted, collected in Malaise traps.

The male is very similar to *P. bengalensis* (Van Lith, 1972), which is known only from the holotype. The latter species differs in the following details: postero-lateral



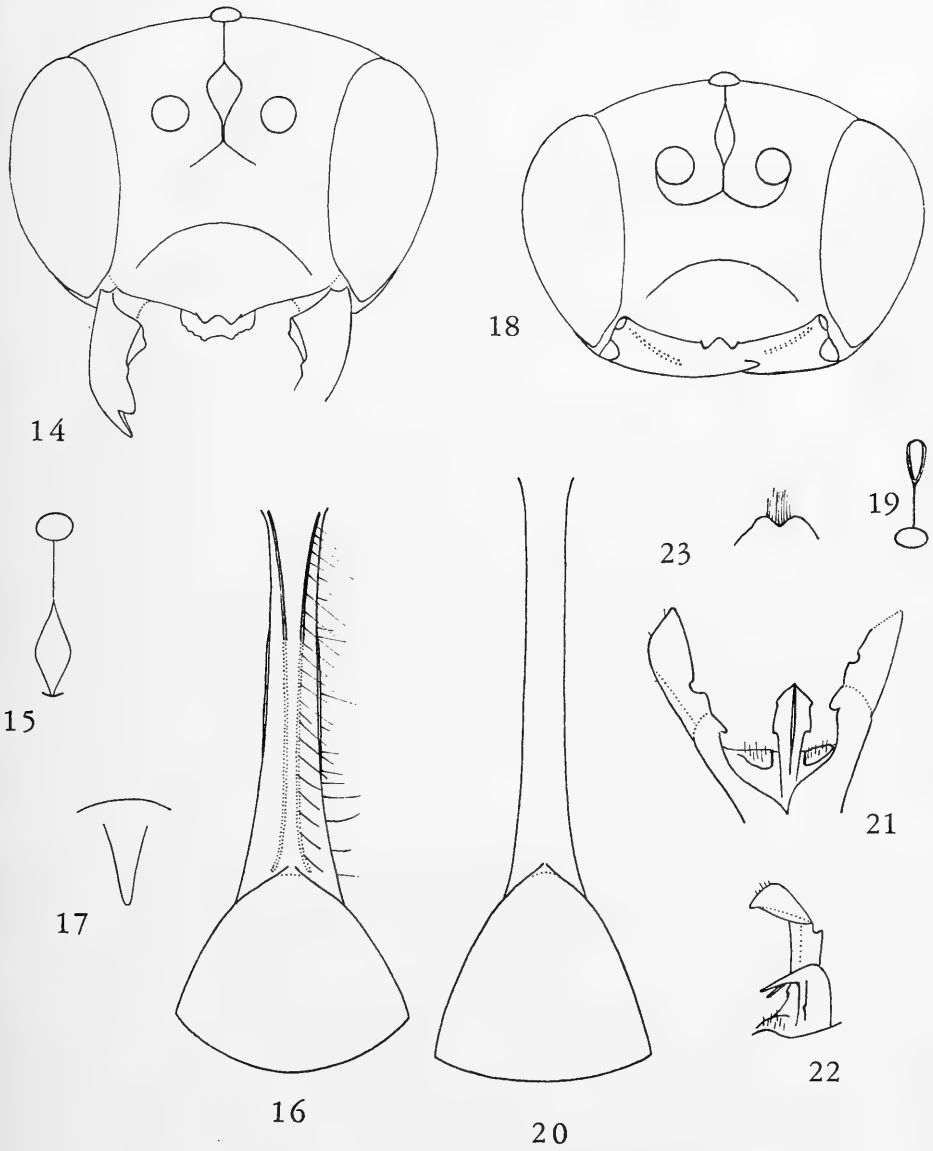


Fig. 14—23. *Psenulus orinus* sp. nov., ♀, holotype, ♂, paratype. 14, face, ♀; 15, median ocellus and interantennal carina, dorsal aspect, ♀; 16, petiole and first tergite, ♀; 17, pygidial area, ♀; 18, face, ♂; 19, median ocellus and interantennal carina, dorsal aspect, ♂; 20, petiole and first tergite, ♂ (sulcus and hairs omitted); 21, ♂ genitalia, dorsal aspect; 22, the same, left stipes and penis valves, lateral aspect; 23, apex of seventh sternite, ♂

groove of propodeum superficial only and sides of propodeum smooth; petiole narrower, apex at most one and a half times as broad as base; stigmata of first tergite protruding. Moreover the antennae of *bengalensis* are much darker and the tyloidea on the twelfth segment is more distinct and larger than in *P. chillcotti*.

*P. chillcotti* belongs to the group of *P. quadridentatus*. The female resembles that of *P. macrodentatus* Van Lith, from Sumatra, but differs in having smaller clypeal teeth, more shining vertex between ocelli and oculi, more coarsely punctate scutum, larger transverse carina below antennae, a curved dorso-lateral groove on the propodeum, darker pronotal tubercles and darker legs.

This species is dedicated to the late Dr. James Gordon Thomas Chillcott, who organized and at first led the Canadian Nepal Expedition, but unfortunately died in Nepal on 20 April, 1967.

A male, collected 3 Aug., 1967, at the same locality, also in a Malaise trap, differs considerably from the three males described above. The coarse punctures on the scutum are completely lacking. Furthermore the tyloidea are only present on antennal segments 3—8 (right antenna) or 3—9 (left antenna), and are of a different shape, much broader, especially on segments 3—6. The squamae of the genitalia are somewhat broader (Fig. 34). The latero-dorsal groove of the propodeum is indistinct. The first recurrent vein of the fore wings ends in the first submarginal cell. However, I do not exclude the possibility that it is an aberrant male of *P. chillcotti* and cannot describe it as a distinct species without further material.

In the British Museum (Natural History), London, is a female from Nepal, which, although it has no gaster, is considered identical with *P. chillcotti*: Ghanpokhara, 5500—7000 ft, 2 May, 1954, coll. J. Quinlan, B.M. Nepal Expedition, B.M. 1954—540.

### *Psenulus puncticeps* (Cameron)

Cameron, 1907: 91, ♀ (*Psen puncticeps*; India: Bombay, not Simla).

Rohwer, 1923: 595—596, ♂ (*Diodontus antennatus*; Singapore).

Van Lith, 1962: 44—46, ♀ and ♂ (*Psenulus antennatus*; Malaya, Java, Bali).

Nepal: 1 ♀, nr Birganj, Lothar, 450 ft, 1—5 Sept., 1967.

The first gastral tergite is red, as in the females from Bali. The tips of the mandibles is worn off, so that the apex seems to be bidentate instead of tridentate, besides the larger inner tooth.

I could not find any difference of importance between the type of *Psen puncticeps* Cameron (1907), which is in the collection of the British Museum (Natural History), and a female from Java, which I considered to belong to *Psenulus antennatus* Rohwer (1923). Cameron's description of *Psen puncticeps* is somewhat misleading. The gaster is not "piceous", but dark red, somewhat discoloured. The propodeum shows the same enclosed area as *P. antennatus*, Cameron describing the "metanotum" as "without a basal area".

The mandibles are quadridentate, as is characteristic for the females of *P. antennatus* from Java and Bali. The punctuation of the scutum is slightly stronger than in these females.

The type does not originate from Simla, as stated by Cameron, but from Bombay and is labelled "Type" (printed on small round label), "Matheran 3.99" (typewritten), "Col. C. G. Nurse Collection 1920—72" (printed), "*Psen puncticeps* Cam. Type Bombay" (probably in Cameron's handwriting), and "B.M. Type Hym. 21.819".

Unfortunately *P. antennatus* was described by Rohwer after a single male from Singa-

pore and but for another male I have seen no further material from Malaya. However, I could compare this latter male with series of females and males from Java and Bali and I think that there is no doubt that *P. antennatus* Rohwer is a synonym of *P. puncticeps* Cameron.

*Psenulus godavariensis* spec. nov.

Male. — Head and thorax black; underside of antennae, mandibles, except dark tips, and palpi yellowish. Dorsal side of pronotum, except darkened sides, a narrow anterodorsal margin and pronotal tubercles yellowish-white. Tegulae yellowish-red. Metanotum yellow with ill-defined brownish area in the middle. Fore and mid legs yellow, trochanters paler, underside of fore and mid femora brownish. Base of hind coxae on fore side with brown spot. Hind legs including trochanters yellowish-red, tarsi brown with paler apices. Veins of wings dark brown. Gaster including complete petiole yellowish-red. Apical spine dark brown.

Clypeus convex, median part of depressed apical margin with two small teeth; distance between tips of teeth about one sixth of total distance there between the eyes. Fine frontal carina, raised part between antennae narrow, ending below antennae in a transverse carina with ends curved upwards to outer side of antennal sclerites. Frons below anterior ocellus with fine and dense, but superficial, punctation, vertex with only a few punctures. Tempora and genae shining, with very fine piliferous punctures. Antennal segments long, 3—12 about two and a half times as long as broad at apex, last segment nearly three times as long as broad at base. No tyloidea.

Scutum with irregular, fine, also with many larger and a few much larger punctures, very fine and dense punctation between median lines. Prescutal sutures distinct, about one third length of scutum. Parapsidal sutures distinct, posteriorly ending in a small pit. Scutellum and metanotum almost impunctate, lateral depressions normal. Enclosed area of propodeum depressed, with oblique carinae, median two carinae diverging, longitudinal sulcus broad and with a few transverse carinae above, narrow on back of propodeum. Surface of propodeum smooth behind enclosed area, basal two thirds of back and sides with coarse reticulate carination but finer than in *P. birganjensis*. Mesopleura, metapleura and anterior margin of sides of propodeum shining, mesopleura, ventral side of thorax and anterior plate of mesepisternum with a few fine punctures. Anterior oblique suture foveolate, widened upper part shining, without transverse carinae. First recurrent vein of fore wings interstitial, second recurrent vein ending in third submarginal cell. Lower side of second submarginal cell about one and a half times as long as upper side. Legs normal, slender. Petiole about as long as first gastral tergite, almost cylindrical, dorsally somewhat flattened, a small elongate-triangular groove at apex. Gaster shining, very finely punctate, apical margins of tergites smooth. Sternites 3—6 finely aciculate.

Pubescence of face silvery, mostly appressed, head and thorax with greyish-white pubescence, partly long, dense on mesosternum. Pubescence of gaster yellowish-golden, a few long stiff hairs before apical margin of sternites, sixth sternite with dense, backwards directed, golden pubescence.

Length, including apical spine, 7 mm.

Genitalia: Fig. 35, 36 and 37.

Female unknown.

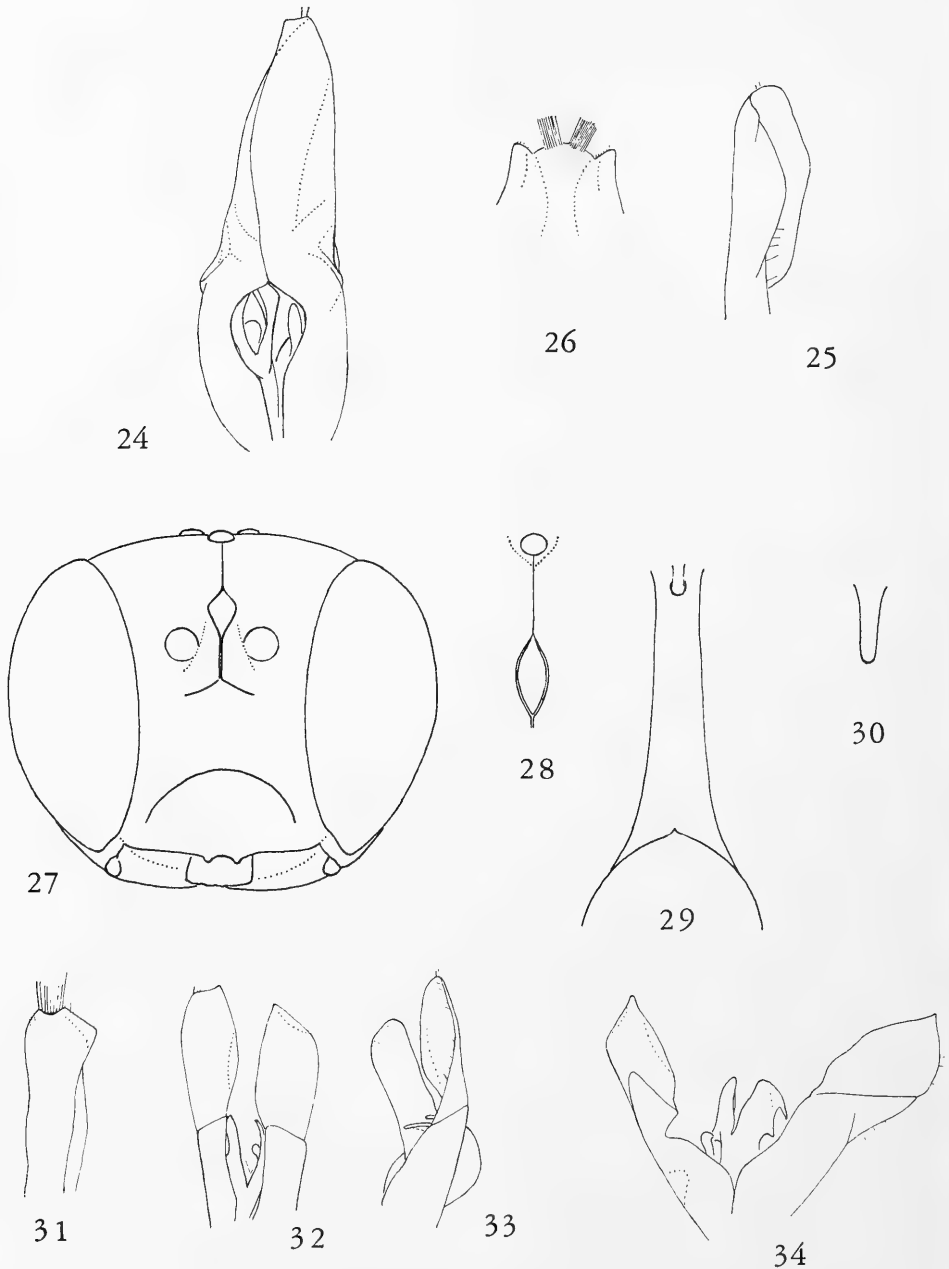


Fig. 24—26. *Psenulus quadridentatus* Van Lith, ♂, Nepal. 24, genitalia, dorsal aspect; 25, apex of left stipes, ventral aspect; 26, apex of seventh sternite. Fig. 27—33. *Psenulus chillcotti* sp. nov., ♀, holotype, ♂, allotype. 27, face, ♀; 28, median ocellus and interantennal carina, dorsal aspect, ♀; 29, petiole, ♀; 30, pygidial area, ♀; 31, apex of seventh sternite, ♂; 32, ♂ genitalia, dorsal aspect; 33, the lateral aspect. Fig. 34. *Psenulus chillcotti* sp. nov., aberrant (?) ♂, genitalia, dorsal aspect

Nepal: 1 ♂ (holotype), Kathmandu, Godavari, 6000 ft, 20—22 July, 1967, Malaise trap.

*P. godavariensis* belongs to the group of *P. interstitialis* Cameron and is probably closely related to *P. ornatus* (Ritsema), *P. birganjensis* sp. nov., *P. kankauensis* Strand (1915) and *P. pembuchiensis* Tsuneki (1971). In view of the marking and the stronger punctate scutum it is considered here provisionally as a separate species.

***Psenulus birganjensis* spec. nov.**

Male. — Head and thorax black, with metallic reflections; the following parts are yellow: mandibles except dark tips, labrum, palpi, pronotum anterodorsally and dorsally, pronotal tubercles, tegulae, two narrow longitudinal lines (which may be lacking) on scutum, broadened posteriorly and neither reaching anterior nor posterior margin, axillae, scutellum including posterolateral margins but except a large vague circular brown spot in the middle, metanotum including postero-lateral margins, four separate elongate marks on propodeum. Anterior margin of clypeus brownish. Scape of antennae yellow, underside of flagellum pale yellowish-brown. Tips of all coxae, whole tibiae and tarsi of fore and mid legs yellow; trochanters and femora of fore and mid legs dorsally yellow, underside brown; hind legs reddish, greater part of trochanters and outer side of femora brown. Veins of wings dark brown. Petiole pale yellowish-red, apical third dark brown, gaster including ventral plate of petiole orange-red. Apical spine dark brown.

Protruding median part of anterior margin of clypeus slightly emarginate, disk dull, superficially punctate. Fine frontal carina, raised part between antennae narrow, ending below antennae in a high transverse carina. Frons and vertex smooth. Antennae long, in frontal aspect third segment about two and a third times, segments 4—12 more than twice as long as broad at apex, last segment about three times as long as broad at base. Segments 3—5 thicker, following segments gradually tapering, segments 6—11 somewhat convex below. No tyloidea.

Scutum and scutellum with very fine punctures, from which fine hairs arise, interstices a few times diameter of punctures, and very few larger punctures. Metanotum with more numerous fine hair-bearing punctures. Enclosed area of propodeum triangular, with distinct oblique carinae, behind enclosed area on both sides a large smooth area, back and sides of propodeum with reticulate, moderately strong carination. Meta-, mesopleura, anterior plate of mesepi- and mesosternum shining, only with minute hair bearing punctures. Anterior oblique suture foveolate, widened upper part with transverse carinae. First recurrent vein of fore wings ending just in second submarginal cell, second recurrent vein ending in third submarginal cell. Upper side of second submarginal cell about half the length of the underside. Legs rather slender. Petiole cylindrical, not reaching as far as end of hind femora. Gaster very finely punctate, dorsally smooth, ventrally finely alutaceous.

Face with appressed silvery pubescence and also with long silvery-white erect hairs. Hairs on head and thorax long, rather dense, yellowish-grey, on gaster shorter and more yellowish, hind margins of sternites with long stiff hairs, sixth sternite with dense yellowish pubescence.

Genitalia (Fig. 38) resembling those of *P. interstitialis*, pale straw-yellow, including volsellae. Apex seventh sternite and apical spine: Fig. 39.

Length, 8.5—9 mm.

Female unknown.

N e p a l: 1 ♂ (holotype), near Birganj, Lothar, 450 ft, 5—12 Sept., 1967, Malaise trap No. 32; 1 ♂ (paratype), same locality, 12—19 Sept., 1967.

This form is provisionally placed in the group of *P. interstitialis* Cameron. Its colour pattern closely resembles that of *P. ornatus* (Ritsema, 1876) from Java, of which only one male is known. *P. birganjensis* differs by the yellow axillae and the shorter antennal segments, segments 4—12 being about twice as long as broad, in *P. ornatus* about two and a half times.

### *Psenulus pulcherrimus* (Bingham)

Bingham, 1896: 443, ♀ (*Psen pulcherrimus*; Tenasserim).

Bingham, 1897: 263.

Van Lith, 1962: 101 (*Psenulus pulcherrimus*).

Van Lith, 1969: 200, ♂ (Vietnam).

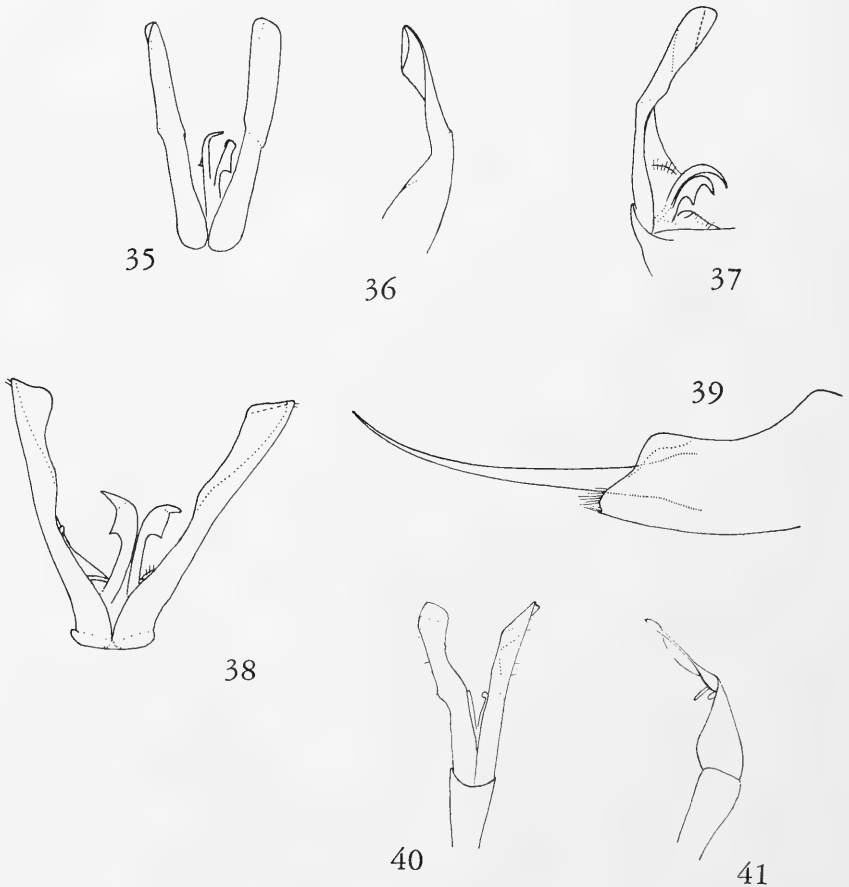


Fig. 35—37. Genitalia of male of *Psenulus godavariensis* sp. nov., holotype. 35, dorsal aspect; 36, right stipes, lateral aspect; 37, right stipes and penis valves, latero-dorsal aspect

Fig. 38—39. *Psenulus birganjensis* sp. nov., ♂, holotype. 38, genitalia, dorsal aspect; 39, apices of seventh and eighth sternites, lateral aspect

Fig. 40—41. *Psenulus pulcherrimus* (Bingham), Nepal. 40, ♂ genitalia, dorsal aspect; 41, the same, lateral aspect

A fine series of two females and seven males was collected. They differ from the nominate subspecies from Tenasserim (female, holotype) and Vietnam (male) only in having more completely, and darker, brown hind femora and the base of the first gastral tergite more or less darkened.

The marking of the scutum is variable. The female and two males collected near Birganj have only a median yellow spot on the scutum, in the female even somewhat reduced. The single female and two out of the five males from Simra have in addition a smaller or larger yellow mark along the tegulae, as in the two sexes from Tenasserim and Vietnam. Also the marking of the scutellum varies, but it covers at least the apical half. Propodeum with the same two large yellow marks as in the holotype, with which I could compare.

Genitalia of male: Fig. 40 and 41.

Nepal: 1 ♀ and 5 ♂, near Simra, Adhabhar, 600 ft, 23—28 Aug., 1967, Malaise traps No. 21, 23 and 24; 1 ♀ and 1 ♂, near Birganj, Lothar, 450 ft, 29 Aug.—5 Sept., 1967, Malaise traps No. 25 and 28, and 1 ♂, same locality, 5—12 Sept., 1967.

This series is interesting, not only because of the relatively great number of specimens from two localities, but also because of the great variability of the yellow marking of the scutum. It may represent a new geographical subspecies, the femora being darker brown and the first gastral tergite being darkened in all specimens. However, in view of the variability of the Nepalese populations and the scarcity of the material from other regions in southern Asia, I hesitate to name this form.

*P. pulcherrimus eburneus* Van Lith (1969), from Bengal, differs by the much paler yellow marking, the completely red first gastral tergite and the four, instead of two, marks on the propodeum.

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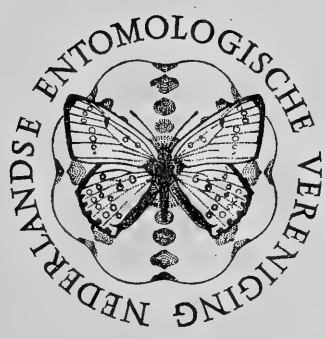
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# TIJDSCHRIFT VOOR ENTOMOLOGIE

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DE NEDERLANDSE ENTOMOLOGISCHE VERENIGING



## INHOUD

L. PETERICH. — Chromatologie, eine Untersuchung der Chromatik der Fauna und Flora auf deren rein chromatische Gesetzmäßigkeiten hin, pp. 143—159, Fig. 1, Pl. 1.



# CHROMATOLOGIE, EINE UNTERSUCHUNG DER CHROMATIK DER FAUNA UND FLORA AUF DEREN REIN CHROMATISCHE GESETZLICHKEITEN HIN

von

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## INHALTSANGABE

Es wurde vermutet, daß die biologische Chromatik — ohne Unterschied zwischen der des Festlandes oder der des Meeres — inklusive ihrer Lock-, Schreck- und Schutzfarben, von rein chromatischen Gesetzmäßigkeiten regiert werden könnte. Gesetzmäßigkeiten, die nicht auf das Farbsehvermögen zurückzuführen sind, sondern auf den unterschiedlichen rein chromatischen Faktoren als solchen beruhen. Dieses bestätigte sich durch eine rein empirische Untersuchung was hier dargelegt werden soll. Ebenfalls: daß die bisher aufgefundenen Gesetzmäßigkeiten alle auf dem Faktor beruhen, daß die Natur scheint's ausnahmslos keine Farbkombinationen hervorbringt, die im offensichtlichen chromatischen Widerspruch zu denen stehen, die sie hervorbringt — meist in unzähligen Fällen, dem gewaltigen Umfang der Biochromatik entsprechend.

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## VORWORT

Der Autor des hier folgenden Artikels befaß sich schon weit mehr als zwanzig Jahre mit der von ihm so benannten biologischen Chromatologie. Als er mich vor vielen Jahren das erste Mal in unserem Naturhistorischen Museum in Leiden besuchte, gab er mir einen Artikel über sein Thema, der 1952 erschienen war. Zu diesem sagte er mir, daß einiges, was er damals geschrieben habe, vielleicht noch nicht zur genüge fundiert sei. Das wolle er nun nachholen. Zunächst mit einer möglichst lückenlosen Untersuchung der Farbzusammenstellungen auf den Lepidoptera. Bekanntlich würden die Farben, etwa der Paradiesvögel, tropischen Fische und Schmetterlinge, allgemein bewundert und wohl von niemandem als geschmacklos bezeichnet. Hierdurch habe man die alte Vermutung: daß die Natur, durch Naturgesetzmäßigkeiten gebunden, nicht jedwede Farbzusammenstellung herstellen könne wie der Mensch — daher auch keine sog. "geschmacklosen". Damit es nicht nur bei dieser Vermutung bliebe, habe er rein praktisch — empirisch untersucht: ob es, trotz des gewaltigen Umfanges der biologischen Chromatik, in ihr gewisse Farbzusammenstellungen nicht gibt, die den Menschen durchaus geläufig sind. Daraufhin zeigte er mir als Vorlagen je zwei Farben nebeneinander — also nur sehr Einfaches. Diese Farbenpaare sind auch in diesem Artikel unter den Nr. 3 bis 6, 20 und

21 abgebildet. (Auf der Farbtafel am Ende dieses Artikels — herausklappbar bei der Lektüre.) Sein Kommentar zu diesen Farbpaaren war: zwar könnte man die Farben, die er verwendet habe, in der Biochromatik nebeneinander finden, doch wohl nicht so, wie er sie nebeneinander gestellt habe. Diese Zusammenstellungen stünden scheinbar im Widerspruch zu den vermuteten Gesetzmäßigkeiten. Jedenfalls hätte er sie in der Biochromatik bisher — und zwar ausnahmslos — nicht finden können; wohl — allerdings nur selten — deutlich voneinander getrennt: meistens durch schwärzliche Farben oder Schwarz. Es sei ja ein großer chromatischer Unterschied, ob Farben voneinander getrennt sind oder direkt nebeneinander stehen.

Daraufhin bat er mich ihm zu sagen, ob ich ihm vielleicht Schmetterlinge nennen könnte, auf denen diese Farben nebeneinander vorkämen — wenn auch in Flächen von geringem Ausmaß. Da mir trotz längerem Nachdenkens kein Schmetterling einfiel, auf dem zum Beispiel Nr. 20 oder 21 vorkommt, begann der Fall mich etwas zu interessieren. Später immer mehr, weil alle die angeführten Farbkombinationen in unserer sehr umfangreichen Schmetterlingssammlung auch in geringem Ausmaß nicht zu finden waren. Trotz wiederholtem stundenlangen Suchen nicht, an dem ich mich auch einige Male beteiligte. Nur selten fand sich hie und da, was dem Abgebildeten mehr oder weniger ähnelte, aber keinen Vergleich mit unseren Vorlagen aushielt: also nicht eine überzeugende Ausnahme. Später haben sich auch meine Kollegen im British Museum of Natural History in London — in dem sich wohl die vollständigste Schmetterlingssammlung Europas befindet — an Peterich's Suche beteiligt. Was bei uns nicht gefunden werden konnte, ließ sich auch dort nicht finden. Bei den zum Teil noch unbeschriebenen Mikro-Lepidoptera, mit denen ich mich schon seit Jahren befasse, ist es auch nicht vorhanden. Unter dem vergebens Gesuchten sind auch Komplementärfarben — ein Begriff, der wohl jedem geläufig ist. Daher wunderte es mich schon nach dem ersten Suchen nach ihnen, daß es meines Wissens nach noch nicht aufgefallen war, daß Komplementärfarben bei den Lepidoptera scheinbar nicht vorkommen; jedenfalls nicht in einigermaßen so starken Farben wie auf Peterichs Vorlagen. Was Blau direkt neben Gelb betrifft, kam der seltene südamerikanische Falter *Agrias bewitsonius bewitsonius* als Ausnahme in Frage. (In London gibt es nur ein, bei uns kein Exemplar von ihm.) In Paris in der Sammlung Fournier im Muséum National d'Histoire Naturelle gibt es von diesem Falter mehrere Exemplare. Um sich Gewißheit zu verschaffen, hat Peterich sie miteinander verglichen. Der Falter — berichtete er mir — sei auf den ersten Blick hin allem Anschein nach eine ausgesprochene Ausnahme; nicht aber bei genauerer Betrachtung. Daher sei er nur eine Scheinausnahme. (Er ist auch in diesem Artikel beschrieben.) Weitere von ihm so benannte Scheinausnahmen hat er bei den Lepidoptera nicht gefunden.

Mit der Zeit erbrachte sein spezielles Studium der Lepidoptera nicht nur das angeführte Resultat, sondern noch eine Reihe sehr unterschiedlicher Art. Von diesen ausgehend, hat er dann die gesamte biologische Chromatik, auf die von ihm gesuchten rein chromatischen Gesetzmäßigkeiten hin, studiert. Das Buch, daß er über seine Resultate geschrieben hat, ist noch nicht erschienen — der hohen Reproduktionskosten der zahlreichen Farbfotografien wegen, die dessen Inhalt sehr anschaulich illustrieren. Da dieses meiner Meinung nach auch uns Entomologen interessieren kann, folgt hier ein Auszug aus seiner Chromatologie.

(Aus dem Holländischen übertragen.)

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## EINFÜHRUNG

Die Vermutung drängt sich geradezu auf, daß die Biochromatik — dem gesamten organischen Leben entsprechend — nicht amorph ist, sondern inklusive ihrer Lock-, Schreck- und Schutzfarben durch Gesetzmäßigkeiten regiert wird, und zwar: rein chromatische. Allerdings mit einigen Ausnahmen, die aber diese Vermutung dadurch stützen, daß sie so selten sind. Es handelt sich bei ihnen um die täuschende Nachahmung amorpher Farbzusammenstellungen, z.B. angefaulte Blätter einiger sogenannter Blattschmetterlinge (*Kallima paralekta*).

Diese auffälligen, vielbesprochenen Ausnahmen — sogenannte Mimikry-Erscheinungen — fallen aber bekanntlich aus dem Gesamtbild der Biochromatik heraus. (Vergleichsweise wie das botanische Aussehen des sog. wandelnden Astes und anderer *Phasmidae* aus dem habituellen Gesamtbild der Insekten herausfällt.) Ansonsten sehen wir auch bei den ausgesprochensten Schutzfärbungen Ordnung, z.B. feine lineare Musterungen die keineswegs amorph sind, wie etwa das Bleistiftgekrizel eines kleinen Kindes an der Wand. Feine und feinste Einzelheiten und Farbnuancen sind ein durchgehendes Charakteristikum der biologischen Chromatik. Wie diese eine biologische Funktion haben können, ist schwer ersichtlich: Aus der Ferne können sie nicht heranlocken, aus der Nähe nicht erschrecken, dazu sind sie viel zu unscheinbar. Und wie könnten sie Tiere schützen? Man muß ihrer ja schon habhaft sein, will man diese Feinheiten überhaupt sehen. Auch dieses stützt die besagte Vermutung.

Von der visuellen Funktionalität her konnten diese Gesetzmäßigkeiten bisher nicht erkannt werden. Sie stehen — das sei hier vorausgeschickt — offenbar auch in keinem Zusammenhang mit dem höchst unterschiedlichen Sehvermögen von Mensch und Fauna. Deswegen nicht, weil sie sich in der gesamten Biochromatik uniform auswirken. Obwohl wir unser Sehvermögen bei unserer Untersuchung ebenso nötig haben wie der Bakteriologe sein Mikroskop, ist unser grundsätzlicher Ausgangspunkt nicht visuellen Charakters, sondern ein rein verstandesmäßig gesuchter und gefundener: — Wenn die Natur (von der angeführten "Vorspiegelung falscher Tatsachen", etwa bei den Blattschmetterlingen, abgesehen) alle Farben der Biochromatik rein chromatisch gesetzlich anordnet, so dürfte es in Flora und Fauna keine Farbzusammenstellungen geben, die ihren Gesetzmäßigkeiten widersprechen. Um diese Gesetzmäßigkeiten zu finden, haben wir eine unserem Ausgangspunkt entsprechende einfache Methode: Zunächst muß festgestellt werden, welche Farbzusammenstellungen in der gesamten Biochromatik in unzähligen Fällen vorhanden sind — offenbar naturgesetzlicherweise, denn sonst wären sie nicht in so hoher Anzahl in der gesamten Biochromatik anzutreffen. Zu jeder dieser häufig vorkommenden Farbzusammenstellungen stellen wir uns jeweils das ihnen chromatisch Entgegengesetzte her. Mit Hilfe dieser — der Biochromatik widersprechenden — Vorlagen, kann dann rein empirisch festgestellt werden, daß in der Biochromatik Gesetzmäßigkeiten regieren, denen zufolge die Natur keine Farbzusammenstellungen hervorbringt, die im Widerspruch zu denen stehen, die sie in Mengen hervorgebracht hat.

Diesen ihren Gesetzmäßigkeiten widersprechen z.B. alle die auf unserer, teils schematischen, Farbtafel am Ende dieses Artikels abgebildeten Farbzusammenstellungen, bei denen ein Minuszeichen steht. Sie konnten trotz jahrelangem Suchen — zumindest bis jetzt — ausnahmslos nicht gefunden werden. Sie stehen im chromatischen Gegensatz zu denen, die in der Biochromatik häufig oder in unzählbaren Fällen vorhanden sind, — daher steht bei ihnen ein Pluszeichen. Daß alle die Vorlagen, bei denen ein Minus-

zeichen steht, im chromatischen Gegensatz zu denen stehen, bei denen ein Pluszeichen steht, soll später dargelegt werden. In manchen Fällen ist dieses aber auch ohne Erläuterung ersichtlich. Deutlich entgegengesetzt sind z.B. Nr. 24 zu 27; Nr. 25 zu 28; Nr. 41, 42 zu Nr. 55, 56; Nr. 48 zu 49; Nr. 50 zu 51; Nr. 52 zu 53; Nr. 57 zu 58; — ferner Nr. 59, 60 zu Nr. 61, 62, 63; Nr. 77 und 78 im Gegensatz zu Nr. 76; Nr. 79 und 80 zu Nr. 81. Nr. 66 steht durch die Wiederholung ein und desselben Motives im Gegensatz zu Nr. 67. Durch die Gegensätze stehen die mit einem Minuszeichen versehenen Beispiele in unmittelbarem Zusammenhang (wie + und —) mit den naturgemäßen, bei denen ein Pluszeichen steht. Nur diese Gegensätzlichkeit zeigt uns an, daß es Gesetzmäßigkeiten gibt — und welche; — wahrscheinlich noch viel mehr als bisher gefunden werden konnten. (Sie sind aber nicht dadurch zu finden, daß man Farbzusammenstellungen herstellt die in der Biochromatik fehlen. Hieraus geht nur hervor, daß diese nicht biochromatisch gesetzlich sind.) Die Farbkombinationen, bei denen weder ein Minus-, noch ein Pluszeichen steht, sind in der Biochromatik nicht häufig — die, bei denen ein "s" steht, sind selten.

Kommen gewisse Farbzusammenstellungen in der gesamten Biochromatik ausnahmslos nicht vor, so impliziert dieses Gesetzmäßigkeiten.

#### GIBT ES EVENTUELL NUR REGELN IN DER BIOCHROMATIK?

Ich hoffe, daß dieser Artikel ein Interesse an der Bestätigung, respektive Falsifikation der rein chromatischen Gesetzmäßigkeiten (die allerdings später noch expliziert werden müssen) mit sich bringt. Das Abgebildete unter dem ein Minuszeichen steht, gestattet eine Suche, um zu prüfen, ob es vielleicht doch noch ausnahmsweise gefunden werden könnte. Sollte sich noch diese oder jene Ausnahme finden lassen, müßte das, was jetzt noch als gesetzlich angesehen werden kann, zur Regel abgeschwächt werden.

Was an Ausnahmen eventuell noch gefunden würde, möchte der Autor sammeln und denjenigen, die sich an der Suche beteiligten, zuschicken, — so nötig, kommentiert.

Die Frage: was zur Regel abgeschwächt werden muß — was nicht, weil sich keine Ausnahmen finden lassen — wird ohne das erwähnte Interesse nicht so bald zu lösen sein; von mir meines beträchtlichen Alters wegen nicht mehr. Für die an ihrer Lösung Interessierten noch das Folgende: Trotz der botanischen Gärten, Aquarien und Terrarien ist das Gebiet der unhaltbaren Farben der Flora und Fauna teils schwer zugänglich. Man denke nur an die Raupen. Hierdurch könnten auf diesem Gebiete noch Ausnahmen gefunden werden. Unbedingt anzunehmen ist das nicht. Es ist nicht sehr wahrscheinlich, daß sich auf ihrem kleineren Teil alles anders verhält; — leicht zugänglich und schwer zugänglich sind ja keine chromatischen Faktoren.

In Bezug auf das, was sich schon einige Zeit in Museen befindet — zweifellos der größte Teil der haltbaren Biochromatik — kann die Suche nach Ausnahmen als vollständig betrachtet werden.

Wenn es sich um Farbnuancen handelt, wie etwa die auf unserer Farbtafel Nr. 3 und 4, ist auf farbige Abbildungen der Objekte meist kein Verlaß. Man muß alles *in natura* sehen. Auch darf das Anschauungsmaterial in den Museen nicht zu alt sein. Wer auf dem Gebiete der Farben und ihrer Nuancen nicht ganz zu Hause ist, bedient sich bei der Suche am besten der hier abgebildeten Vorlagen. Die Biologen, die sich an der Suche beteiligten, meinten zumeist schon vorher, daß dergleichen auf ihrem Spezialgebiet wohl schwerlich gefunden werden könnte. Selten fanden sich Objekte, die auf den ersten Blick



den Anschein erweckten, daß es sich bei ihnen um eine Ausnahme handelte, aber bei genauerer Betrachtung es doch nicht waren. Wir nennen sie Scheinausnahmen, und werden auf sie zurückkommen. Die Suche begann im Rijksmuseum van Natuurlijke Historie in Leiden und wurde dann, der Vollständigkeit halber, im British Museum of Natural History in London, im Muséum National d'Histoire Naturelle in Paris und anderen Museen fortgesetzt.

Da bei dieser Untersuchung auch Nuancen, z.B. wie Nr. 4, eine sehr entscheidene Rolle spielen, das Folgende: Auch wenn Nuancen nur im Ansatz vorhanden sind, kann man sie gewiß durch Züchtung z.B. bei Blumen, dergestalt übersteigern, daß ursprünglich feine Nuancen zu erheblichen Kontrasten werden. Aus diesem Grunde kommen Züchtungen für die Chromatologie nicht in Betracht. Andererseits wäre interessant, durch Züchtung die Kraft der Gesetzlichkeiten zu prüfen, z.B. Farbkombinationen zu erzielen, bei denen es sich nicht nur um Nuancen handelt wie etwa Nr. 3 und 4, sondern um in der Biochromatik offenbar grundsätzlich nicht Vorhandenes, wie Nr. 20, 21, 27, 41, 42, 46, 63, 67.

#### FRAGEN DIE DIE CHROMATOLOGIE MIT SICH BRINGT

Diese Fragen wurden dem Autor immer wieder gestellt, obwohl einige von ihnen ganz außerhalb des chromatologisch Feststellbaren liegen. In diesen Fällen handelt es sich nicht um Antworten auf sie, sondern nur um Hinweise. Eine der stets gestellten Fragen war. "Was berechtigt dazu, das Farbsehen der Fauna in der Chromatologie einfach zu negieren?" Die wahrscheinlich sogar höchst unterschiedliche Perzeption der Farben durch unsere und der Tiere Augen, erhöht die Anzahl der eventuell noch vorhandenen Ausnahmen ebensowenig, wie aus einer Banane zwei werden, wenn ein Mensch deren Farben — wie das vorkommt — auf jedem Auge etwas anders sieht. (Farbmessungen können selbst den Über-Skeptiker davon überzeugen.) Was in der Biochromatik ihrer Gesetzlichkeit zufolge ausnahmslos nicht vorhanden ist, kann in ihr überhaupt nicht erblickt oder durch Farbmessungen aufgefunden werden. Farbsehbegrenzungen bringen keine biochromatischen mit sich; weder unsere noch z.B. die der Bienen, die kein Rot sehen sollen. (In einem späteren Stadium der Chromatologie ist es wohl ratsam Instrumente zu benutzen — Spektrometer usw. —. Mit ihnen könnten die Ergebnisse wohl auch in quantitativer Hinsicht *exakter belegt* und auch die ultravioletten und infraroten Wellenlängen in die Untersuchungen einbezogen werden).

Bis jetzt ist es vom Visuellen her noch keineswegs ersichtlich geworden, daß die in der Biochromatik fehlenden Farbzusammenstellungen, wenn sie in der Flora und Fauna vorhanden wären, nicht auch als Lock- (Nr. 46), Schreck- (Nr. 51) und Schutzfärbungen (Nr. 67) oder sogenannte Erkennungszeichen dienlich sein könnten. Insekten fliegen z.B. an Gräsern befestigten Papierschnitzeln zu, auf die man malt, was es in der Biochromatik nicht gibt; z.B. auf eine weiße Pseudoblüte violette Flecken mitten auf ihre Blätter, Nr. 46.

Der offenbar non-visuelle Charakter dieser Gesetzlichkeit läßt sich vielleicht aus dem Folgenden erklären: Da alles was nicht durchsichtig ist eine Farbe hat, muß es von den winzigen Anfängen der Fauna und Flora auf Erden an, eine (also schon viele Millionen Jahre alte) biologische Chromatik gegeben haben, ehe sich Augen so hoch entwickeln konnten um Farben zu sehen. (Übrigens: Das Farbsehen ist ja — wie uns farbenblinde Tiere zeigen — keine Lebensnotwendigkeit in so hohem Grade wie etwa die

Nahrungsaufnahme.) Wenn die in diesem Sinne prä-visuelle Biochromatik, wie wir annehmen dürfen, nicht amorph sondern chromatisch gesetzlich war, so waren ihre Gesetzmäßigkeiten prä-visuell und somit non-visuellen Charakters wie offenbar die heutigen. Der biologisch-funktionelle Faktor des sich langsam entwickelnden Farbsehvermögens brauchte diese prä-visuellen Gesetzmäßigkeiten nicht außer Kraft zu setzen (ganz abgesehen davon, ob er dazu imstande gewesen wäre). Die Selektion konnte sich ja auch in ihrem Rahmen auswirken. Verbieten diese Gesetzmäßigkeiten doch weder Auffälliges zu Lockzwecken, noch eine hochgradige Anpassung an die Umgebung bei Schutzfärbungen — ohne daß diese deswegen amorph sind (mit Ausnahme der bereits erwähnten Mimikry-Nachahmungen amorpher Chromatik). Bei ihnen hat das vitale Bedürfnis nach vollkommener Tarnung die als solche non-visuellen und in diesem Sinne wahrscheinlich nonvitalen, biochromatischen Gesetzmäßigkeiten offenbar überwunden. (Das Umgekehrte zeigt sich bei den Ausnahmefällen in denen die Natur Tieren Mortales auferlegt; z.B. dem Babirussaschwein des ostindischen Archipels. Ihm wachsen, wenn es älter wird, seine Hauer in großen Bogen tödlich durch den Schädel ins Gehirn.)

Von chemischen Einflüssen her ließe sich das Fehlen gewisser Farbzusammenstellungen in der Biochromatik bisher auch nicht erklären. Nicht zuletzt, weil sich diese Gesetzmäßigkeiten gleichermaßen in Pigmentfarben und Strukturfarben auswirken. Auch hat jedes Schüppchen der Schmetterlinge seine eigene Farbe, desgleichen die Schuppen der Fische und die Federn der Vögel. Durch diese Trennung der einzelnen Objekte wird ein chemischer Einfluß ganz unwahrscheinlich.

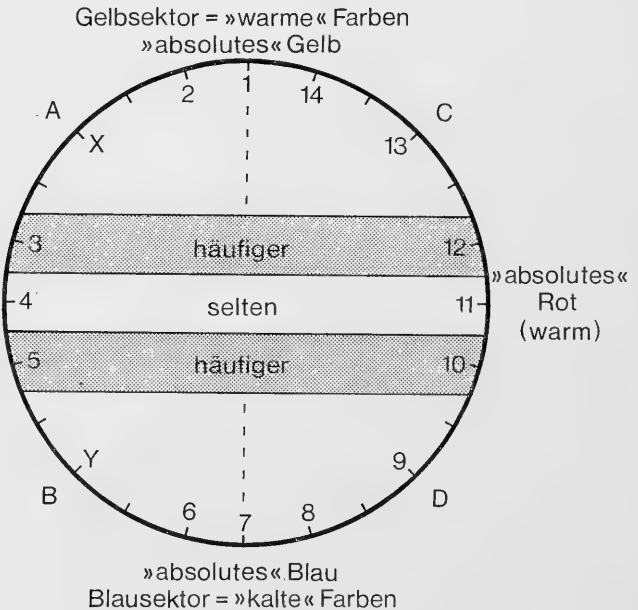
Obwohl es sich bei dem hier Angeführten um interessante Fragen handelt, sind sie insofern für die Chromatologie irrelevant, weil deren Lösung keinerlei Veränderung in der Biochromatik mit sich bringt.

Figur II



«absolutes»  
Grün  
(neutral =  
weder kalt  
noch warm)

Figur I



Zu der Beantwortung anderer, schon öfters gestellter Fragen noch dieses: Ästhetische Begriffe kommen für uns nicht in Betracht. Auch nicht die Aussagen der bekannten Farbenlehren, die dadurch theoretischen Charakters sind, weil in ihnen die sog. Komplementärfarben-Theorie eine bedeutende Rolle spielt. Übrigens gilt diese Theorie heute Vielen als völlig veraltet. Die Farbenpraxis der Natur in Flora und Fauna entspricht dieser Theorie jedenfalls nicht.

Soweit alles das, was unserer Untersuchung ihres ungewöhnlichen Ausgangspunktes wegen, vorausgeschickt ist.

*Terminologie.* Für die Terminologie die wir zur Beschreibung der Gesetzmäßigkeiten brauchen, orientieren wir uns zunächst an dem sog. Farbkreis. Obwohl er durch die Farben die wir nicht sehen (z.B. Ultraviolett) nicht vollständig ist, ist die mit ihm verbundene Terminologie für uns ein sehr brauchbares "descriptives Instrumentarium".

*Zu Figur I:* Die Farben der oberen Hälfte des Farbkreises sind die des Gelbsektors, die der unteren Hälfte sind die des Blausektors. Das absolute Grün und das absolute Rot rechnen wir weder zu dem Blau- noch zu dem Gelb-Sektor. Der Terminus "absolut" ist konventionell und vor allem für die vier sog. Hauptfarben: Rot, Grün, Gelb und Blau gebräuchlich.

Am Farbkreis links A: die Skala vom absoluten Grün an bis Gelb. B: die Skala vom absoluten Grün an bis Blau. Rechts am Farbkreis C: die Skala von Gelb an bis zum absoluten Rot. D: die Skala vom absoluten Rot an bis Blau.

1 = absolutes Gelb; 2 = Grüngelb; X = die Farbe, die zwischen Grüngelb (2) und Gelbgrün (3) liegt. 4 = absolutes Grün (neutral — weder "kalt" noch "warm"); 5 = Blaugrün; Y = die Farbe, die zwischen Blaugrün und 6 = Grünblau liegt; 7 = absolutes Blau; 8 = Violettblau; 9 = Violett und seine Nuancen: Blauviolett und Rotviolett; 10 = Violettrot (das "kalte" Rot); 11 = absolutes Rot; 12 = Orangerot (das "wärmste" Rot); 13 = Orange und seine Nuancen: Rotorange und Gelborange; 14 = Orange gelb. Bei den Doppelnamen ist der zweite der entscheidende. Gelbgrün ist ein gelbliches Grün; Grüngelb ist ein grünliches Gelb. *Für die Farben X und Y haben wir keine bekannten Doppelnamen, die die Farben genau bestimmen.*

(Alle im Text folgenden Nummern: von Nr. 1 bis Nr. 81, beziehen sich auf die Farbtafeln — am Ende des Artikels.)

#### DIE UNTERSCHIEDLICHEN FARBGRUPPEN

**Starke Farben:** nennen wir wie üblich die intensivsten, aus denen man sich in spektraler Folge den sog. Farbkreis gebildet hat. Wir haben eine Anzahl von ihnen auf unserer Farbtafel: Nr. 3 bis Nr. 9; was Blau betrifft: A von Nr. 10, ferner Nr. 20 und Nr. 21. (Die Intensität biochromatischer Farben übertrifft teilweise die, welche man drucken kann.)

**Kalte und warme Farben:** siehe Farbkreis Figur I. Von dem absoluten Grün als auch dem absoluten Rot an, nimmt die Wellenlänge der Farben dem Blau zu ab. Die Farben des Blausektors werden vulgo kalte Farben genannt. Von dem absoluten Grün an (also ohne dieses) werden die Farben des Gelbsektors, inklusive des absoluten Rots, allgemein warme Farben genannt. Wir bedienen uns dieser gebräuchlichen Adjektive kalt und warm aus praktischen Gründen.

Das absolute Grün liegt, was seine Wellenlänge betrifft, in der Mitte des Farbbandes; gilt als neutral. Figur II: + = Farben längerer Wellenlänge = warm; — = Farben

kürzerer Wellenlänge = kalt; dazwischen die Farbe mittlerer Wellenlänge = absolutes Grün = neutral (weder kalt noch warm).

**Gebrochene Farben:** nennen wir die starken kalten Farben, wenn ihre Kälte durch eine Zutat warmer Farbe gebrochen ist (das Blau B von Nr. 10). Gebrochene warme Farben nennen wir die, deren Wärme durch eine kleine Zutat einer kalten Farbe gebrochen ist.<sup>1)</sup>

**Abgeschwächte Farben:** nennen wir die starken, durch Verdunkelung oder Aufhellung abgeschwächten: z.B. Nr. 1 = ein starkes Blau links durch Verdunkelung, rechts durch Aufhellung abgeschwächt.

**Leuchtfarben:** nennen wir die nur um ein wenig abgeschwächten oder gebrochenen starken Farben und diese selbst.

**Halbfarben:** Von uns so genannt, um sie von den abgeschwächten starken Farben und den gebrochenen deutlich zu unterscheiden, zeigen uns z.B. die hellsten bis zu den dunkelsten Holzsorten oder auch die Erdfarben: z.B. Nr. 2.

**Nichtfarben:** sind Schwarz und Weiß und die Grauskala zwischen ihnen — sie zeigen uns kein Farblicht.

#### BIOCHROMATISCHE GESETZLICHKEITEN

1. *Zeichnerische Musterungen* bestehen nie aus vielen starken Farben (Farbtafel Nr. 27, 28, 29) und insofern fast immer aus Halbfarben (Nr. 24, 25), seltener aus Schwarz und Weiß (Nr. 26), weil die aus einer starken Farbe zusammen mit der Nichtfarbe Schwarz oder Weiß weitaus seltener sind (Nr. 31, 32, 33). Noch seltener sind die, die sich aus zwei starken Farben und einer der Nichtfarben (meistens Schwarz) zusammensetzen (Nr. 36, 37). Im chromatischen Widerspruch zu diesen halbfarbenen oder Schwarz-Weiß Musterungen stehen deutlich ihre Übersetzung in starke Farben: Nr. 27, 28, 29; dergleichen konnte in der Biochromatik nicht gefunden werden. (Nr. 24 = Nachfalter *Brahmaea wallichii*; Nr. 25 = Vogel *Squatarola squatarola*; Nr. 26 = Silberfasan *Gennaues nycthemerus* ♂.)

Das zeichnerische Hell-Dunkel und überhaupt der Hell-Dunkel-Kontrast, liegt prinzipiell auf einer ganz anderen Ebene als chromatische Kontraste. Denn Hell-Dunkel ist in seiner stärksten Form Schwarz-Weiß, also farblos. Fotografieren wir die Musterung Nr. 24 schwarz-weiß, bleibt die Essenz der Musterung erhalten (Nr. 30). Bei einer Schwarz-Weiß-Fotografie von Nr. 27 würden die chromatischen Gegensätze, die für Nr. 27 essentiell sind, verschwinden.

Daß die halbfarbenen Musterungen, wie Nr. 24 und Nr. 66, keineswegs nur deswegen vorhanden sind, weil sie in unzähligen Fällen als Schutzfärbungen auftreten, geht aus der Gesamtheit der Biochromatik sehr deutlich hervor!

Wir haben diese besagten Musterungen z.B. auch auf Orchideen, auf den Saaten des *Ricinus* und unter der undurchsichtigen Haut der *Conus*-Muscheln in den schönsten Variationen. Nicht nur das, auch auf Tieren wird uns ihr rein-chromatischer Charakter ersichtlich; denn wir haben diese halbfarbenen Musterungen in unzähligen Fällen gleichzeitig sichtbar neben dem im Sommer sehr auffälligen Weiß und den weithin leuchtend-

<sup>1)</sup> Gebrochene kalte Farben haben wir experimentell, wenn wir auf den gesamten Farbkreis eine gelbliche Glasscheibe legen. Hierdurch wird die Hälfte der kalten Farben gebrochen — derweil die Wärme der warmen Farben gebrochen wird, wenn wir ein etwas bläuliches Glas auf den Farbkreis legen.

sten Farben. Zwei allgemein bekannte Beispiele für diese so häufige Erscheinung sind *Ara ararauna* mit seinem leuchtenden blau-gelben Gefieder, dazu eine fast schwarz-weiße Musterung um sein Auge, und *Pavus cristatus* mit seinen bräunlich gemusterten Flügeln neben dem weithin leuchtenden Blau seiner Brust. In dem Vogelbuch "Birds of the World" (von Oliver L. Austin, Verlag Paul Hamlyn Ltd., London) — mit 754 Abbildungen — fanden sich 117 mit den genannten halbfarbenen Musterungen, von diesen wiederum stehen 90 halbfarbene Musterungen neben Weiß oder leuchtenden Farben. Diese Kontraste sind durchaus nicht nur für die Vögel charakteristisch. Das Zusammentreten von auffälligen und unauffälligen Farben ist eines der ausgesprochensten Charakteristika der Biochromatik — nicht der der Säugetiere. Der Pavian ist eine Ausnahme.

Es gibt in der Natur starkfarbige monochrome Musterungen durch die Verbindung der Nichtfarbe Schwarz mit einer Farbe: Nr. 31 (Fisch *Pomacanthus semicirculatus*), Blau auf Schwarz und Schwarz auf Grün; Nr. 32 (Fasan, *Chrysolophus amherstiae*); Nr. 33 (Goldfasan, *Chrysolophus pictus*); ähnliches schwachfarbig Nr. 34 (Fisch *Mollienisia latipinna*); Nr. 35 ist monochrom, weil Weiß eine Nichtfarbe ist (Fisch *Ostichthys japonicus*); Nr. 36 (Fisch *Halichoerus marginatus*) und Nr. 37 (Fisch *Ostracion lentiginosum*) sind bichrom mit Schwarz-Isolierung der Farben; nicht polychrom aus drei oder mehr Farben bestehend, wie Nr. 38 A, B, C (mit Minuszeichen versehen). Die beschriebenen bichromen Musterungen in zwei starken Farben mit Schwarz sind selten, vor allem von der gesamten Biochromatik her gesehen. Die Kopffedern des Vogels *Onychorhynchus mexicanus* (Nr. 40) gehören bei den Vögeln zu den größten Seltenheiten. Es gibt auch Musterungen, die aus einer starken Farbe und einer stark abgeschwächten Farbe bestehen, meist auch mit Schwarz-Zutaten, so die Musterung auf dem Schmetterling *Deiopeia pulchella*.

Es gibt auch Musterungen in zwei Farben — ohne Schwarz — jedoch nicht in starken Farben. Sie sind sehr selten, Nr. 39 (Kopf des Fisches *Halichoerus marginatus*, Nr. 36).

Die Musterungen in allen ihren Nuancen ist eines der interessantesten Kapitel in der Biochromatik, dessen Ausführung uns aber in diesem Artikel zu weit führen würde.

2. *Die enge Beziehung zwischen Schwarz und fast Schwarzem zu starken Farben.* Diesbezüglich haben wir Nr. 31, 32, 33, 36, 37, 40, 47 (Fisch *Coris angulata*), Nr. 48, 50, 53, 55, 56, 57, 59 und 60. Dieser engen Beziehung widerspräche chromatisch eine gleiche Beziehung starker Farben zu Weiß, mit Minuszeichen: Nr. 41, 42, 43 (nicht 43 A). (Nr. 44, eine der *Viola*-Züchtungen, ist eine Scheinausnahme; auf den einzelnen Blättern: Nr. 45, steht die starke Farbe nicht mitten auf Weiß. Sähe die Blume aus wie Nr. 46, wäre sie eine Ausnahme.) Nicht zu finden waren ferner: Nr. 49, 51, 52. (Zu Nr. 52: Haarfeine weiße Abschlußrändchen fanden sich bei einem der Stiefmütterchen. Weil sie so haarfein sind, können sie die Leuchtkraft der Farbe nicht beeinträchtigen wie ein breiterer Rand.) Nicht gefunden wurde etwas, was Nr. 58 und Nr. 61 entspräche.

3. *Die Gesetzmäßigkeiten im Bezug einer ausgesprochenen Kontinuität, vornehmlich bei Musterungen.* Hierfür gibt es unzählige Beispiele: Dieser Kontinuität entsprechen Nr. 59 und 60, ihr widersprechen Nr. 62 und 63. Ein unscheinbares Motiv Nr. 65 wird kontinuierlich wiederholt (Nr. 66), dem widerspricht Nr. 67.

Wir unterscheiden in der Kontinuität der Musterungen — sagen wir: Stakkato-

Musterungen: Nr. 66 und lineare: Legato-Musterungen: Nr. 24. Die Kontinuität der Musterungen haben wir auch bei Nr. 79 und 80 (keine starken Farben — sondern wie die von Nr. 39); ihr widersprüche Nr. 81.

4. *Flächen in starken warmen Farben treten nicht unmittelbar neben Flächen in starken kalten Farben. Das neutrale Grün tritt zu allen diesen Farben.*

Bei dieser Gesetzmäßigkeit spielt es keine Rolle, ob sich die Farben im Farbkreis gegenüber liegen oder aber, ob sie auf einer der verschiedenen Seiten des Farbkreises stehen, wie z.B. Blaugrün und Gelbgrün. Die starken warmen Farben treten untereinander in allen Kombinationen unmittelbar nebeneinander: die starken kalten Farben gleichermaßen, z.B. warmes Grün und warmes Rot (Farbtafel Nr. 7), als auch kaltes Grün und kaltes Rot (Nr. 8). Nr. 7 und 8, die jeweils eine gemeinsame Wärme respektive Kälte verbinden, treten bezeichnenderweise häufiger zusammen als absolutes Grün und absolutes Rot, Nr. 9. Diese Paare verbindet keine gemeinsame Wärme, weil das neutrale Grün nicht warm ist. Siehe die Verbindungstreifen zwischen den Rots und den Grüns, Figur I, Seite 148 Farbkreis.

Diese Gesetzmäßigkeit widerspricht dem unmittelbaren Zusammentreten kalter und warmer Farben, auch wenn sie im Farbkreis nahe beieinander liegen: Nr. 3, warmes und kaltes Grün; Nr. 4, warmes und kaltes Rot; Nr. 5, warmes Grün und kaltes Rot; Nr. 6 warmes Rot und kaltes Grün. Nr. 10, warmes Rot zu kaltem Blau A (nicht zu dem mit etwas Rotzumischung gebrochenen Blau B). Dasselbe Blau zu ungefähr der gleichen Menge Gelb (nicht abgebildet) — auch ein Kalt-Warm-Effekt — widerspricht der Gesetzmäßigkeit gleichermaßen, wie der Kalt-Warm-Gegensatz Nr. 20, das kalte Violett zu der warmen Farbe X und Nr. 21, das warme Orange zu der kalten Farbe Y. Siehe X, Y, Figur I, Seite 148.

Das absolute Grün tritt — wie gesagt — zu allen Farben des Farbkreises. Im übrigen sind die Rot-Grün Gegensätze in der Biochromatik lange nicht so häufig wie man denken sollte, wenn man an die grünen Pflanzen denkt, die rote Blüten tragen. Das Blattgrün ist bei Knospenblättern und Blütenstielen meist so stark abgeschwächt, sodaß der starke Rot-Grün-Kontrast dadurch nicht zustande kommt, weil das starke Rot dann nur noch neben einem verblaßten Grün steht. Rote Tulpen haben z.B. Stiele, deren Grün ein ausgesprochen gebrochenes und verdunkeltes ist; nicht so bei den roten Tulpen, deren Blätter, bevor sie an den Stiel herantreten, schwärzlich oder weißlich oder etwas gelblich umgefärbt sind, diese Tulpen haben Stiele starken Grüns.

Bei den Lepidoptera gibt es überhaupt kein kräftiges Rot und Grün nebeneinander. Das Rot und Grün welches bei ihnen zusammentritt, ist durch Helligkeit stark abgeschwächt und überdies noch gebrochen, kaum stärker als Olivgrün; das Rot schwachfarbiger als das der Ziegelsteine. Rot- und Grün-Effekte lassen sich weitaus am besten bei den Papageien studieren. Bei ihnen haben wir kein warmes Rot neben kaltem, bläulichen Grün: Nr. 6, mit Minuszeichen; wohl haben wir Nr. 7: warmes Rot und warmes Grün. Ferner Nr. 9: warmes Rot und neutrales Grün. (Nr. 8 fand sich nicht in so starkfarbiger Form bei den Papageien.)

Interessant ist für uns die als Zimmerpflanze beliebte Buntnessel *Coleus* (Labiatae). Auf ihren Blättern haben wir kaltes Rot gegen kaltes Grün, an anderer Stelle warmes Rot gegen warmes Grün, aber kein kaltes Grün gegen warmes Rot. Die Rots, als auch die Grüns dieser Pflanze gehören nicht zu den stärksten Farben der Biochromatik; in dieser ist die Kombination Nr. 7 häufiger als die Nr. 8.

Kalte und warme Farben die nicht in voller Kraft nebeneinander treten, finden wir unter Konditionen, die den Kalt-Warm-Gegensatz bedeutend abschwächen. 1.) Beide Farben sind zu hell für den starken Kontrast (Nr. 11); 2.) zu dunkel (Nr. 12); 3.) eine zu dunkel (Nr. 13). 4.) Eine der Farben tritt in Minorität gewissermaßen nur kontrastpunktisch zur anderen, sodaß der Gegensatz geringer wird als wenn beide Farben in ungefähr gleichem Ausmaß nebeneinander treten. Man muß ja den Effekt im Ganzen, nicht durch die Lupe sehen (siehe Nr. 14 und 15). 5.) Der Kontrast löst sich in Punkten auf (Nr. 16). 6.) Ein prismatischer Übergang zwischen den Farben z.B. erst Blau, etwas Grün, dann Gelb (Nr. 17). 7.) Eine dritte Farbe oder eine Nichtfarbe, z.B. Schwarz, trennt beide Farben voneinander (Nr. 18). 8.) Eine Farbe ist durch Schwarz-Zutaten verdunkelt (Nr. 19). Alle diese Konditionen haben wir im Bezug auf den Kalt-Warm-Kontrast Blau-Gelb dargestellt; sie gelten jedoch für alle starken Kalt-Warm-Kontraste. Nr. 23 (Fisch *Gramma loreto*, früher: *Gramma hemichrysos*) zeigt uns, daß Violett und Orange nur im Verlauf, nicht unmittelbar zusammentreten. Beide Farben nehmen an Intensität ab wo sie zusammentreten. Dieses ist sehr bedeutungsvoll, auch wenn es sich nur um Geringes handelt; und zwar deswegen, weil wir das Entgegengesetzte nicht haben, nämlich: daß die Farben intensiver werden wo sie direkt nebeneinander stehen. Der Kontrast ist hochgradig abgeschwächt wenn beide Farben nur gegeneinander schillern. Durch diese Abschwächungen von Kalt-Warm-Gegensätzen wird die Gesetzmäßigkeit nicht überschritten. Keine Ausnahmen, nicht einmal Scheinausnahmen, sind zwei Objekte unterschiedlicher Farbe nebeneinander, z.B. blaue Blütenblätter und gelbe Stempel!

Am ausgesprochensten abgeschwächt finden wir den Kalt-Warm-Gegensatz bei Nr. 20 und 21. Ein Faktum, was wahrscheinlich wie folgt interpretiert werden kann: je heller, respektive dunkler eine Farbe ist, desto schwächer ist sie. In beiden Fällen nähert sie sich ja: entweder der Helligkeit der Nichtfarbe Weiß, oder der Dunkelheit der Nichtfarbe Schwarz. Gelb ist heller, Rot dunkler als Orange. Daher ist Orange die stärkste warme Farbe des Sektors C Figur I. (Aus diesem Grunde kleidet man denn auch in Holland die Straßenarbeiter Orange.) Aus den gleichen Gründen ist X die stärkste warme Farbe des Sektors A (Figur I, Seite 148). Dementsprechend ist Y die stärkste kalte Farbe des Sektors B und Violett die stärkste kalte Farbe des Sektors D (Figur I). Daher müssen die beiden Kalt-Warm-Kontraste: Nr. 20 und 21 die stärksten sein. Wir sehen es nicht ohne weiteres, aber wir wissen es und können uns daher nicht darüber wundern, daß sie dem Prinzip der Abschwächung der Kalt-Warm-Gesetzmäßigkeit entsprechend am stärksten abgeschwächt sind, mittels der Konditionen, die bezüglich Blau-Gelb auf unserer Farbtafel Nr. 11 bis 19 dargestellt sind. Bezüglich dieser beiden Farbenpaare haben wir keine Fälle bei denen man nicht sofort sieht, daß es sich um keine Ausnahmen handelt. Die Fälle, bei denen auf den ersten Blick hin der Schein trügt — unsere Scheinausnahmen — haben wir nur was Blau und Gelb betrifft. Was läßt sich diesbezüglich vermuten? Gelb ist die hellste der Farben des Farbkreises. In dieser Hinsicht steht es der Nichtfarbe Weiß näher als die anderen Farben des Kreises. Blau hingegen ist eine der dunkelsten Farben — wenn nicht sogar die dunkelste — und nähert sich hierdurch der Nichtfarbe Schwarz. Daher haben wir die dankbar größte Hell-Dunkel-Stufe im Farbkreis wenn Blau neben Gelb tritt. (Der Hell-Dunkel-Kontrast ist prinzipiell kein chromatischer, denn er ist — wie gesagt — in seiner Konsequenz Schwarz-Weiß.) Hierdurch wirkt die große Hell-Dunkel-Stufe zwischen Gelb und Blau dem reinem chromatischen Kontrast entgegen. Wir erkennen es zwar nicht ohne weiteres, doch wir wissen es.

Der Gelb-Blau-Scheinausnahmen wegen haben wir auf unserer Figur I (Seite 148) eine Linie in Pünktchen. Die Scheinausnahmen Blau-Gelb sind sehr selten. So haben wir z.B. bei den Käfern — deren Anzahl an die 600 000 geschätzt wird — wohl nur eine; bei den Schmetterlingen — deren Anzahl an die 200 000 betragen soll — auch nur eine; bei den Fischen und Vögeln nur ganz wenige, bei den Blumen z.B. fand sich bis jetzt noch keine. Einige dieser Scheinausnahmen sollen hier beschrieben werden:

Bei den Lepidoptera haben wir den südamerikanischen Falter *Agrias bewitsonius bewitsonius*. Er zeigt ein leuchtendes Blau neben einem ausgesprochenen starken Gelb — aber nicht ganz so kräftig wie das Blau. Bei einer genauen Betrachtung aber sind diese Farben auf den oberen Flügeln von einer ganz feinen schwärzlichen Linie voneinander getrennt. Auf den unteren Flügeln streuen sich, wo Blau und Gelb sich treffen, gelbe und blaue Schüppchen durcheinander, sodaß sich der Blau-Gelb-Effekt durch die Streuung auflöst. Bezeichnenderweise finden wir in dieser Streuung auch schwarze Schüppchen eingestreut, die einige blaue und gelbe Schüppchen voneinander trennen. In den einheitlichen gelben als auch blauen Flächen finden wir diese schwarzen Schüppchen ebenfalls bezeichnenderweise nicht.

Die auffälligste Scheinausnahme bei den Vögeln ist wohl *Ara ararauna*. Neben dem durchaus kräftigen Gelb seiner Brust steht ein leuchtendes Blau, aber nicht das stärkste, denn dafür ist es zu hell. Zwischen beiden Farben zeigt sich ein ganz klein wenig Grün. Der Vogel zeigt das stärkste Blau auch, aber bezeichnenderweise nicht neben dem Gelb seiner Brust, sondern erst an seinen langen Schwanz- und Flügelfedern. Bei dem *Ara macao* (Nr. 22) sieht es so aus, als ob Gelb und Blau durchaus nicht ruhig in einheitlichen Flächen zusammentreten könnten. Auch zeigt sich ein wenig vermittelndes Grün. Ein sog. Doktorfisch, einer der Acanthuridae, ist wohl die auffälligste Scheinausnahme bei den Fischen. Sein Rumpf ist leuchtend blau, die Rückenflosse in einem noch stärkeren Gelb. Beide Farben sind durch eine feine rote Linie voneinander getrennt. Die große Fläche kalten Blaus steht in ausgesprochener Majorität zu dem warmen Rot der Linie (die Kondition Nr. 15 auf unserer Farbtafel). Eine solche, allerdings noch feinere Linie zeigt sich zwischen Blauviolett und Gelb bei dem Vogel *Poephila gouldiae*. Der Fisch *Pomacentrus coeruleus* ist bei genauerer Betrachtung auch eine Scheinausnahme: Die Leuchtkraft des Gelbs reduziert sich, wo es gegen das Blau tritt, das Blau ist in seiner Leuchtkraft durch Schwarzzutaten reduziert, ähnlich Nr. 19.

Da wir Blau-Gelb Pseudo-Ausnahmen haben, ist es nicht unmöglich, daß sich noch eventuell wahrhafte Ausnahmen finden lassen könnten: z.B. der Käfer *Stigmodera alternata* Luhmholz (Buprestidae), zumindest einer Abbildung nach. Bei dem Exemplar welches ich sah, war das Gelb soviel schwächer als auf der Abbildung, daß dieses Exemplar vermutlich zu alt war. Ausnahmen sind bezüglich der anderen Kalt-Warm Farbenpaare nicht zu vermuten, weil wir sie nicht in so ausgesprochenen Scheinausnahmen finden. Die Beschreibung der weiteren Blau-Gelb Pseudo-Exzeptionen würde hier zu weit führen. Einen durch einen Übergang abgeschwächten Kalt-Warm-Kontrast bezüglich Violett und Orange haben wir auf dem bereits genannten Fisch Nr. 23. Er ist keine Scheinausnahme, weil dieser Übergang schon auf den ersten Blick ersichtlich ist.

Gerade durch diese beschriebenen Konditionen: durch die kalte und warme Farben — gleich ersichtlich — oder in Scheinausnahmen — schwerer ersichtlich — nicht in voller Kraft zusammentreten, tritt die Gesetzlichkeit deutlich hervor. Eine feine schwarze Linie — oder auch eine in einer dritten Farbe — trennen die beiden Farben; oder sie verlieren an Intensität wo sie zusammentreten, zumindest eine der Farben; und andere



Konditionen; derweil die warmen Farben untereinander — respektive die kalten untereinander — konditionslos unmittelbar nebeneinander treten können. Absolutes Rot und absolutes Grün treten auch unvermittelt nebeneinander.

Die Pseudo-Exzeptionen Blau-Gelb sind daher für uns so interessant, weil es bei ihnen so aussieht, als ob die Natur bis an die Grenze der Gesetzmäßigkeit herangeht, sie aber nicht überschreitet. Bezeichnend ist auch, daß die sog. Komplementärfarben: neutrales Grün und absolutes Rot, nicht unter die Gesetzmäßigkeit Kalt-Warm fallen.

Die Gesetzmäßigkeit geht keineswegs so weit, daß die warmen Farben immer nebeneinander treten müßten. Das gleiche gilt auch für die kalten Farben. Wir sehen auch sie voneinander getrennt.

Die Untersuchung der Biochromatik auf diese Gesetzmäßigkeit hin ist weitaus die zeitraubendste. Man muß alles in natura sehen, denn es kommt teils auf Farbnuancen an. Wer untersuchen will, fängt am besten mit den starken Kalt-Warm-Gegensätzen Violett zu X (Nr. 20) und Orange zu Y (Nr. 21) an. (Die starken Farben der Biochromatik sind — wie schon gesagt — teils sehr viel leuchtkräftiger als die, die man drucken kann.) Was die ersten drei Gesetzmäßigkeiten betrifft, kann man sich *teilweise* auch auf farbige Abbildungen verlassen.

Was die empirische Untersuchung der Biochromatik betrifft, wäre es sehr interessant, ob sich noch Ausnahmen zu dem finden lassen, was ohne diese Ausnahmen noch als gesetzlich angesehen werden kann.

Für die nun folgende zweite chromatologische Untersuchung ganz anderen Charakters, wäre dieses aus dem folgenden Grunde bedeutungslos: Bei dieser Untersuchung gehen wir nämlich von den jedenfalls grundlegenden Charakteristika der Biochromatik aus. (Auf unserer Farbtafel mit einem + Zeichen.) Einige Ausnahmen zu ihnen würden ihre quantitative Vorherrschaft nur bestätigen — wie Ausnahmen die Regel.

#### DAS PRINZIP DER OPTIMALEN FARBMANIFESTATION

Für die Interpretation der biochromatischen Gesetzmäßigkeiten (oder eventuell Regeln) verlassen wir das Gebiet der reinen Observation und gehen über zum Verstandesmäßigen.

Für ein eingehenderes Verständnis der Eigentümlichkeiten der Biochromatik führen wir zuerst den Begriff "optimale Farbmanifestation" ein: Farbe ist Licht. Die stärksten Farben haben das meiste Farblicht. Licht manifestiert sich optimal zusammen mit seinem Gegenteil: Dunkel. (Das Licht einer farbigen Lampe manifestiert sich optimal in der Nacht; im weißen Sonnenlicht ist ihre Wirkung weitaus schwächer.)

Wir sehen, daß die Natur nach diesem Prinzip "vorgeht". Die starken Farben stehen auf Schwarz (Nr. 56) oder fast Schwarzem (Nr. 55), und nicht auf Weiß, und haben hierdurch eine optimale Wirkung.<sup>1)</sup> Weiß ist ja weit heller als alle starken Farben, sodaß diese Farben auf Weiß Dunkel-Erscheinungen sind, anstatt Licht-Erscheinungen, (Nr. 41 und 42). Vor allem gilt dieses für die dunkelsten der starken Leuchtfarben: Grünblau, Blau, Violettblau und Blauviolett. Diese Farben auf Weiß fehlen ganz und gar in der Biochromatik (Nr. 41, 42, 43). Es wäre eine völlige Fehlmanifestation ihrer Leuchtkraft. Auf Schwarz oder fast Schwarzem ist ihre Manifestation optimal (Nr. 55, 56).

<sup>1)</sup> Zur Vermeidung von Mißverständnissen: Der Begriff "optimale Manifestation" hat keine biologische Bedeutung; sie ist "funktionslos".

Diese chromatische Optimalität kann nicht aus funktionellen Gründen erklärt werden. Das, was ihr entgegengesetzt ist, könnte ja ebensogut Locken (Nr. 27), Schrecken (Nr. 51) oder tarnen (Nr. 67).

Neben Weiß können Leuchtfarben schon auftreten; auch die genannten dunklen (z.B. Nr. 43 A, Violett neben Weiß bei einem afrikanischen Schmetterling), wobei sie aber nur auf einer Seite Dunkelercheinungen sind. Mitten auf Weiß finden wir die dunklen Leuchtfarben nie, geschweige denn zwei oder drei von ihnen (Nr. 43 B).<sup>1)</sup>

Hellere Farben, wie etwa Orangerot, finden wir schon eher mitten auf Weiß, aber auch nicht in großen Farbflecken, vergleichbar mit der japanischen Fahne (Nr. 68 A). (Nebenbei gesagt: Die Fahne ist ein visuell effektives Erkennungszeichen, die Kombination widerspricht aber dem chromatischen Optimalitätsprinzip der Biochromatik. Wie dieses Beispiel zeigt, können wir die rein chromatische Optimalität nicht ohne weiteres visuell erkennen, wohl aber verstandesmäßig aufspüren.)

Das starke Rot einzelner roter Flecken die wir auf Weiß finden, ist — und das ist bezeichnend — durch Schwarz konditioniert; sei es, daß Schwarz die Leuchtfarbe umringt (Nr. 48); z.B. bei dem Falter *Parnassius apollo*, oder, daß Schwarz neben das Rot tritt und hierdurch auf einer Seite seine Leuchtkraft hebt, z.B. bei dem Fisch *Coris angulata* (No. 47). (Handelt es sich um viele, kontinuierliche Flecken (Nr. 64), so kommt ein andersartiger Faktor in Frage; wir werden auf ihn zurückkommen.)

Der chromatische Gegensatz zu diesen Erscheinungen, d.h. von Weiß umringte Leuchtfarben auf einem dunklen Hintergrunde, ist noch nie gefunden worden (Nr. 49). Es gibt Fälle, bei denen Schwarz von einer Leuchtfarbe auf nicht ganz dunklen Hintergründen umringt ist (Nr. 50): bei Fischen, sehr häufig bezüglich ihrer Augen. (Die Abbildung bei Nr. 50 ist einigermaßen irreführend: solche Flecken gibt es nie auf Schmetterlingsflügeln, wie die Zeichnung suggeriert.) Weiße Flecken umringt von einer starken Farbe, gibt es nicht (Nr. 51). Starkfarbige Falterflügel zeigen manchmal schwarze Oberecken oder Ränder, nie weiße. Die letzteren können wir finden bei schwachfarbigen Flügeln.

Die Leuchtkraft einer starken Farbe ist auch recht wirkungsvoll in der Gestalt eines kleinen Punktes auf einem ganz dunklen Hintergrunde. Noch besser für die Farbmanifestation sind zahlreiche (einfarbige) Fleckchen auf Schwarz, wie es sie bei manchen Lepidopteren gibt (Nr. 59, 60). So etwas ist auf Weiß nicht zu finden (Nr. 61). Auch verschiedenfarbige Pünktchen oder Fleckchen auf Schwarz gibt es nicht — in einem solchen Falle würde sich keine der Farben optimal manifestieren (Nr. 62). Es braucht uns nicht zu verwundern, daß von Fleckchen unterschiedlicher Farben auf Weiß gar keine Rede ist (Nr. 63).

Wenn sich die helleren Leuchtfarben manchmal auf Weiß finden lassen — wenn auch zumeist von Schwarz begleitet — die Leuchtfarben wie Blau, Blauviolett, ließen sich nicht mitten auf Weiß finden, selbst nicht unter dieser Kondition.

Zusammenfassend: Von der Tatsache her, daß Schwarz die Leuchtkraft der Farben optimal hebt, lassen sich die folgenden Kombinationen erklären: Nr. 31, 32, 33, 34, 36, 37, 40, 47, 48, 50, 53, 56, 57, 59. Gleichzeitig erklärt sich, daß wir dergleichen wie Nr. 41, 42, 43, 46, 49, 51, 52, 58, 61 nicht haben; denn, wie gesagt, beeinträchtigt Weiß die Leuchtkraft der starken Farben.

<sup>1)</sup> Eine der gezüchteten *Violaceae* ist, die bereits angeführte Scheinausnahme (Nr. 44). Auf den einzelnen Blättern steht Violett nicht mitten auf Weiß (Nr. 45). (Sähe die Blume aus wie Nr. 46, wäre sie tatsächlich eine Ausnahme.)

Jetzt zu dem Thema der zeichnerischen Musterungen in Halbfarben, oder Schwarz und Weiß. In diesen Musterungen kommt ein zweites Optimalitätsprinzip zum Ausdruck: die des Hell-Dunkel-Gegensatzes. Ein kleines Experiment kann das deutlich machen: Decken Sie bitte Nr. 27 und Nr. 28 mit der Hand zu. Schwerlich, daß Sie sich die Anzahl der Farben und welche es sind, ins Gedächtnis zurückerufen können. Kein Wunder, denn es handelt sich bei ihnen um eine konglomerat-artige und in diesem Sinne amorphe Fehlmanifestation aller dieser starken Farben. Dieses ganz im Gegensatz zu Nr. 24 (*Brahmaea wallichii*) und Nr. 25 (*Squatarola squatarola*), die ein optimales zeichnerisches Hell-Dunkel-Spiel in Halbfarben darstellen. So kompliziert dergleichen Musterungen auch sein können (von denen wir unzählige in der Biochromatik haben), sie können nie konglomerat-artig sein, weil der Hell-Dunkel-Gegensatz nur einer ist, während es zwischen den vielen starken Farben eine Menge Gegensätze gibt. Die Essenz dieser Musterungen bleibt auch in der Photographie erhalten (Nr. 30). Nr. 27 und 28 aber setzen sich aus so zahlreichen Gegensätzen starker Farben zusammen, daß sich hierdurch ein Konglomerat ergibt, in dem sich keine der Farben optimal manifestieren kann.

Wir können auch von der optimalen Manifestation eines ausgesprochen unscheinbaren Motives in einer Halbfarbe sprechen (Nr. 65) wenn sich dieses ständig wiederholt (Nr. 66) eine Optimalität der Manifestation durch Multiplikation. Dementsprechend haben wir in der gesamten Biochromatik eine außerordentlich große Anzahl ganz unterschiedlicher Musterungen, die sich durch die Wiederholung ein und desselben unscheinbaren Motives ergeben. Dieser Optimalität entgegengesetzt wäre eine Musterung aus ganz unterschiedlichen unscheinbaren Motiven (Nr. 67). Diese haben wir nicht. Die Optimalität der Wiederholung haben wir bei Nr. 59, 60 und 64; ihr widerspricht Nr. 62 und 63. (Zu Nr. 64: durch diese Optimalität ist es vielleicht erklärlich, daß wir in diesem Falle zahlreiche rote Flecken auf Weiß haben — nicht aber einen roten Fleck mitten auf Weiß.) Die Wiederholung desselben Motives ist eines der Grundprinzipien der menschlichen Ornamentik. Als Schutzfärbung wäre Nr. 67 gewiß ebenso dienlich wie Nr. 66 oder Nr. 24.

Wir wollen uns in diesem Artikel mit den obigen Beispielen begnügen. Eine ausführliche Darlegung dieses Themas wurde bereits veröffentlicht in der *Acta Biotheoretica* (Peterich, 1972)\*). Der Versuch, für die biochromatischen Eigenartigkeiten eine Erklärung zu finden, ist meiner Meinung nach an sich wichtiger als die ihm vorangehende rein empirische Forschung. Wie gesagt erscheint es uns unwahrscheinlich, daß die biochromatischen Gesetze endgültig auf chemische oder biologisch-funktionelle Gründe zurückzuführen sind. In welcher Richtung müssen wir dann die Erklärung suchen?

In der organischen Natur sehen wir eine Dualität: Einerseits haben wir den Aspekt des Nutzens, der Zweckmäßigkeit, welche in hohem Grade das Aussehen der Organismen bestimmt, und andererseits "das unerklärliche Reich des Schönen", wie Prof. Adolf Portmann es einmal ausgedrückt hat, während eines Vortrages in Basel.

Weil Ordnung, Geordnetheit ein allgemeines Charakteristikum der organischen Welt ist, war es anzunehmen, daß die Biochromatik nicht amorph, sondern nach Gesetzen gestaltet ist. Auch war es denkbar, daß diese Gesetzmäßigkeiten empirisch gefunden werden konnten. Es hat sich nun herausgestellt, daß der Charakter dieser Gesetzmäßigkeiten sich unserem Verstande als weitgehend zugänglich erwies, — und wohl auf Grund ihrer

\*) Für die die vorliegende Farbtafel angefertigt wurde.

optimalen Auswirkung. Dieses war nicht zu erwarten, weil sie zu dem sogenannten "unerklärlichen Reich des Schönen" gehören, in welches wir nun durch sie einen Einblick nehmen können.

Durch die Gesetzlichkeiten, die sich als rein chromatische erwiesen haben, erhebt sich die Frage: welcher Herkunft sie sein könnten; darüber gibt uns weder ihre optimale Auswirkung noch ihre wahrscheinlich prä-okulare Herkunft, eine Auskunft.

Wir haben Beispiele dafür, daß die aus dem vitalen Gebiete stammenden Bedürfnisse: nämlich die Zweckmäßigkeit der Nachahmung amorphes Chromatik (z.B. *Kallima paralekta*) die ansorten vorhandene ornamental auf uns wirkende gesetzliche Ordnung, der Biochromatik überwunden hat. Auch auf dem morphologischen Gebiete besteht diese "Ornamentalität". Sie wirkt sich am deutlichsten aus bei den "niederen" Lebensformen, etwa bei den Foraminiferen und Radiolarien, auch noch z.B. bei Coelenteraten, Echinodermen oder Arthropoden. Vergessen wir auch die Pflanzen nicht. Bei der Weiterentwicklung der Anatomie der "höheren" Tiere scheint diese Ornamentalität abzunehmen, insbesondere bei den Säugetieren. Die Zweckmäßigkeit wirkt anscheinend der Ornamentalität entgegen. Vielleicht können wir von einem Gegensatz von Vitalem zu rein Ornamentalem sprechen, und in diesem Sinne ist es denkbar, daß die chromatische, wie auch die formale (morphologische) Ornamentalität des organischen Lebens nicht vitaler, sondern non-vitaler Herkunft ist — einfach auf der Tatsache beruht, daß die ganze Natur (die anorganische, als auch die organische) nicht amorph, nicht chaotisch ist. In den Eisblumen im Winter haben wir ein Beispiel von diesem fundamentalen Ordnungsgesetz der Natur — sie sind bis ins Feinste strukturiert, nicht-amorph; und bei ihnen ist es ja sicher, daß hier keine Zweckmäßigkeitsfaktoren vorliegen.

Wir wissen nicht ob es möglich ist, oder je sein sollte, unsere Frage zu beantworten. Viel hängt davon ab, ob es überhaupt gelingen wird dieses Gebiet in die experimentell-manipulative Forschung einzubeziehen.

#### ZUSAMMENFASSUNG

In diesem Artikel konnte nur ein Teil des vorhandenen Faktenmaterials angeführt werden. Vor allem das, was Blumen und Tiere in natura oder zumindest in Lichtbildern besser und deutlicher illustrieren als in Reproduktionen. Durch dieses Manko konnten auch die Gesetzlichkeiten nur auf eine sehr allgemeine Weise zur Kenntnis gebracht werden. Wir strebten danach, das Essentiellste herauszuheben. Es wurde darauf hingewiesen, was zu kontroversalen Diskussionen führen könnte, z.B. was Züchtungen betrifft.

Für die Beschreibung der Gesetzlichkeiten haben wir zum Teil Gebrauch gemacht von der mit dem Farbkreis verbundenen Terminologie. Die gefundenen Gesetzlichkeiten sind mittels Induktion aufgestellt, als empirische Generalisationen. Dem bisherigen Stand der Chromatologie nach sind die wesentlichsten:

1. Zeichnerische Musterungen bestehen nie aus vielen starken Farben und insofern fast immer aus Halbfarben; weil die aus einer starken Farbe zusammen mit der Nichtfarbe Schwarz oder Weiß weitaus seltener sind. Noch seltener sind die, die sich aus zwei starken Farben und einer der Nichtfarben (meistens Schwarz) zusammensetzen.
2. Die enge Beziehung zwischen Schwarz und fast Schwarzem zu starken Farben.
3. Die Gesetzlichkeit im Bezug einer ausgesprochenen Kontinuität, vornehmlich bei Musterungen.

4. Flächen in starken warmen Farben treten nicht unmittelbar neben Flächen starker kalter Farben. (Auch hier eine Kontinuität: Warm zu Warm, respektive Kalt zu Kalt.) Das neutrale Grün tritt zu allen Farben.

Es ist darauf hingewiesen worden, daß es prinzipiell bei der chromatologischen Untersuchung keine Rolle spielt, wie Tiere Farben sehen; im Allgemeinen: wie die subjektiven Farbeindrücke sind. Auch wurde erwähnt, daß die unterschiedlichen Farbsehbegrenzungen keine biochromatischen Begrenzungen mit sich bringen. Es wurde vermutet, daß die biochromatischen Gesetzmäßigkeiten ihres non-visuellen Charakters wegen, älter sein dürften als das Farbsehvermögen. Auch wurde gesagt, daß die Farbkombinationen, die auf Grund der chromatischen Gesetzmäßigkeiten in der Biochromatik fehlen, gleichermaßen als Lock-, Schreck- und Schutzfarben dienlich sein könnten, wie die in der Biochromatik vorhandenen. Vermutet wurde, daß in einem späteren Stadium der Chromatologie der Gebrauch von Instrumenten (Spektrometer etc.) anzuempfehlen ist. Das Thema einer optimalen biochromatischen Farbmanifestation wurde mit einigen Beispielen angeschnitten. Die Frage wurde gestellt: welcher Herkunft die biochromatischen Gesetzmäßigkeiten sein könnten. Eine Erklärung ihrer Existenz auf chemischem Niveau oder biologisch vitalem, ließ sich bisher nicht finden. Auf gewisse wissenschaftlich-theoretische Fragen z.B.: was eine Gesetzmäßigkeit in der Wissenschaft genau ist, ist der Autor nicht eingegangen, weil er sich auf diesem Gebiete der Logik der Wissenschaft nicht auskennt. Die Frage: Biochromatische Regeln oder Gesetzmäßigkeiten, wurde erörtert. Der Autor hofft, daß diese Frage ein Interesse an der Suche nach eventuellen Ausnahmen zu den Gesetzmäßigkeiten mit sich bringt, obwohl diese nur für die erste empirische chromatologische Untersuchung wichtig sind. Nicht so für die zweite, die von dem in unzähligen Fällen in der Biochromatik Vorhandenen ausgeht.

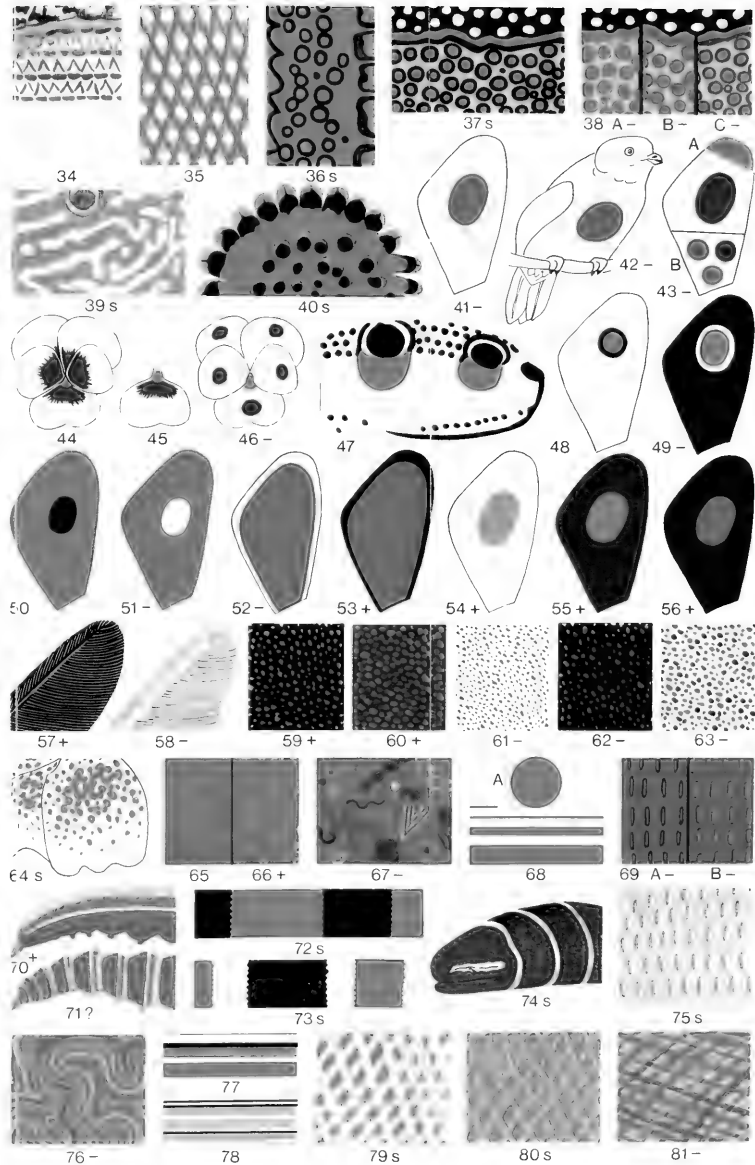
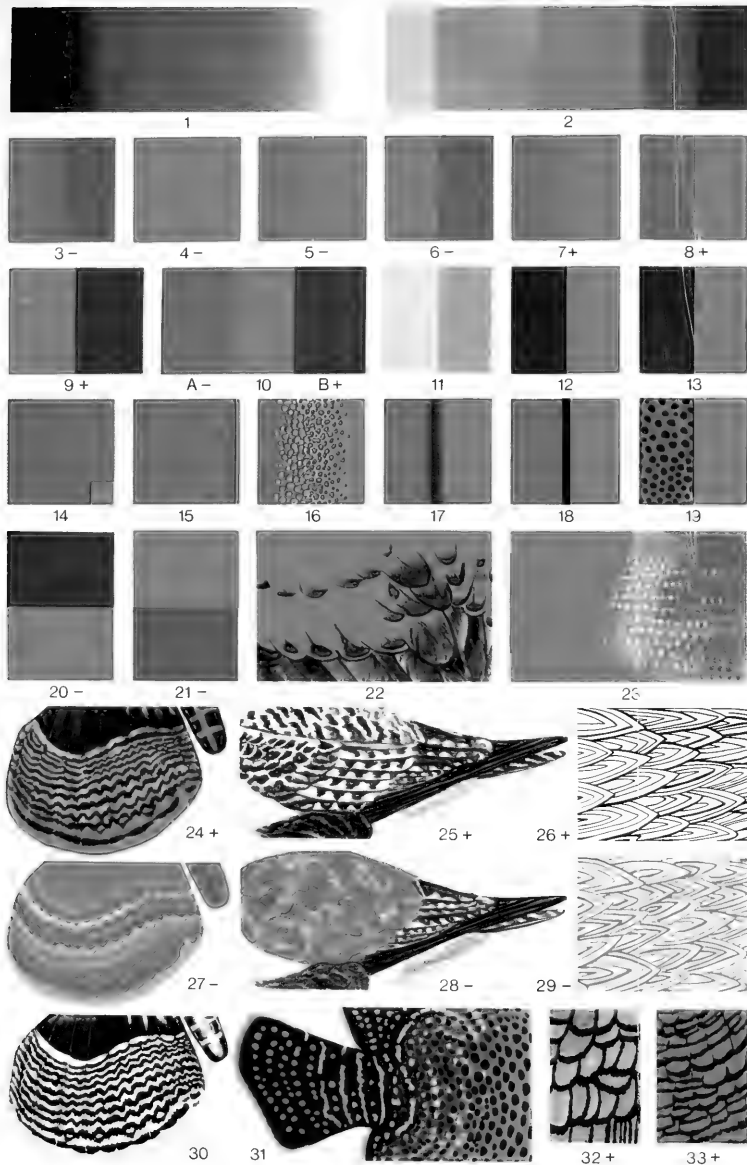
#### MEIN DANK

Für seine Hilfe möchte ich hier meinen Dank sagen an: Dr. A. Diakonoff, vom Rijksmuseum van Natuurlijke Historie zu Leiden, der mir sehr viele Jahre mit Rat und Tat geholfen hat. Viel zu danken habe ich auch Mr. W. H. T. Tams und Mr. T. G. Howarth, vom British Museum of Natural History in London. Zugleich auch meinen Dank allen Biologen, die mir in den beiden genannten und anderen Museen bei der Suche nach Ausnahmen und Scheinausnahmen auf die Gesetzmäßigkeiten der Biochromatik hin geholfen haben. Hier auch meinen Dank an Herrn Prof. Dr. M. Jeuken und Drs. W. van Laar, vom Instituut voor Theoretische Biologie der Universität zu Leiden. Van Laar war der Erste, der sich ausgiebig mit allen Facetten der Chromatologie befaßt hatte. Nicht zuletzt hier meinen Dank der Hamburger Grafikerin Christel Achner, die mir jahrelang, vor allem durch ihren scharfen Blick und stets sehr kritische Einstellung, eine sehr wertvolle Mitarbeiterin war und überdies die Farbtafeln für diesen Artikel angefertigt hat.

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A PROPOS D'HYBRIDISME NATUREL CHEZ LES

ORNITHOPTÈRES (LEPIDOPTERA: PAPILIONIDAE)

par

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## RÉSUMÉ

L'auteur étudie ici les caractères d'*Ornithoptera priamus miokensis* Ribbe et démontre qu'il est un hybride naturel entre *bornemanni* Pagenstecher et *urvilleana* Guérin. Mais il réitère son opinion qu'*alottei* Rothschild est très probablement une bonne espèce et non un hybride comme il a été affirmé.

## SUMMARY

The author develops here the thesis that *Ornithoptera priamus miokensis* Ribbe is a natural hybrid between *bornemanni* Pagenstecher and *urvilleana* Guérin and offers evidence that *alottei* Rothschild is very likely a good species and not a hybrid, as it is sometimes believed.

## INTRODUCTION

Le dossier de l'hybridisme chez les Ornithoptères est fort mince. On n'a jamais réussi à les croiser artificiellement et l'hybridisme naturel se borne à quelques affirmations qu'*alottei* Rothschild est un hybride et non une bonne espèce.

Or, dans les pages qui suivent, j'étudie les caractères de *priamus miokensis* Ribbe de l'Archipel du Duc d'York et montre que cette sous-espèce est un hybride naturel entre ses deux voisins géographiques, *priamus bornemanni* Pagenstecher de Nouvelle-Bretagne et *priamus urvilleana* Guérin de la Nouvelle-Irlande et de l'Archipel des Salomons. D'autre part, sur la base d'arguments solides, je propose de maintenir à *alottei* son statut d'espèce valide, car il est douteux qu'il soit un hybride entre *victoriae regis* Rothschild et *priamus urvilleana*, même si ces deux espèces sont sympatriques avec lui à Bougainville.

### *Ornithoptera priamus miokensis* Ribbe

Cette sous-espèce a été nommée plutôt que décrite par Ribbe en 1898 et, depuis, n'a guère été l'objet que de commentaires rares et isolés. Elle vole dans l'Archipel du Duc d'York, composé des îles de Mioko, Ulu, du Duc d'York proprement dite et de quelques îlots. Cet archipel est situé dans le Déroit de St-Georges séparant la Nouvelle-Bretagne de la Nouvelle-Irlande. Une assez forte minorité des spécimens sont bleus, une fraction sont verts, alors que la majorité sont bleu-vert, en proportions variables. M. R.A. Carver m'informe (in litt.) qu'à l'éclosion, le plus grand nombre des spécimens sont entièrement verts et que beaucoup d'entre eux virent plus ou moins au bleu dans les heures qui suivent. Ce fait est intéressant, mais non inédit chez les Ornithoptères. Rothschild l'a déjà signalé chez *O. lydius*.

Il y a quelques mois, j'ai obtenu de MM. H. Borch et R. A. Carver, résidant à Rabaul, 56 couples de *miokensis* provenant des trois îles sus-mentionnées. J'en détaille ci-après les caractères et les compare avec ceux de 36 couples de *bornemanni* de Nouvelle-Bretagne et de 12 couples d'*urvilleana* de Bougainville, sans prendre immédiatement en considération 12 couples capturés en Nouvelle-Irlande, nous verrons plus loin pourquoi. Tous les spécimens sont déposés dans mes collections, sauf un couple de *miokensis* qui est au Rijksmuseum van Natuurlijke Historie, à Leyde, Pays-Bas. Pour alléger le texte, je cite les caractères, disant chez *miokensis* . . ., chez *bornemanni* . . ., alors que ces considérations sont basées uniquement sur le matériel cité plus haut, qui est trop restreint pour que les résultats aient une entière valeur statistique.

#### Taille

1. L'envergure varie entre 135 et 150 mm. chez *urvilleana*. Chez *bornemanni*, elle oscille entre 115 et 130 mm. Chez *miokensis*, la taille est nettement plus variable et l'envergure est comprise entre 110 et 140 mm.

#### Forme des ailes

2. L'aile postérieure est assez régulièrement arrondie chez *urvilleana*, sans angle apical antérieur bien marqué et avec le bord apical nettement crénelé. Chez *bornemanni*, l'aile postérieure est nettement triangulaire, avec l'angle apical antérieur saillant et les bords costal et apical plutôt rectilignes; le second est pas ou à peine sinueux et se trouve dans le prolongement de celui des ailes antérieures. Chez *miokensis*, la plupart des spécimens ont l'aile postérieure triangulaire, avec le bord apical non sinueux; 7 d'entre eux ont l'aile assez arrondie, avec le bord apical crénelé.

#### Coloration du dessus des ailes

3. Les aires métalliques des deux ailes sont bleu franc chez *urvilleana*, mat et non satiné; occasionnellement une légère nuance violette ou verdâtre est visible chez certains spécimens. Chez *bornemanni*, la couleur est verte, vive et brillante, surtout aux ailes antérieures; certains spécimens ont toute la surface des ailes postérieures vert assez foncé, avec une nuance légèrement bleuâtre.

Il n'est pas facile de décrire la couleur du dessus des ailes de *miokensis*, d'abord à cause du nombre et de l'importance des variations et ensuite parce que la délicatesse et la subtilité des nuances sont telles qu'il est difficile de les traduire en mots. Je distinguerai ici deux qualités chromatiques, la couleur (bleue ou verte) et le ton (mat ou brillant). Les spécimens sont décrits tels qu'ils apparaissent en éclairage perpendiculaire, la lumière venant de derrière l'observateur.

Des 56 exemplaires que j'ai examinés, un seul montre le vert brillant de *bornemanni* et 4 autres ont leurs aires colorées brillantes, quoique leur éclat soit nettement inférieur à celui de *bornemanni*; ces 4 spécimens sont bleu clair, d'une nuance turquoise, légèrement teintée de verdâtre; nous les retrouverons plus bas. Tous les autres insectes, qu'ils soient plus ou moins bleus ou verts, ont un ton mat et terne qui rappelle celui de l'ardoise.

En ce qui concerne la couleur, sur 55 spécimens, 22 sont entièrement bleus, sans trace de vert. La couleur est terne et un spécimen montre une légère nuance mauve.

Six spécimens sont nettement mais très partiellement bicolores: la partie apicale des

bandes radiale et anale des ailes antérieures est verte sur une longueur variable; la couleur est la plus verte à l'apex de l'aile et vire progressivement au bleu lorsqu'on s'avance vers la base; l'angle externe de la bande anale est bleu.

Quinze spécimens présentent les mêmes caractères, mais en plus accusé; le vert est nettement plus étendu du côté du corps et teinte légèrement l'aile postérieure qui est bleu-vert; ici aussi, c'est à l'apex de l'aile antérieure que le vert est le plus franc et l'angle externe reste bleu.

Cinq spécimens sont uniformément vert-bleu et avec la même variation d'intensité: le vert est le plus pur à l'apex de l'aile antérieure et l'angle externe est bleu.

Six spécimens enfin sont entièrement et franchement verts, sauf à l'angle externe où la bande anale est encore bleutée, mais comme il a été dit plus haut, si le vert a l'intensité de celui de *bornemanni*, le ton est le mat ardoise d'*urvilleana*.

Un seul spécimen, un des bleus aux couleurs brillantes cités plus haut, a une coloration différente; les deux bandes des ailes antérieures sont bleu clair et les ailes postérieures sont légèrement et uniformément nuancées de vert.

Ce gradian si constant dans la variation de l'intensité du vert suggère que cette couleur dépend d'un organisateur exerçant son action à partir de l'extrémité de l'aile antérieure.

#### Coloration du dessous des ailes

4. Les taches des ailes antérieures sont bleues chez *urvilleana*, sauf celles de l'apex de l'aile qui sont lavées de vert. Chez *bornemanni*, toutes les taches sont uniformément vert franc, mais occasionnellement la base de celles des cellules discale et Cu2-2A (sensu Miller) vire au vert-bleu. Chez *miokensis*, 1 exemplaire a toutes les taches uniformément bleues; chez 34, celles de l'apex de l'aile sont teintées de vert dans la même proportion que chez *urvilleana*; chez 21 elles sont presque entièrement vertes, mais celles de la base des cellules discale et Cu2-2A sont constamment bleutées.

5. La partie discale des ailes postérieures est bleue chez *urvilleana* et tout le pourtour antérieur et externe est teinté de vert-bleu délavé. Chez *bornemanni*, la surface est entièrement et uniformément vert franc, mais la base de la cellule Cu2-2A vire occasionnellement au vert-bleu ou au bleu. Chez *miokensis*, 16 exemplaires montrent les mêmes proportions du bleu et du vert que chez *urvilleana*; chez 25, le vert est plus franc et nettement plus étendu que chez ce dernier; chez 14, le vert prédomine et le bleu est considérablement réduit et localisé sur une zone d'étendue variable dans la partie postérieure de la cellule discale et à la base de la cellule Cu2-2A; chez 1 spécimen seulement le bleu est entièrement absent.

#### Dessins du dessus des ailes

6. La bande anale est interrompue au milieu de la cellule du même nom chez *urvilleana* et cet intervalle n'est que très rarement sablé de bleu. Chez *bornemanni*, cet intervalle est présent chez la moitié des spécimens et il est y toujours sablé de vert. *Miokensis* montre les mêmes variations, en mêmes proportions que chez *bornemanni*.

7. La bande médiane des ailes antérieures est absente chez *urvilleana*, mais de très rares spécimens possèdent une très fine ligne d'écaillés bleues, à peine visibles, sur la limite postérieure de la cellule discale. Chez *bornemanni*, la moitié des insectes possèdent une fine bande médiane bien visible et envoyant d'assez longs prolongements sur la base des M et Cu. Chez *miokensis*, la bande médiane est toujours totalement

absente et je ne l'ai observé que deux spécimens chez qui quelques écailles colorées sont visibles.

8. Les taches discales noires des ailes postérieures sont constamment au nombre de 5 chez *urvilleana*; la première étant ouverte contre le bord de l'aile, je n'en tiens pas compte ici; les 4 autres ont le plus souvent un diamètre nettement supérieur à l'intervalle qui les sépare. Chez *bornemanni*, les taches discales sont beaucoup plus petites et séparées par des intervalles supérieurs à leur diamètre; elles sont le plus souvent au nombre de 3, mais certains spécimens en ont 4, 2 ou 1. Chez *miokensis*, 20 spécimens ont quatre taches discales grandes et bien nettes; 28 exemplaires ont 3 taches assez petites et 7 autres insectes ont une petite tache nette, accompagnée de 2 autres réduites à l'état de nuages plus ou moins marqués.

9. La couleur bleue des ailes postérieures s'avance jusqu'au bord de l'aile chez le tiers des *urvilleana* que j'ai vus, ne laissant qu'un très mince liseret marginal noir; chez les autres spécimens, le bord noir est assez large et contient fréquemment une enclave bleue irrégulière au niveau des cellules M1-M2 et M2-M3. Chez *bornemanni*, le bord noir est toujours assez large, avec occasionnellement une enclave verte. Chez *miokensis*, je n'ai vu qu'un seul spécimen chez qui la couleur s'avance jusqu'au bord de l'aile, quoique l'extrémité des nervures soit souligné de noir; tous les autres ont un liseret marginal noir plus ou moins large; parmi eux, 36 ont l'enclave métallique irrégulière décrite plus haut.

10. La tache sous-costale jaune est présente chez  $\frac{3}{4}$  des *urvilleana*; elle est parfois moyenne ou petite et souvent minuscule. Chez *bornemanni*, elle n'est présente que chez un spécimen sur six et elle est toujours très. Chez *miokensis*, elle n'est absente que chez 9 spécimens; chez 4 autres, elle est également absente mais la membrane est fortement teintée de vert cet endroit; chez 12 spécimens, la tache est présente mais réduite à un point minuscule; chez 13 autres, elle peut être qualifiée de petite tache; chez 17 autres, elle a 6-8 mm de long et 3-4 mm de large; chez 1 spécimen, elle a 11-4.5 mm et rempli presque toute la cellule sous-costale; je n'en ai vu d'aussi grande que chez quelques *hecuba* et *euphorion*.

11. La cellule sous-costale n'est jamais entièrement noire chez *urvilleana*. Chez chacun des *bornemanni* et *miokensis* j'ai vu 1 spécimen ayant cette cellule uniformément noire, sauf un léger sablé métallique très localisé.

12. Les points submarginiaux jaunes sont à ma connaissance toujours absents chez *urvilleana*. Chez *bornemanni*, j'ai vu 2 spécimens qui montrent chacun un point jaune. Chez *miokensis*, ces points sont toujours absents.

#### Dessins du dessous des ailes

13. La tache métallique de la cellule discale des ailes antérieures est courte et située à l'apex de cette dernière chez les  $\frac{2}{3}$  des *urvilleana*; chez l'autre tiers, elle est plus longue. Chez *bornemanni*, la plupart des exemplaires ont la tache cellulaire très longue. Chez *miokensis*, 10 spécimens ont la tache cellulaire très petite et en position apicale, alors que chez 46 autres, elle s'étend sur toute la longueur de la cellule.

14. Les taches discales noires des ailes postérieures sont très grandes chez *urvilleana* et au nombre de sept; la dernière, située au tornus, est constamment présente et souvent énorme. Chez *bornemanni*, les taches discales sont nettement plus petites et le plus souvent au nombre de 6, celle du tornus n'étant présente que chez le

tiers des spécimens et étant toujours très petite. Chez *miokensis*, 5 exemplaires seulement ont des taches discales aussi grandes que celles d'*urvilleana*, y compris celle du tornus; chez les 51 autres, elles sont plus petites et celle du tornus ne manque que chez 5 d'entre eux; chez les 46 spécimens, cette tache est de taille très variable et pas toujours proportionnelle à celle des taches discales, car elle est parfois très grande quand ces dernières sont moyennes ou petites.

15. Le tornus est faiblement teinté de jaune gris chez *urvilleana*. Chez *bornemanni*, il est largement envahi de jaune-orange. Chez *miokensis*, 19 spécimens ont le tornus jaune-gris comme chez *urvilleana* alors que les 37 autres l'ont orange.

16. La cellule discale est assez largement bordée de noir sur ses limites antérieure et apicale, chez *urvilleana* et les cellules R1-Rs, Rs-M1 et M1-M2 sont parfois ennuagées de noir. Chez *bornemanni*, la cellule est très finement bordée de noir sur sa limite antérieure et les cellules sus-nommées non poudrées de noir. Chez *miokensis*, 11 spécimens ont la cellule discale assez largement bordée de noir et parmi eux 3 seulement montrent certaines cellules sablées de noir; 44 exemplaires ont la cellule discale finement bordée de noir, comme *bornemanni* et 1 seul ne présente pas cette bordure.

17. Les taches submarginales jaunes sont présentes et en nombre variable chez la moitié des *urvilleana* et les  $\frac{2}{3}$  des *bornemanni*. Chez *miokensis*, j'ai compté 38 spécimens sur 56 ayant des taches marginales visibles si peu que ce soit.

#### Dominance des caractères

Examinons maintenant la dominance relative des caractères d'*urvilleana* et de *bornemanni* et en quelles proportions on les retrouve chez *miokensis*. Le nombre des spécimens examinés est certainement trop faible pour que les résultats aient une valeur statistique. J'utilise donc des épithètes au lieu de pourcentages.

Pour les caractères suivants, *urvilleana* domine:

3. Couleur de dessus des ailes: dominance de plus de moitié.
3. Ton de dessus des ailes: dominance presque complète.
4. Couleur des taches sous les ailes antérieures: dominance forte.
5. Couleur des taches sous les ailes postérieures: dominance forte.
7. Bande médiane des ailes antérieures: dominance complète.
10. Tache sous-costale jaune: dominance très forte.
14. Tache tornale sous les ailes postérieures: dominance forte.

Pour les autres caractères, c'est *bornemanni* qui domine:

2. Forme de l'aile antérieure: dominance presque complète.
6. Bande anale des ailes antérieures: dominance complète.
8. Taches discales sur les ailes postérieures: dominance de plus de la moitié.
9. Bord noir sur les ailes postérieures; dominance complète.
13. Tache sous la cellule discale des ailes antérieures: dominance forte.
14. Taches discales sous les ailes postérieures: dominance forte.
15. Couleur orange du tornus: dominance forte.
16. Bordure noire sous la cellule discale: dominance forte.
17. Taches marginales jaunes sous les ailes postérieures: dominance forte.

Sur 16 caractères considérés, *urvilleana* domine fortement pour 7 d'entre eux et *bornemanni* chez 9. Cette dominance n'est que partielle chez 14 caractères. Il n'y en a que deux où la dominance est tout à fait constante: la bande médiane des ailes antérieures

est absente comme chez *urvilleana* et la bande anale est comme chez *bornemanni*. Un seul caractère intermédiaire entre ceux des sous-espèces, la taille.

#### Association des caractères

Je n'ai trouvé que deux caractères qui soient constamment associés et ils le sont pour des raisons évidentes. Sous les ailes postérieures le tornus est faiblement teinté de jaunegrise chez *urvilleana* et largement coloré d'orange chez *bornemanni*. Chez *miokensis*, la teinte du tornus est toujours proportionnelle à l'étendue relative du bleu et du vert.

Mais d'autres caractères que l'on pourrait s'attendre à trouver associés ne le sont nullement. Ainsi, l'extension du vert sous les ailes est toujours beaucoup plus forte aux ailes postérieures qu'aux antérieures alors que c'est le contraire sur les ailes. Egalement, certains spécimens très verts sous les ailes postérieures ont de très grandes taches discales noires. Enfin, l'intensité du vert sous les ailes n'est nullement proportionnelle à ce qu'elle est dessus: chez 14 exemplaires les plus verts dessous, 2 sont entièrement bleus dessus, sans trace de vert, 3 sont faiblement teintés de vert dessus alors que 9 sont fortement teintés de vert ou entièrement verts.

#### Cumul des caractères

Un seul *miokensis* est en tous points identique à *bornemanni*, sauf qu'il a plus de bleu à la face inférieure de la base des deux ailes. Tous les autres, si verts soient-ils, ont le ton mat d'*urvilleana* et sont donc bien différents de *bornemanni*. 3 spécimens seulement ont une coloration identique à celle d'*urvilleana* dont ils paraissent indistinguables, mais leurs ailes postérieures ont une forme voisine de celle de *bornemanni* et leur taille est inférieure à 125 mm. Les autres exemplaires allient des caractères intermédiaires en des proportions les plus diverses.

#### Conclusions

De la longue étude qui précède, nous pouvons conclure que *miokensis* présente uniquement des caractères qui se retrouvent chez *urvilleana* et *bornemanni*. J'en ai détaillé plus haut 17. Sauf une exception, ces caractères ne sont jamais associés, sont présents chez *miokensis* à tous les degrés de cumul et montrent tous les états intermédiaires possibles. L'explication qui s'impose est que *miokensis* est un hybride à de multiples degrés entre *urvilleana* et *bornemanni*. Il est probable que des spécimens de ces deux formes traversent occasionnellement le Détroit de St-Georges et volent dans les Iles du Duc d'York où ils se reproduisent entre eux et, plus fréquemment, avec des hybrides des générations précédentes. Le génotype de *miokensis* est donc entièrement dérivé de celui des deux formes sus-mentionnées dont les gènes peuvent être associés de multiples façons et dans toutes les proportions possibles.

On peut aussi se demander si des spécimens de *miokensis* ne traversent pas aussi le détroit et ne mêlent pas leurs gènes avec ceux des populations pures de Nouvelle-Bretagne et de Nouvelle-Irlande. Il semble bien que ce soit le cas. Certains *bornemanni* montrent des aires bleues sous les deux ailes et le dessus des postérieures peut être nuancé de bleu. Mais il est difficile de dire si cette couleur est due à la présence de gènes d'*urvilleana* égarés chez *bornemanni*, car d'autres sous-espèces de *priamus* montrent aussi le dessous des ailes largement envahi de bleu, telles *hecuba* et *priamus* typique. Il n'est pas question de gènes étrangers chez ces deux dernières.



Le cas des *urvilleana* de Nouvelle-Irlande est plus évident. Sur 12 spécimens que j'ai vus, la majorité ont les taches discales noires des ailes postérieures plus petites que chez les spécimens de Bougainville et la taille de la moitié des spécimens est nettement inférieure. 4 d'entre eux ont le dessus des ailes nettement teinté de vert, à l'apex des ailes antérieures et sur le pourtour des postérieures. Sous les ailes, le vert est très étendu, surtout aux postérieures. Ceci suggère fortement que les populations d'*urvilleana* de la Nouvelle-Irlande ont reçu des gènes de *bornemannii* qui leur ont été transmis par *miokensis*. C'est pour cela que j'ai comparé plus haut *miokensis* à des *urvilleana* de Bougainville.

### Ornithoptera allottei Rothschild

Une autre espèce d'Ornithoptère a la réputation d'être un hybride: *allottei*, car presque tous ses caractères sont intermédiaires entre ceux d'*urvilleana* et *victoriae regis*. Dans une note récemment publiée (1970), j'ai exprimé l'opinion qu'il s'agit en réalité d'une bonne espèce, ai cité une quarantaine de ses caractères et lui ai assigné une position dans l'arbre phylétique du sous-genre. J'ai montré que la situation d'*allottei* entre *urvilleana* et *regis* est une impression purement esthétique et non pas une vraie position phylétique. Ces trois formes ne constituent pas une séquence linéaire de spécialisation croissante, mais *urvilleana* et *regis* ont évolué dans deux directions différentes, alors qu'*allottei* est demeuré plus primitif qu'eux.

En citant la bibliographie de cette espèce, j'ai commis une grave omission que je répare ici. En 1930, Rousseau-Decelle publia une bonne redescription de l'espèce, accompagnée de deux excellentes photos. Il affirma qu'il s'agit d'un hybride entre les deux formes citées plus haut et cita à l'appui une trentaine de caractères intermédiaires. Je n'ai donc pas été le premier à détailler les caractères d'*allottei*.

Après la parution de mon article, des remarques (*in litt.*) de plusieurs correspondants me montrèrent que la thèse de l'hybridisme est encore largement accréditée. La même année (1970), D. K. McAlpine publia une note réaffirmant cette opinion et critiquant la place que j'ai assignée à *allottei* dans mon arbre phylétique. L'auteur australien, qui ne cite pas non plus Rousseau-Decelle, avance plusieurs arguments en faveur de l'hybridisme — comme la rareté des spécimens, la stabilité des hybrides de la F1, etc. — qui ont mon agrément, mais qui me paraissent insuffisants pour être convaincants. Je ne citerai que trois points avec lesquels je suis en désaccord.

1. "It would be unsafe to assume a form to be an hybrid simply because it is intermediate morphologically between two commoner forms." "A careful study . . . reveals not a single morphological development which can be considered peculiar to the supposed species." ". . . this could be expected if the genotype of *allottei* included only genetic material derived from the two parent species . . ." Ces trois phrases provenant du même alinea contiennent à la fois une contradiction et deux erreurs. L'auteur pense qu'il serait téméraire de considérer qu'une forme est un hybride simplement parce qu'elle est intermédiaire entre deux autres, mais c'est néanmoins exactement ce qu'il fait. Ensuite, le fait qu'une espèce soit intermédiaire entre deux autres ne prouve pas que tous ses gènes soient les mêmes que ceux de ces dernières; les exemples du contraire sont nombreux dans tous les ordres d'insectes. Enfin, *allottei* possède en fait un petit nombre de caractères que l'on ne retrouve pas chez ses parents putatifs. Je ne les ai pas cités dans ma note de l'an dernier. Les voici:

Chez *alottei*, les ailes postérieures sont largement et uniformément sablées de noir sauf sur leur pourtour. Chez les *urvilleana* de Bougainville, seule la cellule est assombrie, alors que chez *regis*, l'aile postérieure est entièrement métallique. Rares sont les *urvilleana* chez qui la couleur noire déborde de la cellule et plus rares encore les *regis* qui montrent des nuages sombres dans la région péri-discale. Il serait bien étonnant que tous les *alottei* connus soient issus du croisement d'individus ayant une coloration exceptionnelle.

Un second caractère est que, chez *alottei* la bande apicale légèrement métallisée des ailes postérieures s'étend sur tout le pourtour de l'aile, de l'extrême base jusqu'à la cellule Cu1-Cu2. Chez *regis*, cette bande, qui est plus brillante, n'est présente qu'à l'apex de l'aile, entre les cellules Ms-M1 et Cu1-Cu2. Chez *urvilleana*, elle est absente.

Un troisième caractère, plus important encore et plus frappant, est la couleur verte des ailes antérieures, du pourtour des postérieures et du dessous des deux ailes, qui est très pure et fort différente de celle des deux autres sous-espèces. Ces trois caractères ne peuvent pas avoir été acquis des deux progéniteurs supposés et tout porte à croire qu'ils sont dûs à des gènes spécifiques à *alottei*.

2. Reprenant provisoirement mon opinion qu'*alottei* est une bonne espèce, McAlpine critique le fait que je l'ai fait se différencier de *victoriae* après *alexandrae* et non avant, comme cela devrait être le cas selon lui. Or, mon arbre phylétique, aussi bien que le texte qui l'accompagne, montrent explicitement que chacune de ces deux solutions soulève des difficultés. Entre deux objections, j'ai choisi la moindre, conformément au principe de la plus grande économie des moyens d'explication et ai considéré ce choix comme la solution de plus grande probabilité. Les objections de McAlpine montrent clairement qu'il n'a malheureusement pas lu mon texte, ne comprenant probablement pas le français.

3. Un autre point sur lequel je reprendrai McAlpine est qu'il s'attend à ce que ses conclusions soient contestées par les collectionneurs d'Ornithoptères, à cause de la "rareté fabuleuse" d'*alottei* et du prix énorme qui a été payé pour un spécimen. Que l'essence des choses soit confondue avec leur valeur financière est en effet courant dans notre société. Quoique le problème d'*alottei* ne comporte évidemment qu'une alternative simple — c'est un hybride ou une bonne espèce — je veux bien croire qu'il y a une certaine part d'irrationnel dans les motivations des tenants de chacune des deux solutions, mais elle est à rechercher à un niveau plus profond. Depuis bien avant La Fontaine on sait que l'homme a tendance à valoriser ce qu'il possède et à dénigrer ce qu'il ne peut pas obtenir. Peut-être ces différences d'opinion ne sont-elles qu'une forme de l'éternel conflit entre ceux qui possèdent et ceux qui ne possèdent pas? Le fait qu'au moins trois spécimens aient été récoltés dans la nature par des chasseurs indigènes en 1970 seulement contribuera certainement à diminuer le prestige dont on a doté *alottei* et suggère que l'on finira par découvrir une vraie population de cette espèce.

De toute façon je n'ai pas prétendu prouver, ni par ma note de l'an dernier, ni par ce qui précède, qu'*alottei* est une bonne espèce, mais simplement que j'ai de bonnes présomptions en faveur de cette opinion. Il est évident que seuls des essais d'hybridation artificielle ayant donné des résultats positifs pourront résoudre ce problème sans équivoque.

Je ne pense pas inutile de terminer en signalant l'existence d'un des ♂ de ma collection présentant des caractères fort intéressants et bien différents de ceux des spécimens qui ont été figurés jusqu'ici. Aux ailes antérieures, la bande radiale est nettement plus large

que celle du spécimen de ma figure 1 (1970), la cellule R4-R5 étant largement colorée. Aux ailes postérieures, la bande périphérique brillante est très large, d'un vert franc, assez foncé et mat. La surface sablée de noir est nettement réduite. Les taches discales noires sont au nombre de 3 à droite et de 2 à gauche; elles sont grandes, très nettes et situées en dehors de la zone sablée. A la face inférieure de l'aile, il y a des traces irrégulières de couleur jaune dans la cellule R1-Rs; à l'aile droite seulement, la couleur jaune perce la membrane et est visible de dessus. En outre, il y a trois grandes taches jaunes sous les cellules M1-M2, M2-M3 et M3-Cu1, la seconde seulement étant visible de dessus où elle a les dimensions de  $1,5 \times 3$  mm.

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NOTES ON *PAMMENE IGNORATA* KUZNETSOV, 1968

(LEPIDOPTERA, TORTRICIDAE)

by

HARVARD UNIVERSITY  
NIELS L. WOLFF  
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## ABSTRACT

*Pammene ignorata* Kuznetsov, 1968, was described after two ♀ from the U.S.S.R.; the male was unknown. In the present paper 16 specimens, ♂ ♀, from Denmark and Sweden, are recorded, formerly confounded with *P. gallicolana* Lienig & Zeller. The Siberian and Far Eastern localities are distant 6000 and 8000 km, respectively. Four more finds, one from Siberia, two from the Far East and one from Lithuania, at a distance of 450 km from Scandinavia, are now added.

While studying Scandinavian material of the *Pammene argyrana* group in order to clear nomenclatorial problems (Wolff, 1968), in 1957 I came across a Danish female specimen from the island of Falster, collected about 80 years earlier, which defeated identification.

The colour and the pattern of the fore wings resembled those of *Pammene gallicolana* Lienig & Zeller, but the shape of the wing was different and the dorsal blotch less contrasting than in specimens of that species from Germany. The genitalia differed strikingly from those of all other species of the group familiar to me, especially by the characteristic antrum, showing in the mount as a well-defined triangle.

Although surmising that the specimen was undescribed, I left it out of further treatment in my paper, out of need for additional material. Ten years later another Scandinavian specimen with identical genitalia turned up, collected on the island of Öland, Sweden, 8-9.VI.1967, by Mr. Ingvar Svensson.

An attempt to have the first Swedish specimen identified at the British Museum (Natural History) proved unsuccessful. Upon this Dr. A. Diakonoff of Leiden, who did not know the species either, volunteered to bring the Danish specimen and the mount along with him to the Zoological Institute of Leningrad at the occasion of the 13th International Congress of Entomology, 1968, in order to discuss the matter with Dr. V. I. Kuznetsov.

Dr. Kuznetsov recognized the species at once as his *Pammene ignorata* from the Far East, at that time just described, but published later in the same year (Danilevski & Kuznetsov 1968: 383, fig. 256). The description is based on two females, the holotype from the Far East, Primorski Krai (Maritime District), near Ussuriysk, Suputin nature reserve, 17.VI.1966; and the paratype from Siberia, Autonome Buryat Republic, Kabansk, 26.VI.1959. Therefore at that time four female specimens of the species were available.

My recent search for the species in the field and in collections brought to light the following six additional specimens from Scandinavia:

- Denmark: Sjælland, Boserup Skov 20.VI.1971 (H. Hendriksen leg.).  
 Lolland, Roden Skov 6.VI.1964 (H. Hendriksen leg.).  
 Lolland, Kosteskoven 28.VI.1962, 24.VI.1965 (Kaj Pedersen leg.).  
 Lolland, Krenkerup 5.VI.1968 (E. Pyndt leg.).
- Sweden: Skåne, Benestad 16.VI.1970 (I. Svensson leg.).

The fact that all ten specimens were females invited to still further study. The record of *Pammene gallicolana* as a true Danish species dates from 1956, when Mr. Bradley compared a Danish male from the island of Falster with the type specimen of *gallicolana* in the British Museum; they proved to be conspecific (cf. Wolff, 1968: 328). My fig. 11 of the valvae of the type specimen is after a sketch, kindly sent by Mr. Bradley.

A renewed close examination of all slides of male genitalia of the supposed "*gallicolana*" available now disclosed the existence of small but constant and therefore significant differences from those of the *gallicolana* males from Germany, originating partly from the collection of the Zoological Museum, Copenhagen, partly from the collection of Mr. E. Jäckh, of Bremen, as well as from the illustrations of the male genitalia of *gallicolana* by Bentinck & Diakonoff (1968, pl. 58 f. 117a) and by Hannemann (1961, fig. 197, although here erroneously taken for *argyrana*) — and also from the drawing of the type (Wolff, 1968, fig. 11).

A significant difference appeared to be the shape of the valva, in the Danish material showing a more or less pronounced angulation of the outer contour, not present in the material from elsewhere. So, while the female genitalia of *gallicolana* and *ignorata* differ considerably, those of the males differ but very slightly, so slightly in fact, that this difference has easily been overlooked up till now. A close re-examination of the genitalia of the type of *P. gallicolana* (slide no. 4370 BMNH) carried out by Mr. Bradley now confirmed this constant difference from *P. ignorata*.

At present the following eight Scandinavian males of *P. ignorata* are known to me:

- Denmark: Falster, Hannenov 16.V.1948 (N. L. Wolff leg.). Falster, Sundby 5.VI.1914 (Sønderup leg.). Lolland, Bremersvold 11.VI.1914 (Sønderup leg.). Lolland, Hamborgskoven 10.VI.1951 (E. Pyndt leg.). Bornholm, Randskløve 3.VII.1960 (van Deurs leg.).
- Sweden: Öland, Högsrum 6.VI.1959. Värmland, Ränneberget 18-19.VI.1968. Västmanland, Ängsö 15.VI.1971 (all I. Svensson leg.).

The search for the unknown male of *Pammene ignorata* thus ended with the discovery that it had already been examined and illustrated, although incorrectly interpreted. All Danish and Swedish "*gallicolana*", females as well as males (a total of sixteen specimens), belong to *ignorata* instead.

The following pictures, previously published (Wolff 1968), and stated to represent *gallicolana*, thus show *ignorata* ♂: figs. 10, 12, 13, 28 and 37.

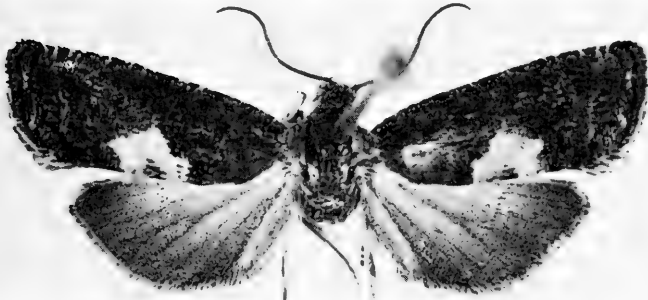
On my recent inquiry about the present state of the knowledge of *P. ignorata* in Russia, Dr. Kuznetsov kindly communicated the following Russian finds:

- Amurland, Khabarowsk (about 600 km N. of Vladivostok).  
 Ussuriland, Ussuriysk (N. of Vladivostok).  
 Transbaykal, Kabansk (N. of Irkutsk).  
 Lithuania, Obeline (near Kaunas).

The locality in Lithuania approaches the Scandinavian locality in Öland by about 450 km. The new Russian material included a single ♂, the genitalia of which —



1



2

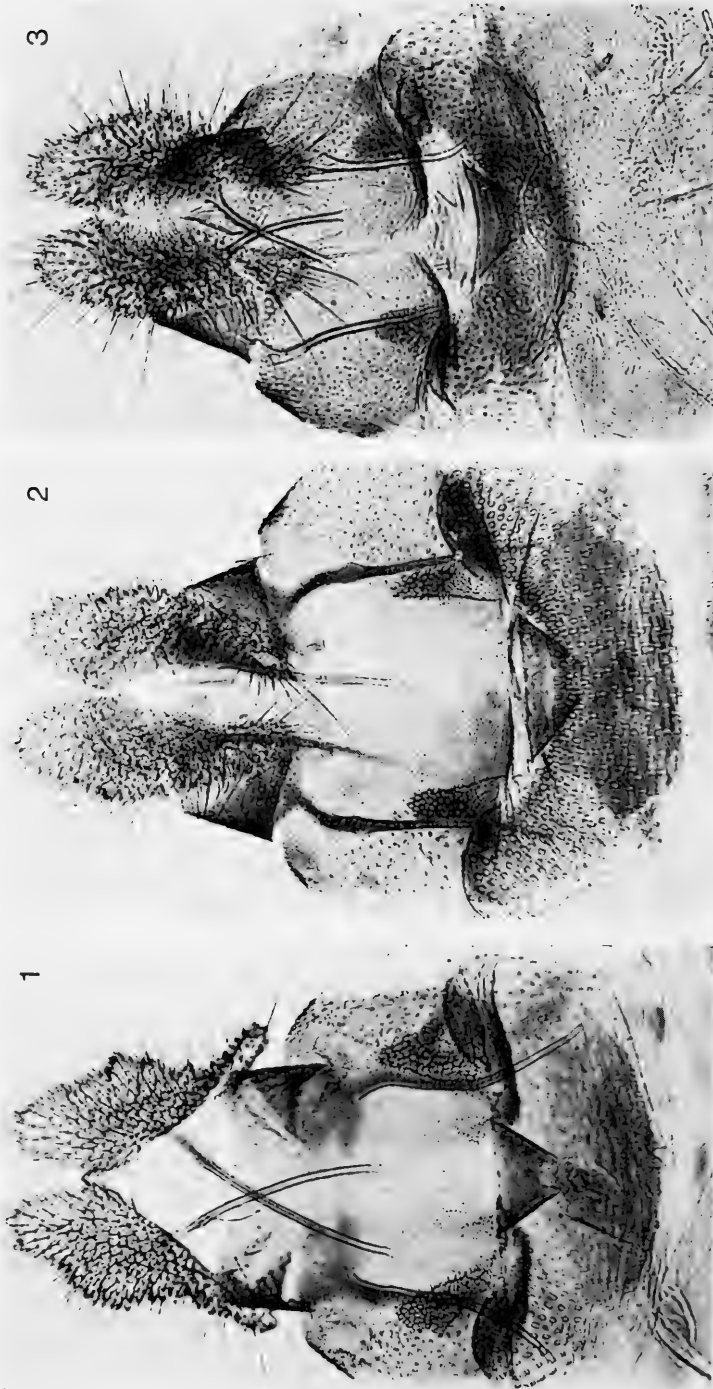


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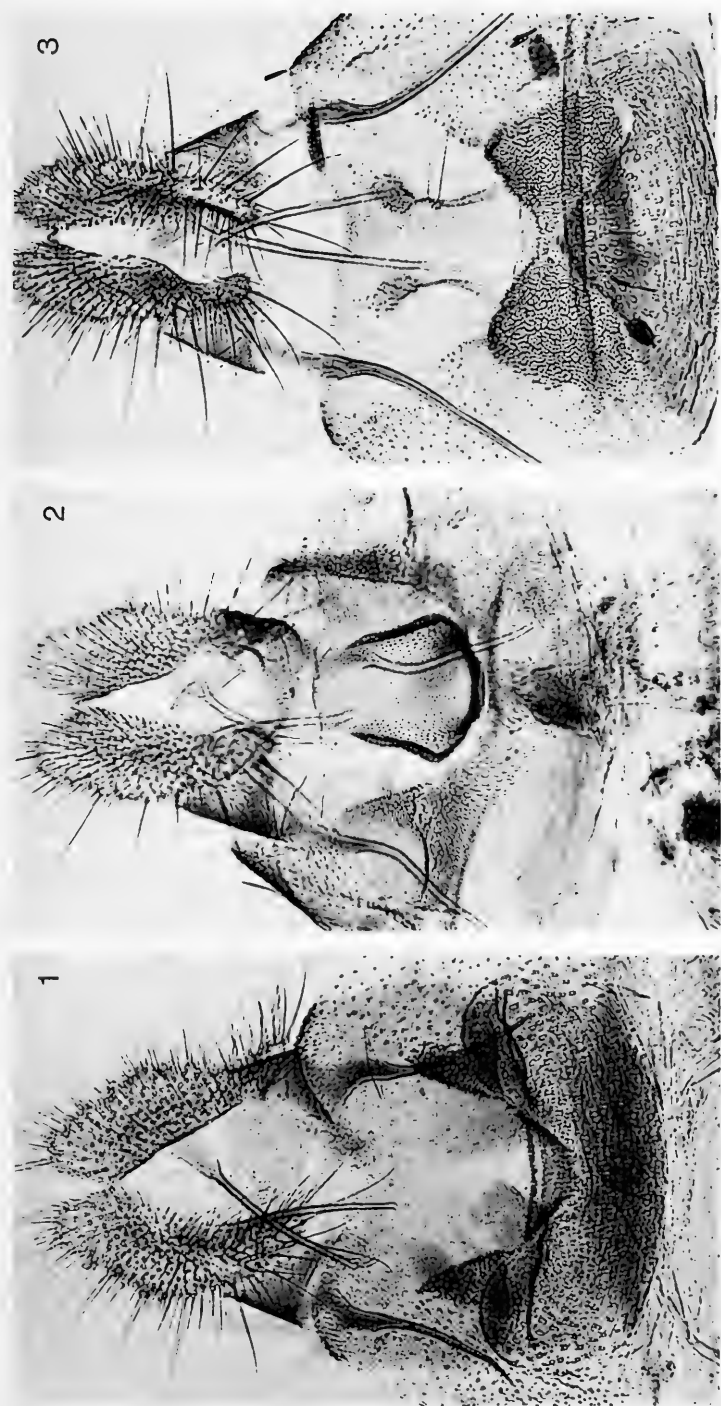
4

Pl. 1, Fig. 1—3. *Pammene ignorata* Kuzn. Denmark. 1, ♂ Lolland; 2, ♂ Falster; 3, ♀ Lolland; 4, *Pammene gallicolana* Lien. & Zell. ♂ Germany, Speyer ( $\times 6\frac{1}{2}$ )

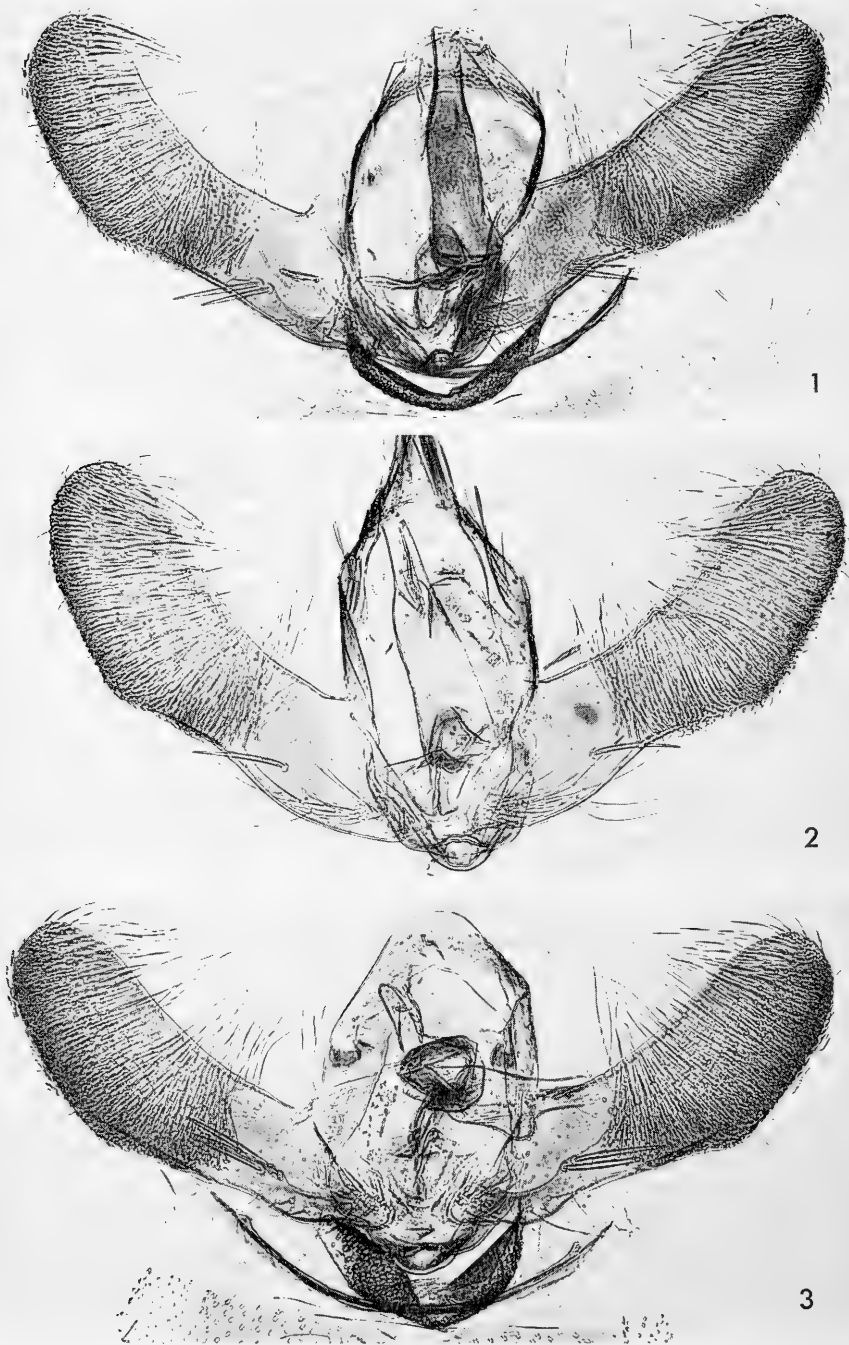


Pl. 2, Fig. 1—3. Female genitalia of *Pammene ignorata* Kuzn. Denmark. 1, Falster, prep. NLW 2190; 2, Lolland, prep. NLW 3745 (the same specimen as shown on Pl. 1 Fig. 3); 3, Lolland prep. NLW 3434 (X 60)

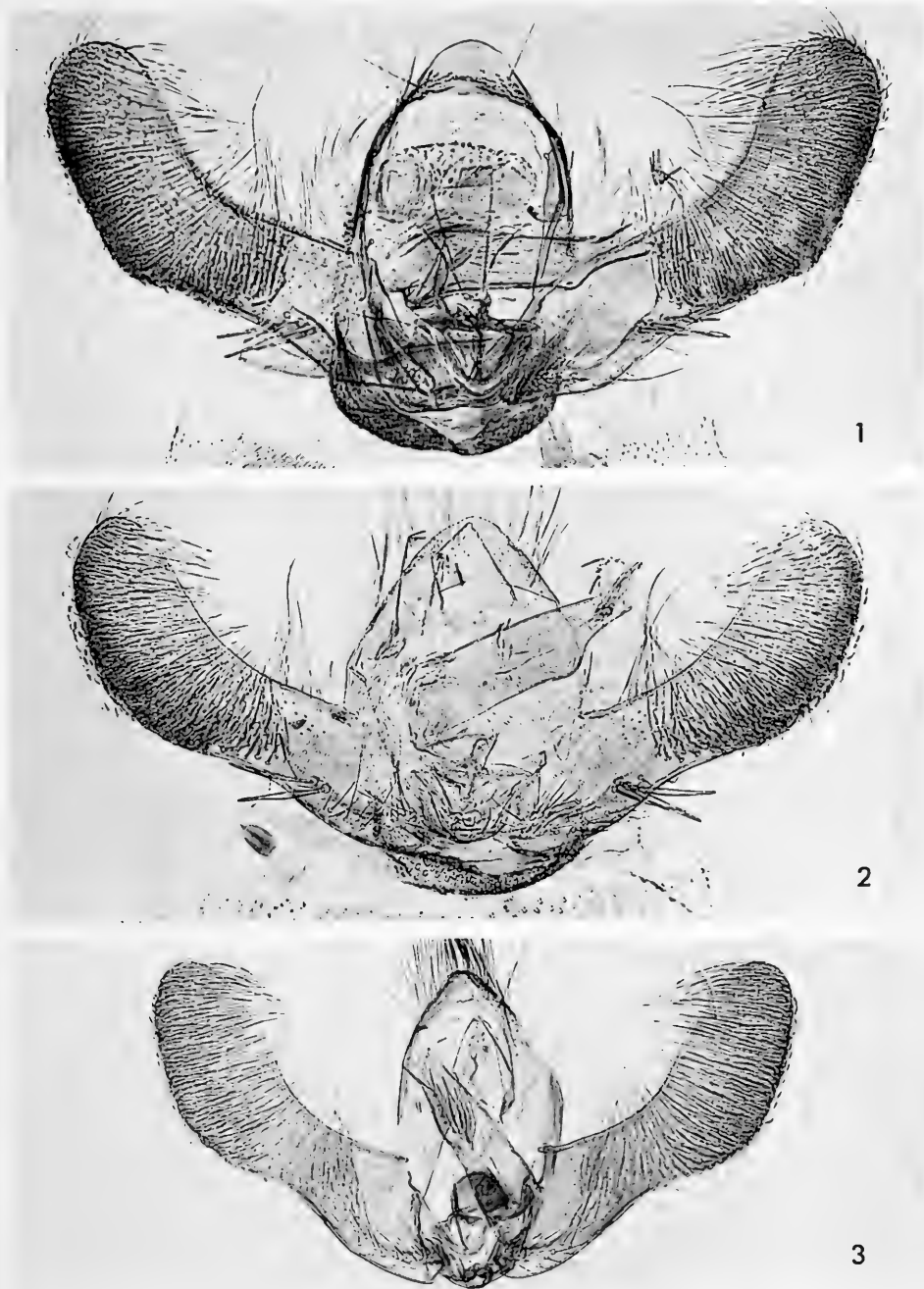




Pl. 3, Fig. 1—3. Female genitalia of *Pammene* spp. 1, *P. ignorata* Kuzn. Sweden, Öland, prep. I. Sv. 4378; 2, *P. gallicolana* Lien. & Zell. Germany, Lausitz, prep NLW 2171; 3, *P. albuginana* Guen. Denmark, Lolland, prep. NLW 3744 (x 60)



Pl. 4, Fig. 1—3. Male genitalia of *Pammene ignorata* Kuzn. Denmark. 1, Lolland, prep. NLW 2138; 2, Falster, prep. NLW 1160 (the same specimen as shown on Pl. 1 Fig. 2); 3, Bornholm, prep. NLW 4007 ( $\times 70$ )



Pl. 5, Fig. 1—3. Male genitalia of *Pammene* spp. 1, *P. ignorata* Kuzn. Sweden, Öland, prep. I. Sv. 4584; 2, *P. gallicolana* Lien. & Zell. Germany, Speyer, prep. NLW 3743 (the same specimen as shown on Pl. 1 Fig. 4); 3, *P. albuginana* Guen. Denmark, Sjælland, prep. NLW 2094 ( $\times 70$ )



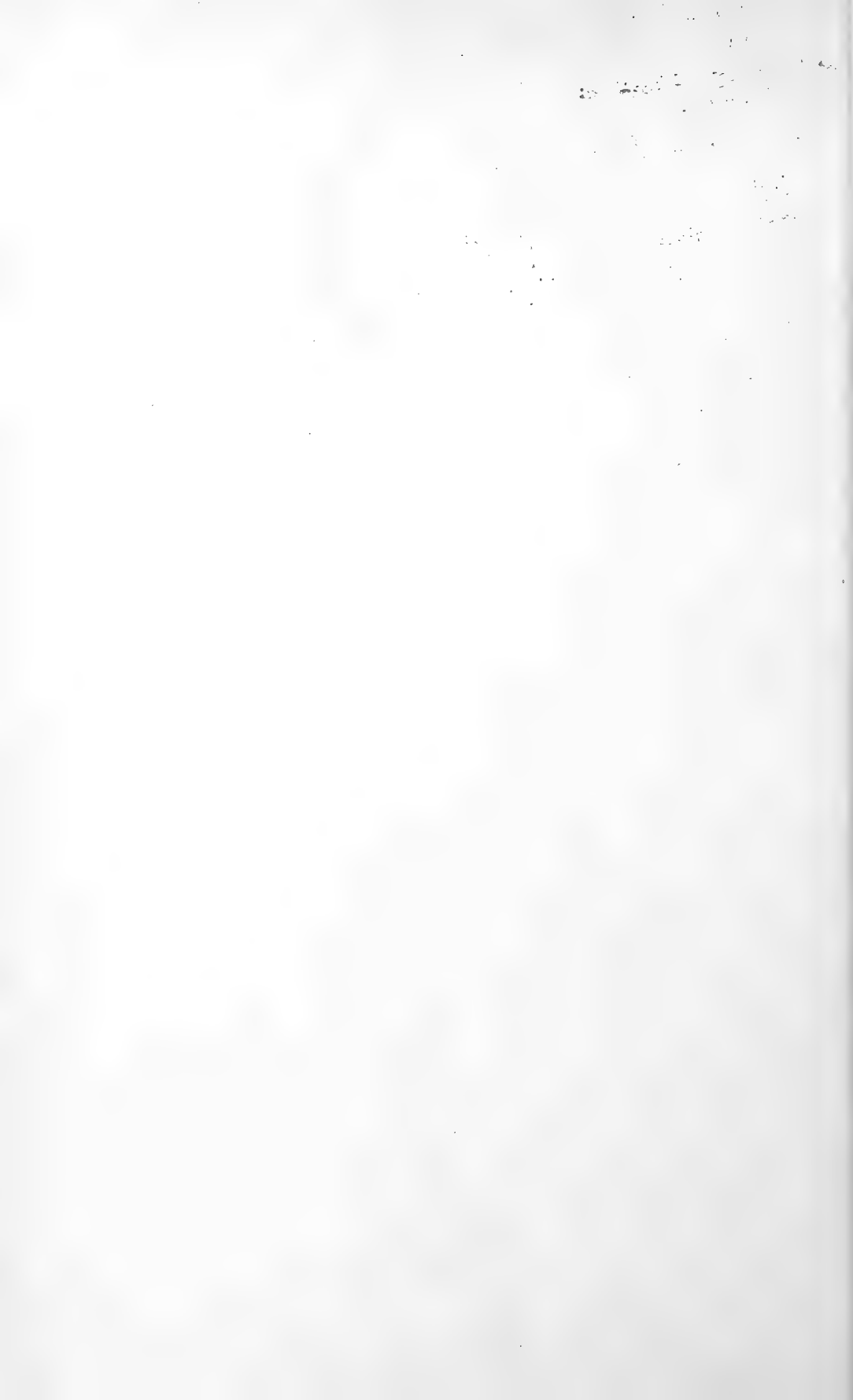
according to the accurate drawing included — match those of the Scandinavian specimens. Dr. Kuznetsov kindly permitted me to make use of his above data in the present paper.

Pl. 1 shows two Danish ♂ and a Danish ♀ of *Pammene ignorata* and, for comparison, a German *P. gallicolana* ♂. Pl. 2 depicts the female genitalia of three Danish *P. ignorata*. In Pl. 3 the female genitalia of a Swedish *P. ignorata* are presented beside those of a German *P. gallicolana* and a Danish *P. albuginana*. Pl. 4 demonstrates the male genitalia of three Danish *P. ignorata*, while in Pl. 5 the male genitalia of a Swedish *P. ignorata* are compared with those of a German *P. gallicolana* and a Danish *P. albuginana*.

The author wishes to acknowledge his gratitude to Mr. J. D. Bradley (Commonwealth Institute of Entomology, London), Dr. A. Diakonoff (Rijksmuseum van Natuurlijke Historie, Leiden) and Dr. V. I. Kuznetsov (Zoological Institute of the Academy of Sciences, Leningrad) for their kind assistance, as well as to the many lepidopterists who readily placed their specimens at his disposal. Mr. B. W. Rarmussen (Zoological Institute, Copenhagen) deserves special thanks for his careful preparation of the microphotographs.

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## POLLINATION OF *FIGUS COSTARICANA* AND *F. HEMSLEYANA* BY *BLASTOPHAGA ESTHERAE* AND *B. TONDUZI* IN COSTA RICA (HYMENOPTERA: CHALCIDOIDEA, AGAONIDAE)

by  
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### ABSTRACT

Pollination was studied in *Ficus costaricana* and *F. hemsleyana* in San Jose, Costa Rica. The pollinators, *Blastophaga estherae* and *B. tonduzi*, have two pairs of pollen organs: corbiculae on the fore coxae and pockets on the underside of the mesothorax, both open organs. On the inner side of each corbicula, there is a distinct comb. Loading of corbiculae and pockets is effected by the fore legs before the female wasp leaves her native syconium. Pollen is lifted from the open anther onto the underside of the thorax and afterwards shoveled to the thoracic pockets with the aid of the combs. Pocket emptying and subsequent pollination are effected at the end of each oviposition act. Pollen is shoveled back from the pockets to the corbiculae and taken from these by the arolia of the fore legs. The pollen is shaken off from the legs onto the stigmata by beating the fore legs on each other. The role of the coxal corbiculae is twofold: since in just-emerged wasps the corbiculae are full of pollen, they serve as reservoirs for pollen transport; in addition, they are also used as temporary pollen containers for extraction and deposition of pollen during the pollination act.

### INTRODUCTION

The mode of pollination in the common fig (*Ficus carica* L.), by the small chalcidoid wasp, *Blastophaga psenes* L. which had long been studied by numerous botanists and zoologists (Condit, 1947; Grandi, 1929), was believed to be the prototype of fig pollination in general. It was thought that in all *Ficus* species the pollinating wasps became passively dusted with pollen on their way out of the native figs, and thereby carried the pollen to young receptive figs.

Recently it has been found that in the majority of other fig species the situation is not as simple as in the common fig. Independently, and almost simultaneously, Ramirez (1969), in Costa Rica, and Galil and Eisikowitch (1969), in East Africa, discovered the specific organs which serve for pollen transport from old figs to young ones in various species of *Ficus*. In several agaonid wasps which are the pollinators of *Ficus* species of the *Urostigma* Section in Central America, Ramirez (1969) found two types of pollen-carrying organs, viz. "coxal corbiculae" on the fore coxae and "sternal corbiculae" on the underside of the mesothorax. In contrast to the open organs described by Ramirez, Galil and co-workers (Galil and Eisikowitch, 1969; Galil and Snitzer-Pasternak, 1970) found only closed organs ("pollen pockets") on the mesothorax in *Cerosolen arabicus* Mayr and *Blastophaga quadraticeps* Mayr, the pollinators of *F. sycomorus* L. and *F. religiosa* L., respectively.

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Pollen corbiculae and pockets of agaonid wasps were actually illustrated in earlier publications (Grandi, 1916, 1917, 1919, 1923; Galil and Eisikowitch, 1968), but nothing was said on the function of these organs. Indeed, even Grandi did not notice their specific structure and role in pollination.

Hitherto, only very little has been published on the structure and action of the pollen corbiculae and pollen pockets.<sup>3)</sup> The thoracic pollen pockets of *Blastophaga quadraticeps* are the only ones which have actually been studied in some detail (Galil and Snitzer-Pasternak, 1970). Pocket loading was observed in *F. religiosa*, whereas pocket emptying and the pollination process were described in *F. sycomorus* only (Galil and Eisikowitch, 1969). The study of the open corbiculae and pockets of the agaonid wasps which pollinate the *Ficus* spp. of the *Urostigma* section in Central America would help us to understand the mechanism of action in the more complicated closed organs of other wasps.

The objective of the present work was to take a closer look at the structure of the coxal corbiculae and thoracic pockets of *Blastophaga estherae* Grnd. and *B. tonduzi* Grnd. (the pollinators of *Ficus costaricana* (Liebm.) Miq. and *F. hemsleyana* Standl., respectively), originally discovered by Ramirez (1969, 1970) and to study their mode of action.

#### MATERIALS AND METHODS

Observations on the syconia of *F. costaricana* and *F. hemsleyana* and their pollinators were carried out in the San Jose area (Costa Rica, Central America) and at the campus of the University of Costa Rica during February—March, 1971. The low to middle-sized trees bear easily accessible spreading branches (Plate 1, fig. 5). Many of them flower during the winter and provide abundant material at all developmental stages.

The structure of the figs of both *Ficus* species studied and the structure and behaviour of their pollinators, respectively, are very similar. From the biological aspects, the differences between them are only quantitative, i.e. in the size and shape of the syconia, in the size of the corbiculae and pollen pockets of the wasps, and in the duration of the different processes involved in pollination. For technical reasons, the more suitable of either species was selected to illustrate a particular stage.

For a more detailed study of the corbiculae, the pockets, and the adjacent parts of the wasp body, serial microtome sections were prepared. The wasps were fixed in Bouin-Dubosq-Brazil, embedded in celloidin-clove oil and microtomed at  $6\mu$  in transverse and longitudinal sections. The sections were stained in Delafield's haematoxylin and counterstained in eosin Y. Due to folding of the coxae parallel to the longitudinal axis of the body, sections of the thorax included corresponding sections of the coxal corbiculae as well (Plate 1, figs. 9, 10, 11).

Corbiculae and pockets were studied in microscope whole mounts of the fore legs and the mesothorax, respectively (Plate 1, fig. 8; Plate 2, figs. 14, 15). The tergites of the mesothorax were cut away. The remaining ventral part of the mesothorax and the prothorax with the two fore legs were fixed in FAA, dehydrated and mounted in Permount. For a more detailed study of the structure of corbiculae and pockets, scanning electron micrographs were prepared (Plate 2, figs. 12, 13).

<sup>3)</sup> In the present work the coxal pollen organs are named "corbiculae", according to Ramirez (1969). For the more complicated thoracic organs, the term "pockets" is used, according to Galil and Eisikowitch (1969).



For ensuring better inhabitation by the wasps, branches bearing uninhabited receptive B<sup>4</sup>) figs were enclosed in small jars, together with D phase figs, prior to the release of the wasps. The newly emerged female wasps immediately penetrated into the B phase figs so that oviposition and pollination could be followed more easily.

## OBSERVATIONS

### *Syconia* and Pollinators

In *F. costaricana* and *F. hemsleyana*, as in most species belonging to the *Urostigma* section of the genus *Ficus*, syconia develop in pairs in the axils of foliage leaves. The syconia of *F. costaricana* are almost sessile whereas those of *F. hemsleyana* are distinctly pedunculate. Receptive syconia of the female phase (B) in both species, which are about the same size (up to 11 x 12 mm), are broad at the top and taper toward the base (Plate 1, Fig. 6). In *F. costaricana*, the cavity of the B fig is relatively wide (up to 7 x 3 mm). As is usual in *Urostigma*, the figs are bisexual. The short- and long-styled female flowers (gall and seed flowers, respectively) are easily distinguishable by the size of the stigmata and the thickness of the styles which are larger in the gall flowers (Figs. 1, 2). The male flowers which are scattered among the female flowers throughout the surface of the fig cavity remain small and closed. Their number ranges from 30 to 40 per syconium.

At the male phase (D) the figs are more rounded, about 17 mm in diameter (Plate 1, Fig. 7). In *F. costaricana* they become yellowish with red spots. The male flowers which are found among the pedunculate galls and sessile seeds ripen and become more prominent since the anthers (one per flower) protrude out of the open perianth scales (Fig. 3).

During the male phase (D), the scales of the ostiole do not loosen. The female wasps leave the figs via small holes in the vicinity of the ostiole bored by the males. Generally there is only one hole, but, occasionally, two and three holes may also be found.

At the approach of final ripening (phase E), the fig grows in size, softens and becomes more reddish than at phase D. There is no characteristic smell.

The pollinators, namely *Blastophaga estherae* in *F. costaricana* and *B. tonduzi* in *F. hemsleyana* possess both corbiculae and pockets (Ramirez, 1969, 1970). In *B. tonduzi*, they are about 1.5 times larger than in *B. estherae* (150 $\mu$  in the former, as against about 100 $\mu$  in the latter). The corbiculae are elongated depressions occupying about two-thirds of the coxae of the fore legs on their inner surface (Plate 2, Figs. 13, 15). The depressions are fringed on one side by a row of long and stiff comb-like bristles (cb). When the coxae are pressed to the thorax from beneath, the corbiculae (c) face upwards, with their combs interlacing in the middle (Plate 1, Fig. 9). The pockets (PP) are rounded depressions on the underside of the mesothorax, partially covered by a flap

<sup>4</sup>) According to Galil and Eisikowitch (1968) the developmental phases of figs were named as follows:

Phase A (Pre-female): Young syconium prior to the opening of the ostiole.

Phase B (Female): Ostiolar scales loosen, female flowers ripen, sycophilous wasps penetrate into the syconium and oviposit into the ovaries.

Phase C (Interfloral): Wasp larvae and fig embryos develop within their respective ovaries. Ovaries occupied by the larvae are transformed into galls.

Phase D (Male): Male flowers mature, wasps reach the imago stage, fertilized female wasps leave syconia via channels bored by the males.

Phase E (Post-floral): Both syconia and the seeds inside them ripen.

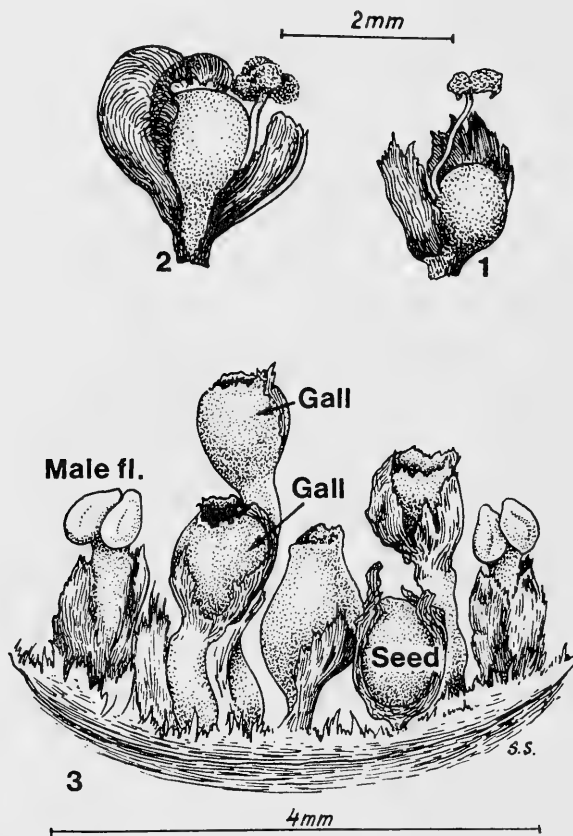


Fig. 1. Female seed flower of *Ficus costaricana*. Fig. 2. Female gall flower of *Ficus costaricana*. Fig. 3. Cross-section through a male phase (D) syconium of *Ficus costaricana*, showing galls, seeds and male flowers

(Plate 1, Fig. 8; Plate 2, Figs. 12, 16). Due to their larger size, the pockets of *B. tonduzi* are closer to each other, when the thorax is viewed from below (for *B. estherae* see Plate 2, Fig. 14). The pockets are delimited from both sides by two groups of bristles, the first of these consisting of about ten stiff and long setae (Plate 2, Fig. 12).

On the underside of the body, between the sternites of the pro- and mesothorax, there is a wide depression bordered from above by a wavy flexible membrane (M) which bridges the gap (Plate 1, Figs. 10, 11). When the fore coxae are pressed upwards, a chamber is created (I) that is delimited from above by the membrane, from below by the pair of corbiculae, and by the pro- and mesothorax from the anterior and posterior sides, respectively. It appears that this intersegmental depression and the strong longitudinal muscles along the whole thorax enable the wasp to bend its prothorax deeply downwards, towards the mesothorax. In this posture, the stretched procoxae are pushed ahead, sliding upon the underside of the mesothorax and reaching the pollen pockets on both sides.

The relative positions of the intersegmental chamber, the coxal corbiculae and the pockets can be seen clearly in a series of longitudinal microtome sections along the thorax,

starting in the middle (Plate 1, figs. 10, 11). At first, the inner border of the fore coxa appears with the comb (fig. 10). In further sections, the coxa is cut through the corbicular depression (fig. 11). The wavy intersegmental membrane is distinct. The pockets, which are situated more laterally, appear only in the peripheral sections (compare Plate 2, fig. 16).

### Pocket Loading

As in agaonid wasps having only thoracic pockets, loading of the pockets and corbiculae in the females of *F. costaricana* and *F. hemsleyana* takes place immediately after the wasps have left their galls, before their release from the male-phase (D) figs. The process is essentially similar in the two *Ficus* species, but since in *F. hemsleyana* it is more readily observable, because of the larger pollen organs of *B. tonduzi* and the longer duration of the act itself, that species was chosen as the chief object for the study of pocket loading.

Filling of the pockets and corbiculae with pollen consists of several movements involving various parts of the body of the pollinator.

1) Approaching the anthers. When the female *B. tonduzi* wasp leaves its gall, it removes the remnants of the exuvia stuck onto its head and antennae with its fore legs and straightens out the wings by passing the hind legs above and below the wings several times. The wasp now starts pushing its head between the pistils in search of male flowers which are dispersed among the galls and seeds throughout the surface of the fig cavity. Only open anthers are used for pollen loading. When the dehiscence slit is still narrow, the wasp widens the opening by means of the scapes of the antennae.

2) Pollen lifting: The female wasp presses the flagella of the antennae into the anther while the scapes keep the opening wide. The mandibles which move behind the scapes crumble the pollen within the anther. Now the fore legs move very quickly, one after the other, dipping the arolia in the anther and raising them backwards to the thorax. Many pollen flakes appear hanging from the underside of the thorax. Some are pressed into the intersegmental chamber by up and down movements of the coxae of the fore legs. Altogether, up to 40 successive pollen lifting movements of the fore legs, as described here, were counted for each female wasp.

3) Filling of pockets: This is accomplished with the assistance of the coxae of the fore legs. The wasp stands firmly on the middle and hind legs and the coxae of the fore legs are pressed upward onto the thorax. At the same time the neck of the wasp stretches downwards and its back becomes hunched. The fore coxae which glide on the lower surface of the thorax, comb the pollen into the pockets which are within reach of the coxae at this posture. The shoveling movements are repeated several times and, as a result, the pockets and corbiculae become filled with pollen, while pollen flakes are no longer visible on the underside of the thorax. When the anther does not contain enough pollen, the wasp passes to another male flower. Each pollen lifting cycle terminates by pocket filling movements. The whole process is very lengthy and may continue several minutes.

The effect of the shoveling movements in the filling of the pockets with pollen can easily be shown by artificial loading of the pockets with spores of the fungus *Pisolithus tinctorius* (Mich. ex Pers.) Coker et Couch. These spores are about the same size as the pollen grains of *Ficus* (see Galil and Snitzer-Pasternak, 1970). Whenever the spores

were deposited on the underside of thorax and then shoveled backwards by a flattened, broad needle, the pockets were found to be filled with spores; when a pointed needle was used, the pockets remained almost empty.

Because of the fineness of the structure and the swiftness of the movements of the legs, it is very difficult to observe the details of pollen lifting. Nevertheless, it is likely that the combs of the coxae are used to sweep the pollen and that the wide and flexible membrane bordering the intersegmental chamber from above is instrumental in the bending of the thorax, so that the coxae can reach the pockets.

The wasps are very absorbed in the process of pollen loading. The opening of the fig and the strong illumination, indispensable for observations with the dissecting microscope, do not appear to disturb them. Even when the fig is turned over or the stamen on which the wasp stands and works, is detached from its place, the wasps continue their actions uninterruptedly.

### Pocket Emptying: Pollination

Receptive figs of the female phase (B) of *F. costaricana* are easily recognisable by the flat ostiole. When the ostiole opens, a narrow slit appears between the two upper scales which can be seen from above. Generally only one female wasp was found in the fig cavity. Only when a neighbouring tree reached the releasing D phase, there were sometimes 2-3 wasps in one fig. It appears that after the entrance of the wasp, the ostiole closes and does not admit additional wasps (see Ramirez, 1970). Some time after inhabitation by the wasps, the ostiolar area of the fig bulges considerably.

B figs of *F. costaricana* are very suitable for observations of pocket unloading and pollination. Although the fig is not large, its cavity is wide and distinct. Therefore, when the fig is cut open, the chances of the wasp within remaining intact are considerable. But the chief advantage of *F. costaricana* for the study of pollination lies in the behaviour of the female wasps during oviposition.

As in many other *Ficus* species (for *F. religiosa*, see Galil and Snitzer-Pasternak, 1970; for *F. sycomorus*, see Galil and Eisikowitch, 1969), extraction of the pollen from the pockets and subsequent pollination occur at the end of each oviposition act. When pollination is completed, the wasp withdraws her ovipositor from the pistil of the female flower and starts walking on the surface of the fig cavity in search of another female flower. The response of the female wasp to external disturbances during the two phases is very different. If the fig is cut open in the interval between two successive oviposition acts, the insect starts running on the stigmata of the female flower and generally escapes outside. For that reason, it happens but seldom that two or more oviposition acts may be observed in succession. On the other hand, if the fig is cut open in the middle of oviposition when the ovipositor is still inserted into a pistil, the wasp is not disturbed as easily, generally completes the oviposition act, and carries out pollination at its end as usual. The oviposition act of *B. estherae* lasts 3.5-4 minutes (compare 50-100 seconds for *B. tonduzi* and 50-70 seconds for *Cerastolen arabicus*, the pollinator of *F. sycomorus*, according to Galil and Eisikowitch, 1969). Therefore, it is comparatively easy to catch the female in the middle of the oviposition act while its ovipositor is still inserted into the style of the female flower and to observe the pollination act properly.

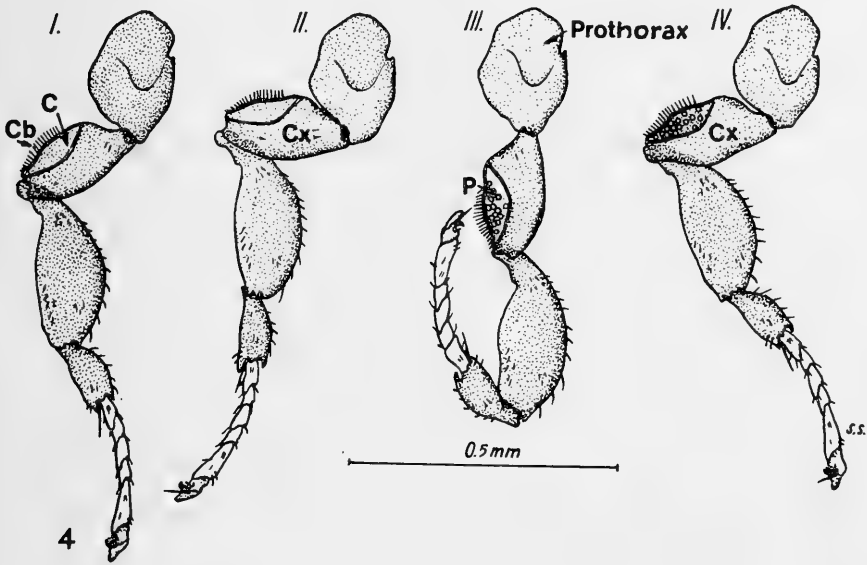


Fig. 4. Position of the fore leg of *Blastophaga tonduzi* during the four steps of the pollination act. Cx, coxa; C, corbicula; Cb, comb I. Preparation. II. Shoveling. III. Extraction of pollen. IV. Shaking of pollen

Pollination by *B. estherae* is more complicated than by other hitherto observed agaonids possessing only thoracic pockets. The act may be divided into several steps easily discernible according to the movements of the fore legs and other parts of the body (fig. 4).

1) Preparatory step (oviposition): The wasp stands firmly on its six legs (fig. 4 I), with the ovipositor inserted into a style. The body is comparatively stationary, except for slight trembling of the tip of the abdomen. The head does not move and there is no biting of the neighbouring stigmata as has been observed in *F. sycomorus* (see Galil and Eisikowitch, 1969).

2) Combing of pollen from pockets to corbiculae: Pollination now starts. The wasp raises its fore legs (fig. 4, II), stretches its neck and head forwards and downwards and the thorax becomes hunched. The fore coxae, which become pressed to the thorax, move to and fro as if performing a combing action. The posture of the body and fore legs is exactly the same as at the end of the pollen loading phase (see above). The shoveling movements of the fore coxae upon the underside of the thorax are also the same, but the direction seems to be reversed from the pockets towards the prothorax. It appears that during this step, pollen is transferred to the intersegmental chamber and coxal corbiculae.

3) Transfer of pollen from coxal corbiculae to arolia of the fore legs: The change in the position of the legs taking place now is very abrupt (Fig. 4, III). The wasp remains standing on the middle and hind legs, and the fore coxae are still pressed to the thorax; but the subcoxal parts of the fore legs starting with the femora, which up to now were hanging passively downwards, fold upon themselves with the tarsi becoming

parallel to the femora and the arolia projecting upwards (fig. 4, III). The combined organ produced by pressing together of the femora and tarsi, with the tibiae connecting them from below, makes several pendulous movements, thereby pressing the arolia upwards and backwards, towards the coxal corbiculae and the intersegmental chamber. As a result of these movements, the arolia reach the coxal corbiculae and the intersegmental chamber, and shovel some pollen out of them. A few pollen grains were detected on the arolia afterwards.

4) Pollination proper: The change occurring now is not less surprising than the previous one. The tibiae and tarsi of both legs bend down without touching the surface (fig. 4, IV). Both legs strike their tarsi on each other as if shaking off something onto the stigmata below. This movement is most probably the depositing of pollen grains on the stigmata, that is, pollination. At least during the entire process, no other movements were observed which could be interpreted as being the pollination act itself.

In contrast to pocket loading during which large flakes of pollen are transferred and shoveled into the pollen pockets each time, pollen unloading is effected gradually by installments, so that only a few pollen grains are extracted from the corbiculae and deposited on the stigmata at the end of each oviposition episode. Hence, the pollen loads of a single wasp may suffice for pollination of a great number of flowers.

#### DISCUSSION

It must be borne in mind that in spite of the use of the term "corbiculae" for the coxal pollen organs of *Blastophaga*, these corbiculae are very different from the similarly-termed organs of bees, not only in location and structure, but also in function. The pollen carried in the corbiculae of bees is destined for the feeding of larvae. In the most evolved types, as in the honey bee *Apis mellifera*, the pollen accumulated in the tibial corbiculae, is slightly wetted by nectar so that a sticky mass is produced which is no longer suitable for pollination. In bees such as *Andrena* and *Halictus* on which the accumulated pollen remains powdery, pollination may occur only accidentally. On the other hand, in most agaonids, the pollen loaded in the corbiculae and in the pockets is not used for nutrition, either for the adult wasps or for the larvae. Its sole purpose is pollination. Unlike pollination by bees, pollination in *Ficus* is carried out deliberately and not as a by-product of other activities.

In the pollinators of *F. costaricana* and *F. hemsleyana*, the structure of the pollen organs is comparatively simple. Due to the absence of a complete cover, the pollen pockets are not opened for loading and closed afterwards, as in the pollinators of *F. religiosa* and *F. sycomorus*. On the other hand, the behaviour of the wasps becomes more complicated, since the coxal corbiculae are used as shovels, in addition to their role as pollen containers during transport and as temporary pollen repositories during pollination.

It is likely that the description of the pollination process in *F. costaricana* and *F. hemsleyana* is typical not only for the New World *Urostigma* species, but also for many of the Old World species of the same section. However, no information is as yet available on this point. *B. quadriceps*, the pollinator of the only Old World *Ficus* of the *Urostigma* section hitherto studied, is exceptional in terms of the structure of the pollination apparatus and behaviour during pollination. In contrast to most pollinators

of *Urostigma* figs, *B. quadraticeps* lacks coxal corbiculae and its pockets are closed organs.

The study of pollination in the Central American *Urostigma* clearly shows that the different *Ficus* pollinators which, at first sight, appear quite similar to each other, are actually far from uniform. Superimposed on the general resemblance, there is considerable variability in structure and behaviour of the wasps in the different sections of the genus *Ficus* and sometimes also in species of the same section. Hitherto only very few species were studied in some detail. It is worthwhile to extend the studies of pollination ecology to other sections and to new localities so as to obtain a broader view of the evolution of the interrelations between the figs and their pollinating wasps.

#### ACKNOWLEDGEMENTS

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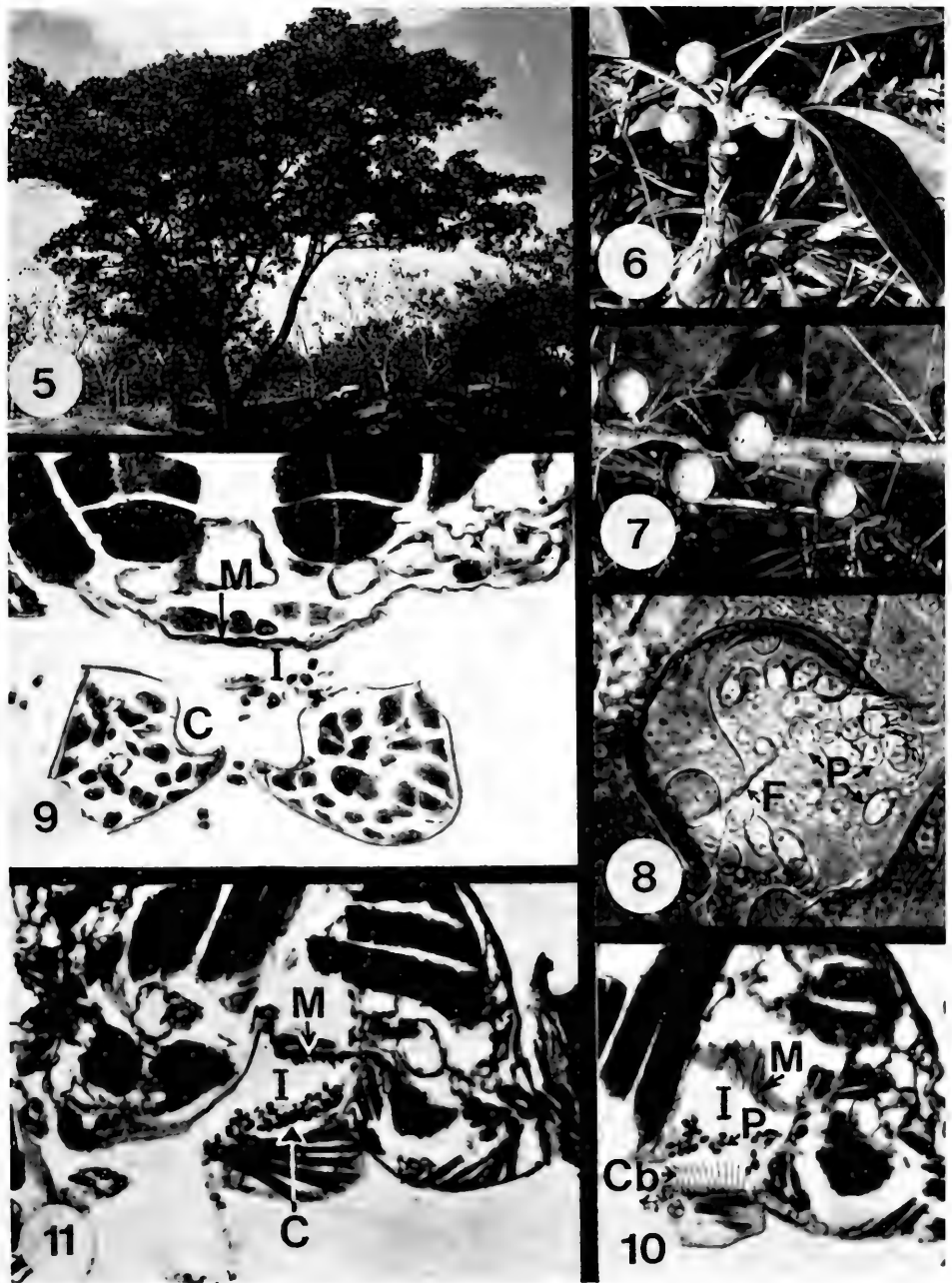


Plate 1. Fig. 5. Tree of *Ficus costaricana* in San Jose. Fig. 6. Branch of *F. costaricana* bearing female phase (B) figs (x 0.5). Fig. 7. Branch of *F. costaricana* bearing male phase (D) figs (x 0.4). Fig. 8. Ventral view of the pollen pocket of *Blastophaga estherae*. F, flap. Fig. 9. Cross-section through the thorax of *Blastophaga tonduzi* at the intersegmental chamber (I), showing fore coxae (Cx) with the corbiculae (C) and membrane (M). Fig. 10. Nearly median longitudinal section of the thorax of *Blastophaga tonduzi*, showing the intersegmental chamber (I) with pollen grains and fore coxae (Cb) with comb. M, membrane. Fig. 11. Inner parasagittal section of thorax of *Blastophaga tonduzi*, showing intersegmental chamber (I) with pollen grains and median section of coxal corbicula (C)

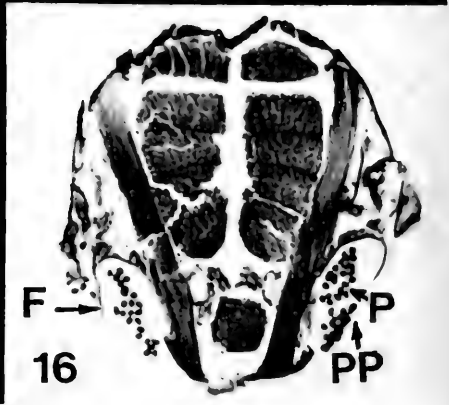
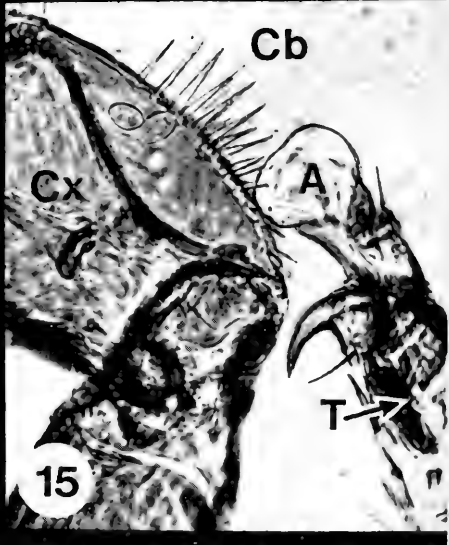
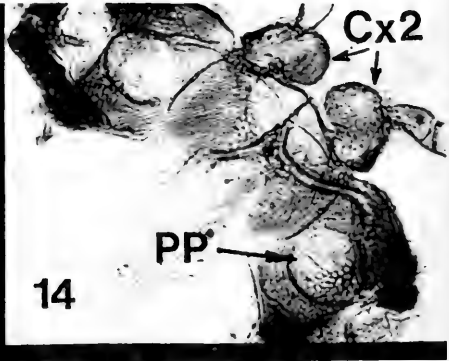
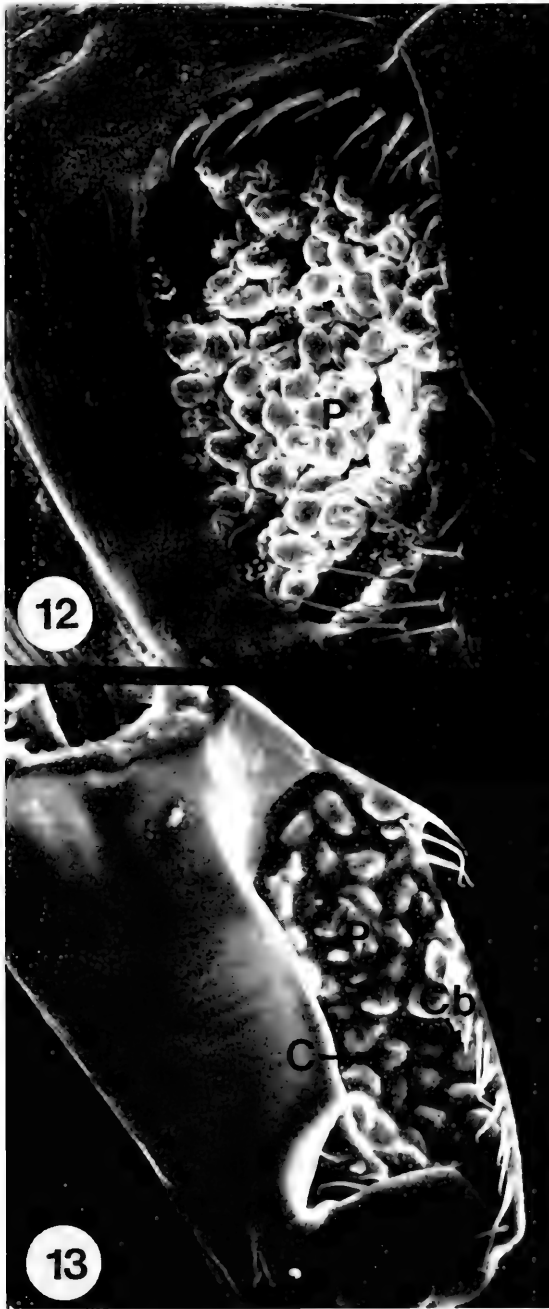


Plate 2. Fig. 12. Scanning electron micrograph of pollen pocket of *Blastophaga tonduzi* (x 470). P, pollen grains. Fig. 13. Scanning electron micrograph of coxal corbiculae of *Blastophaga tonduzi* (x 470). P, pollen grains, C, corbicula, Cb, comb. Fig. 14. Ventral view of mesothorax of *Blastophaga estherae* showing pollen pockets (x 100). Cx, coxae of mid legs; PP, pollen pockets. Fig. 15. Coxa (Cx) and arolium (A) of folded fore leg at pollen extraction, step 3 of pollination act (x 300). T, tarsus. Fig. 16. Cross-section through mesothorax of *Blastophaga tonduzi*, showing pockets (PP) with pollen grains (P) (x 120). F, flap

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## INHOUD

G. THOMSON. — Geographical variation of *Maniola jurtina* (L.) (Lepidoptera, Satyridae), p. 185—226, Pl. 1—2.



# GEOGRAPHICAL VARIATION OF MANIOLA JURTINA (L.) (LEPIDOPTERA, SATYRIDAE)

by

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## ABSTRACT

The form and geographical variation of the male genitalia of *Maniola jurtina* are described and the distribution of the various types encountered is examined. An analysis of the structure is combined with a close examination of the possible evolution of the species. The morphological and genitalia correlations are studied, forming the basis of a revision of the sub-species and geographical races of *jurtina* in which two new sub-species are described.

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## 1. INTRODUCTION

Possibly there is no more familiar butterfly species than the Meadow Brown (*Myrtill* in France, *Ochsenaug* in Germany, *la Loba* in Spain, *Altmän Slättergräsfjäril* in Sweden and *Bruin Zandooje* in Holland) nor one which is more welcome, heralding the appearance of summer, at least in central and northern Europe. In spite of this (or perhaps because of it) a full understanding of the species has evaded the few specialists who have given it some attention, the consequence, no doubt, of lack of material or, more commonly, a lack of objectivity in assessing the relative value of *jurtina* characteristics. Work in some major areas has still to be begun, notably larval variation and host plant associations, cytology, temperature and humidity effects and the genetics of most of the wing markings.

As much taxonomically important information on the species was collected (Thomson, 1969) to serve as a basis for further study, but the shortcomings of the resulting paper were no doubt as well known to the author as to anyone. Work from that time continued with increased enthusiasm to such an extent that, with the acquisition of a number of representative series, several long unresolved problems have now been tackled and to a great extent these have been solved. The appeals of Lempke (1935) and Pionneau (1936) for a study of the French *jurtina* were not taken up by any entomologist in or out of that country. Now, thanks to the generosity and co-operation of a number of French colleagues,

what I consider to be a satisfactory organisation of the French races of *jurtina* has been completed. In other regions such as north-west Spain, north Africa and even Iran, a much clearer picture than that which existed before has been built up.

Without doubt, many of the answers came directly or indirectly from a study of the genitalia. This work, inspired by that of Dr. L. G. Higgins, was both time consuming and extremely rewarding. What originally seemed to be an enigma, namely the apparent lack of correlation between the genitalia and known phenotypes, turned out to be the key to an understanding of the geographical forms of *jurtina*. It is, perhaps, rather surprising that so little notice has been taken of the work of Le Cerf (1912, 1913) on the genitalia of the species. Although it is nearly sixty years since his details were published of the differences between the male armature of the eastern part of the butterfly's range (*persica* and *ghilanica*) and what he called "*jurtina*", "*hispulla*" and "*fortunata*", authors of countless papers and articles in the entomological literature continued to report "form *hispulla*" from the eastern part of the species range. However, even Le Cerf was deceived by the fact that the material he considered to be *jurtina* came from an intermediate region and, had he examined the genitalia from British or east-Swedish insects, he would have indeed been surprised by what he saw. In fact his *persica* genitalia were of the typical eastern type (usually called *jurtina*).

Muschamp (1915) observed that the genitalia of what he called *jurtina* and the southern European *hispulla* Esper differed from each other, although his record of the discovery was decidedly misleading:

'.....I am inclined to believe that the valve is not exactly the same in the southern var. of the species; the valve of *hispulla* is blunter and more squared off in almost every case.....'

In the first instance he did not say from where in the "south" his material came, which, in the light of recent investigations, would render such details essential and, secondly, because of the form of the valve it is difficult to know what he meant by "more squared off". Nor does his illustration help as he failed to say whether or not the drawing of the *jurtina* armature (which I suspect derives more from imagination than science) represents the "southern var."

So the situation remained until 1950, when Professor Gustaf de Lattin (1950) claimed for *hispulla* specific rank. Furthermore, he realised that the Turkish insects were not a *hispulla*-form and that *hispulla* was restricted to the western Mediterranean. H. de Lesse (1952) restated de Lattin's views separating *hispulla* as a good species and illustrating the structure of a specimen from Seine et Oise (France) as *jurtina* which, being of what had come to be known as the *hispulla* type, showed that even he did not fully understand the nature of the valve variation. De Lattin (1958) published additional information in the form of a distribution map, but the limits of the ranges of the valve types do not correspond with what has since been found.

Details of the supposed distribution of the genitalia types were given by Bernardi (1961, 1966) who confused the issue somewhat as he obviously did not fully appreciate the individual variability of the structure and, having based his results on only a few mounts (probably only one or two — although he does not say), came to some rather strange conclusions regarding speciation in the genus *Maniola*. The scientific value of his work on the butterfly is so reduced by his inadequate sampling that it will be necessary only to deal with certain aspects of it in the relevant sections of this paper. Bernardi

believed that the distribution of *jurtina* (*bispulla*) extended from the Canary Islands and North Africa through the Iberian Peninsula to south France and including the Balearic Islands, Corsica, Sardinia, Sicily and Malta. The remainder of the species range, and also Corsica, he said, was populated by the species *janira* with the exception of that occupied by *megala* which he considered to be distinct.

Important and extensive work was recently undertaken by Higgins (1969) who claimed that the range of the western or "old *bispulla*" genitalia was much more westerly and northern, than had been presumed, extending from the Canary Islands, through north Africa, Sicily, Corsica, Sardinia, south and west France to Great Britain. The eastern (*jurtina*) type, he reported, was found in Finland to Austria, Italy and eastwards. Between the two regions he found an area in which they meet and fuse.

Dr A. F. Tauber (Vienna) has recently studied the species in "the east" (1968, 1969, 1970) and his work has raised some interesting questions, but, like Bernardi, his samples were inadequate although there are indications of another zone of secondary intergradation in Turkey. A paper on this subject is in preparation.

Clearly, it was necessary to find out more about the true nature and extent of the variation of the *jurtina* genitalia, particularly relating to the known geographical forms of the species. My previous work on the species completely ignored the structural variation of the genitalia, so from 1969, until the time of writing, I have undertaken an extensive examination of the structure throughout its range, from Finland in the north, to the Canary Islands in the south and from the Irish Arans in the west, to the southern shores of the Caspian Sea in the east. This paper is the result of that work. In it I have related the structural variation to that of the known phenotypes. In the taxonomy I have gone to much trouble to avoid name changing and the proliferation of taxa in this already "over described" species. Some older taxa (e.g. *mirtyllus* Fourcroy) have been resurrected to this end. Possibly the most controversial arrangement is the acceptance of Verity's decision about the type locality of *jurtina* and thus the typical sub-species which has so often been cited as Sweden. This has necessarily meant the reintroduction of the name *janira*. However, some specialists have over the years accepted the type locality restriction of Verity, including De Lattin, Bernardi and no less an authority than Hemming (1958), so, in this respect, I am not proposing an entirely original solution. Furthermore, it leaves the name *fortunata* Alpheraky available for the Canary Islands form, should this be considered necessary. The total taxonomic change thus consists of the reintroduction of two 'older' taxa, the sinking of a single taxon as a junior synonym and the description of two new subspecies.

Perhaps more than with any other familiar species *jurtina* has suffered from a galaxy of taxa unaccompanied by adequate descriptions. I have, therefore, included detailed descriptions of races where these are not already readily available or where the original or subsequent descriptions are misleading.

Acknowledgement is due to so many people who have helped in some way with this work that I can only mention a few and trust that in the case of the others my appreciation is understood. Special thanks go to R. F. Bretherton, E. C. Pelham-Clinton, R. L. Dickson, T. G. Howarth, J. H. Robert, A. Valletta, the Royal Scottish Museum and the British Museum (Natural History) for the supply and access to specimens and information, also A. Finnie who took most of the genitalia photographs for this paper.

## 2. METHOD AND MATERIAL

### Slide mounts

Because of the structure of the male valve in the *jurtina* group it is somewhat difficult to make more than very general comparisons of its shape, size and proportion by the usual optical methods. The structure has been described by Muschamp (*loc.cit.*) as very irregularly shaped for a Satyrid, being "made up of concave and convex hills and valleys". I have attempted to rationalise the dimensions of the structure by the usual three-dimensionally mounted genitalia, but without success. It was discovered, purely by accident, that a much simpler approach to the problem would yield the results for which I was searching. This method is now described.

The male genital armature of *jurtina* is comparatively exposed. Removal of the valve — the right valve was used in this research — can be simple and quick from both fresh and dry specimens, although both have minor drawbacks which require some care to be taken. These are, however, of no real significance if one is aware of them. If the specimen is freshly killed, light pressure applied to the sides of the abdomen will expose the genitalia. The valve to be removed can be pulled out further with fine pointed forceps, when it will normally remain in an exposed position. A pair of fine dissecting scissors are inserted, one blade between the two valves, and the other between the valve to be removed and the hairy valve cover as far to the rear of the structure as possible. The removed valve should be handled as little as possible and it is best if it falls directly onto the slide. When the desired position on the slide is achieved a cover slip is placed on it without pressure, this being applied only when the two sides of the cover slip are taped. Mounting the valve from fresh specimens has the disadvantage that the liquids which exude from the structure can be troublesome if they obstruct vision, but it is seldom serious in extent. To remove the valve from a dry specimen a pair of very fine pointed forceps are inserted closed between the two valves which are carefully separated. The valve to be removed is gripped firmly by the forceps and gently broken off as far back as possible. This will nearly always be at the valve's junction with the ninth segment (*vinculum*). It is mounted on the slide in the same way. Mounting dry has the disadvantage that occasionally the structure cracks when pressure is applied to the slip. However, as with the mounting of fresh individuals, the wastage rate is very low.

The large number of mounts required for the study of the valve variation could have been undertaken only by this method in reasonable time. About thirty or forty preparations can be made in an hour.

### Photographic

The use of a photographic enlarger to make permanent records of temporary mounts of the androconial scales in *Pieris* has already been suggested (Thomson, 1970a). A much more sophisticated approach can be used with valve mounts giving remarkable results if care is taken with focus and exposure. Photographic prints have the advantages that they can be examined under any conditions without the microscope; several can be compared at the same time and they take up much less storage space than conventional mounts. Furthermore, it will be seen in the main part of this paper that accurate measurements can easily be taken from these "micro-photograms" in a way which would be



difficult or impossible otherwise. In the case of a Satyrid valve the enlargement required is small,  $\times 12$  being convenient for most work, although  $\times 18$  would produce better results if a greater degree of accuracy was required. The enlarger is set using a transparent or translucent scale so that the desired magnification is uniform and repeatable. The focus is carefully checked. This will remain constant provided the mounts are on the same thickness of slide. For most work any orthochromatic bromide paper (grade two or three) is adequate. The criterion is whether or not details other than the outline of the structure are required. Occasionally the dorsal edge of the *jurтина* valve is 'turned over' and a false impression of the shape would be obtained if this went unobserved. The chitinous exoskeleton is of a reddish colour, making longish exposures necessary with orthochromatic materials, thus losing some of the internal detail and the 'hairs' which are so characteristic of the structure. This can be overcome by using panchromatic paper (e.g. Panalure of Kodak), although one must work in darkness or inconvenient panchromatic lighting conditions. Using bromide paper produces a white image on black, but this could be reversed by projecting first onto film, using the negative to produce a positive print. However, this adds nothing to our knowledge of the valve and I do not see any real value in this form of reversal unless considerable magnification is required.

In spite of the variability of the valve large samples as are necessary when studying the wing markings in the species are not necessarily essential, as the nature of the population is usually clear after looking at only a few mounts. This is not so in the zone of secondary intergradation and, although a sample of ten to fifteen was considered adequate for pure eastern and western types, a larger number of twenty or thirty had to be measured if considerable variation was detected.

### Collection and samples

The material came from a large number of localities throughout the *jurтина* range, but very few from its eastern part from where specimens are, for political or geographical reasons, very difficult to obtain. A special sample series was taken on our trip across France in 1970 (Thomson, 1970c) to correlate east-west longitudinal direction to the change in the valve form. Together with the material, collected by colleagues and friends in France and Belgium, it was possible to plot the change in both the north and the south of that country. In total in excess of eight hundred male valves were mounted and measured from eighty nine localities, while about ten thousand *jurтина* were examined, many in great detail, in the preparation of this paper. The specimens were in my own collection, private collections and in the Royal Scottish Museum, Edinburgh.

## 3. THE MALE GENITAL ARMATURE

### Description

An exhaustive description of the male genital armature would be superfluous here, as this can be found elsewhere (Le Cerf, 1912, 1913; De Lesse, 1952). Variation occurs in the brachia (gnathos), the aedeagus and to a greater extent in the valves tending towards one of the main forms in Europe and the Near East with an intermediate ("blend") zone. A third form is found in Iran and the extreme east of Turkey. These types will be called

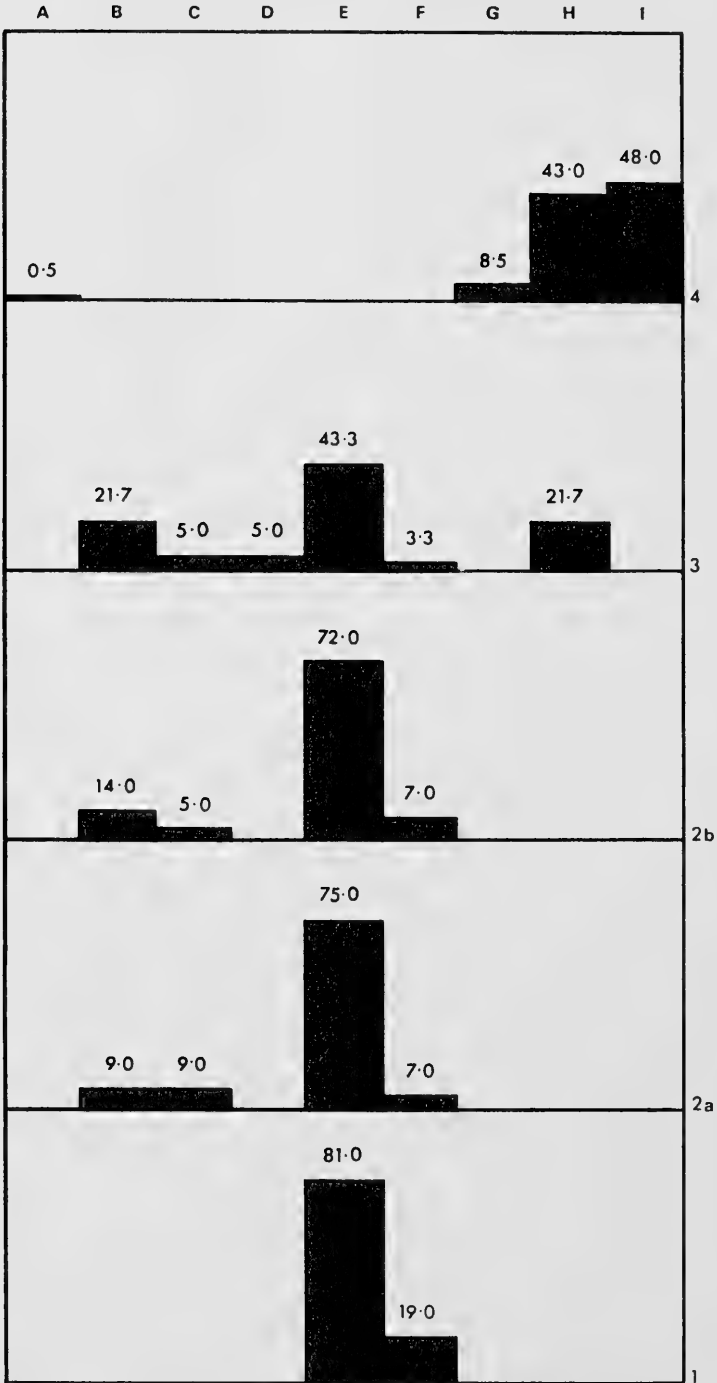


Fig. 1. The relative proportion of valve types in *Maniola jurtina* in: 1. south west (North Africa, Spain, Portugal, Balearic Islands, Malta and southeast France); 2a. west France; 2b. Britain; 3.

Fig. 1. The relative proportion of valve types in *Maniola jurtina* in: 1. south west (North Africa, Switzerland, Germany, Hungary, U.S.S.R., Italy, Crete, Corsica, Finland, east Sweden). A — relict primitive; B — relict transitional type *a*; C — relict transitional type *b*; D — secondary transitional; E — western type *a*; F — western type *b*; G — eastern type *a*; H — eastern type *b*; I — eastern type *c*

eastern type (*jurtina* sensu Higgins and *persica* Le Cerf) and the primitive type (*ghilanica* the western type (*bispulla* sensu Higgins and De Lesse and *fortunata* sensu Le Cerf), the Le Cerf). It should be noted that Le Cerf's "*jurtina*" is intermediate in character. These three types are figured. For an interpretation of some of the terms which I have used in the following description (see page 23 and 27).

#### WESTERN Type (Pl. 1 Fig. 11).

Brachia markedly swollen at the base to almost twice the width of the "neck" of the uncus. Aedeagus slightly swollen at its extremity. Valve usually moderately large, rarely very large. Dorsal edge moderately long, sometimes very long and nearly always strongly concave. Dorsal process variable but always longer than its width at its extremity, frequently almost pointed or sharply rounded but sometimes with a short flat top. Dorsal edge, dorsal process and distal edge to the distal process smooth and free from irregularities. Ventral edge usually strongly convex and sometimes forming an acute angle with the distal edge.

#### EASTERN Type (Pl. 1 Fig. 10).

Brachia narrow and gradually tapering to their extremity without marked swelling at the base; narrower at the base than the "neck" of the uncus. Aedeagus straight, with little or no swelling towards the extremity. Valve variable in size and proportion ranging from very long (in the south) to very short (in the north). Dorsal edge usually short, rarely strongly concave. Dorsal process very short and broad, nearly always flat-topped and much wider than its height, but occasionally rounded, to form a long convex curve to the distal process. The dorsal edge, dorsal process and distal edge to the distal process more or less irregular. Ventral edge gently convex, only occasionally strongly curved.

#### PRIMITIVE Type (Pl. 1 Fig. 9).

Brachia narrow and gradually tapering to their extremity without marked swelling at the base; narrower at the base than the "neck" of the uncus. Aedeagus straight with little or no swelling towards the extremity. Valve rather large. Dorsal edge usually very short, hardly ever strongly concave. Dorsal process very short and broad, nearly always flat-topped and wider than its length. The distal edge of the dorsal process to the distal process (which is rather long) is decorated with a "fringe", variable in extent, but very irregular outwardly. This fringe appears to be attached to the outer surface of the valve. Ventral edge convex, but only slightly so.

It should be noted that a fringe-like structure is present in some, but by no means most, eastern valves. Although it is likely that this structure is homologous to that found in the primitive type, its manifestation in most cases demonstrates their differences more than their similarities. In the case of the eastern form the position of the fringe on the valve is extremely variable, occurring anywhere from the distal process to the inner edge of the dorsal process, occasionally appearing in other parts of the valve surface and other unrelated areas. While the eastern type valve is more usually without it, the western type sometimes, but infrequently, shows evidence of this unusual feature. The primitive type

always has a fringe which is quite clearly an irregular appendage to the distal edge of the valve.

#### Comparison with other *Maniola* species

It is extremely interesting to relate the form of the genital armature of *jurtina* to the other *Maniola* species: *telmessia* (Zeller), the insular *nurag* (Ghiliani) from Sardinia and *cypricola* (Graves) from Cyprus. In all three species the valve is much closer to the western type, although in *telmessia* there are some traces of an intermediate element. The frequent misconception that *telmessia* lacks the "Jullien Organ" should be cleared up here. These structures are, in fact, always present in *telmessia* but they are much thinner and more easily removed than those in most *jurtina*. Examination under the microscope will reveal, in cases where the genitalia appear to lack the "organ" that they have been knocked off, either in nature, or in the preparation of the mount and the point from which they have been removed will be seen quite clearly. I have encountered one such individual *jurtina* from London. Specimens of *telmessia*, apparently lacking these structures, occur frequently enough, so that Verity described race *telmessiaeformis* as a form of *jurtina* which resembled *telmessia* in all respects, except that it had the "Jullien Organ". The explanation for this is now quite clear. The evolutionary implications of the valve form in these species will be discussed later.

#### 4. VALVE VARIATION

##### Valve types and their distribution

The variation in the shape of the *jurtina* valve is considerable by any standard, yet, in spite of this, it is relatively easy to recognise the primitive, eastern, western and even transitional types when these occur. Furthermore, similar, if not identical, forms occur frequently enough, not only in the same locality but in widely separate areas, so that it has been useful to classify these according to the form of the dorsal process, in order to be able to refer to them later. These main types are figured. The reasons for my use of terms "primitive", "secondary" and "relict" in this context will become clear in the ensuing discussion.

**p r i m i t i v e t y p e** (Pl. 2, Fig. 1) — dorsal process distally edged with an extremely irregular "fringe", usually extending to the distal process and apparently attached to the outer surface of the valve.

**r e l i c t p r i m i t i v e t y p e** Pl. 2, Fig. 2) — more or less similar to the primitive type and distinguished from others by the presence of the "fringe", but the body having an outline more or less like that of the eastern type. (Bernardi illustrates the *janina* type as having a "fringe" or crest attached to the inner surface of the valve. As I have said, this feature is inconsistent in the eastern type and occurs rarely in the western. The irregular dorsal and distal edge should not be confused with this).

**r e l i c t t r a n s i t i o n a l t y p e a** (Pl. 2, Fig. 3 and 4) — dorsal process rather short or short and broadly rounded, with little or no flattening at its extremity.

**r e l i c t t r a n s i t i o n a l t y p e b** (Pl. 2, Fig. 5) — dorsal process very short and almost or sharply pointed.

secondary transitional type (Pl. 2, Fig. 6) — dorsal process long, with a rather broad, flat top.

western type a (Pl. 2, Fig. 8) — dorsal process long, with a more or less rounded extremity.

western type b (Pl. 2, Fig. 7 and 9) — dorsal process long, with a pointed or very sharply rounded extremity, or with a short flat top.

eastern type a (Pl. 2, Fig. 10) — dorsal process distally forming a long convex curve to the distal process. (This is the type found in ssp. *megala* by Bernardi and used as evidence for raising the status of the race).

eastern type b (Pl. 2, Fig. 11) — dorsal process fairly short with a flat or almost flat top.

eastern type c (Pl. 2, Fig. 12) — dorsal process very short with a long flat top.

A long examination of the valve types in localities from which material was available, indicated that the distribution of the eastern and western types broadly coincided with that described by Higgins, although the limit of the western range was rather further east in France and the transitional region probably a little less widespread than previously thought. The only notable point of difference was that the genitalia type in Corsica was transitional and not western. What was considerably more interesting was that there appeared to be a consistent difference between the populations of north Africa, Spain, Portugal and south-east France and those of western France and Britain. The relative proportion of the valve types in the latter group was virtually identical. A histogram showing the proportion of the various valve types in each region is given (Fig. 1). It is worth noting that the composition of the western populations is similar in terms of the relative proportion of each of the western types and that the west French and British samples differ from the southern group in the presence of the relict transitional elements. This distribution of types is also found in the transitional zone where eastern, as well as western forms are found.

The distribution of the primitive type is difficult to ascertain, not only because of the few collections which are made in Iran and eastern Turkey, but also because in this part of the world *jurtina* is both very local and, at least sometimes, quite uncommon. It is almost certain, however, that it is the most restricted of the three main types. It is also unique in the fact that, from the slim evidence available, there is no transitional locality similar to that found between the eastern and western zones. Populations in the East in which this valve type occurs are composed entirely of them.

Although the presence of a primitive type valve as a rarity within the eastern range would seem unlikely, two such forms turned up at Verbier in the Swiss Valais and Cortina d'Ampezzo in north-east Italy, two high altitude localities. The significance of this is increased by the discovery of the relict transitional valves within the western zone. These were first thought to be eastern types, but a closer examination of them, in the light of my investigations as a whole, made it obvious that they were, in fact, indicative of the insect's evolution.

There are, therefore, five main population groups:

1. the south-western — north Africa (with the Canary Islands), Spain, Portugal, the Balearic Islands, Malta, south-east France and probably also Sardinia. In this region the "pure" western genitalia are found substantially free from relict transitional elements.

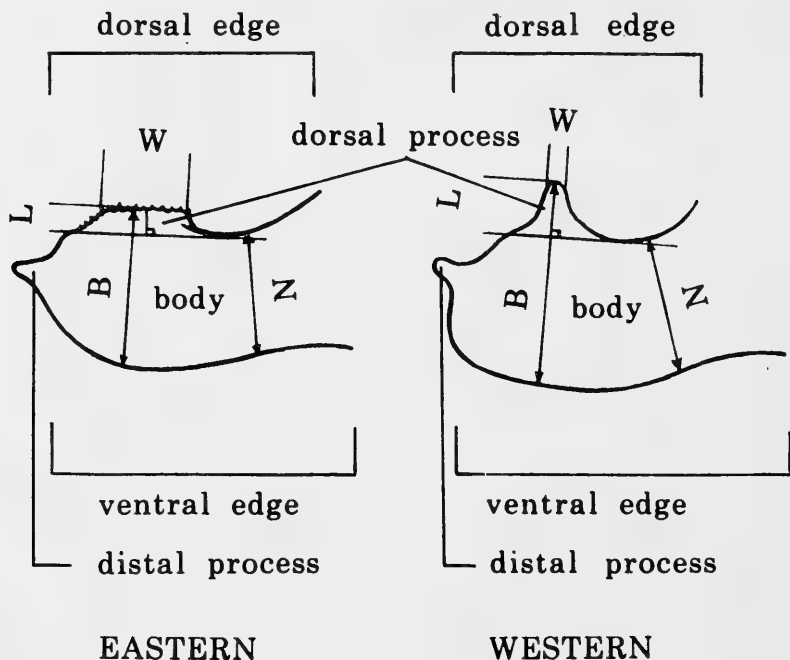


Fig. 2. Diagrammatic representation of the two main *jurtina* valve types, showing terms used and measurement parameters.

By far the most common valve type is the western type *a*, followed by type *b* which comprises about one fifth of the population.

2. the west French and British — France north and west of the Cevennes to Brittany bordering on the transitional zone to the east, and all of the British Islands. Here the relict transitional elements are found as a very small part of a basically western zone.

3. the transitional — west Sweden, (presumably Norway), Denmark, the Netherlands, Belgium and France, east of a line running from the Pas de Calais, just east of Paris to the Franco-Italian border on the Mediterranean coast and Corsica and bounded to the east by the Alps, Jura, Vosges and the Ardennes. In this complex region western, eastern and transitional types occur in more or less equal proportions. Most frequent are the relict transitional, western type *a* and eastern type *b*.

4. the eastern — east Sweden, most of Germany, Switzerland, Italy, and eastward throughout the range of the species excluding the region occupied by the primitive type.

5. the primitive — north-east Iran, the Elburz Mountains and south-west shores of the Caspian Sea, (possibly to) north-east Turkey. Only the primitive type valve occurs.

The distribution of the valve types is shown in Map 1.

#### Explanation of the valve distribution

The *Maniola* species *cypricola*, *telmesia* and *nurag* are so much an integral part of the evolution of *jurtina* that they are considered here as the result of a single evolutionary event. Although no explanation of the ancestry of our insect fauna can be free from doubt or criticism, I can think of no other explanation of the development of these species

that would fit the facts better than that which I am about to detail.

Without the presence of occasional genitalia types which I have called "relict transitional" in the west and "relict primitive" in the east, it would be very difficult indeed to say with any degree of certainty how the present distribution of the valve types came about. As it is, it would be difficult to explain the presence of such forms in such widely separate localities as Scholes (Yorkshire, England), Banstead Downs (Surrey, England), Falais and Bordeaux (France), if it were not that these individuals do, in fact, represent relict elements of a past fauna and that the western type genitalia were more recent than the eastern. Similarly, the presence of what I call the "primitive" valve in the eastern range substantiates this claim and gives us a good indication of the way in which the structure has developed. From this I deduce that the race or races of the mountains of Iran are the oldest surviving ancestors of the insect, from which *jurtina* has come — possibly a montane species. The eastern races which possess the primitive valve, fly at an altitude of about two thousand meters and frequently well over it. It is worth noting that the relict primitive valves so far found were from montane localities, Verbier, at 1500—1750 m (probably the highest locality in western Europe) and Cortina d'Ampezzo, at 1250 m. There are few places in the western range where *jurtina* flies at high altitude, but it can be taken at 1650 m in the Atlas Mountains in Morocco. The highest western type locality in western Europe, from which I have specimens, is Mt. Ventoux, Vaucluse (France) taken at 1250 m. The Col du Tende (Alpes Maritimes) at 1450 m is a transitional locality.

If we accept that the species has come from the east, we are faced with the question of how *telmessia* and *cypricola* have evolved there with western type genitalia, but I believe that this gives us the key to the solution. I have come to the conclusion that *jurtina* travelled westwards in two streams, originating either east of the Caspian Sea, or, what is more likely, from the area we now call Iran. The more northern migration moved westwards, either north of the Caspian Sea, or from Iran north over the Caucasus then westwards. The other took the southern route through Iran. The structure at this time could well have looked much like the primitive type we now know. While the northern stream extended its range very slowly westwards evolving little, the southern stream, favouring the warmer conditions, probably spread quickly through Iran, Turkey, south Greece (and the land mass now remaining as the Greek Islands), Sicily, Corsica, Sardinia, north Africa and the Canaries to Spain, west France and Britain evolving very rapidly to a type much like the relict transitional. However, an isolated group established itself north of the Elburz Mountains — what we now call *ghilanica* — retaining the primitive valve and genitalia. When Cyprus, Rhodes and Lesbos were split from Turkey and Angiastri from Greece, the western type valve had almost fully developed. The northern stream continued its slow westward spread, probably interrupted by frequent glaciations, to the Alps, south into Italy and north to Scandinavia. A branch which had already evolved the eastern type genitalia, swung into Greece and across the Bosphorus to Turkey. Here it met and dominated the western type, except for a few individual populations which had developed to such an extent that they were able to retain their identity as *telmessia* and in another form, as *cypricola*. This stream might well have also met the relict races of north Iran, but these were able to survive to this day. Meanwhile, the southern stream had evolved the western characteristics particularly in Spain and north Africa where they were isolated by the Pyrenees. A most important event then took place: the western types spread eastwards, meeting what had now developed into the eastern types which were moving westwards,

forming a zone of secondary intergradation in the region in which we now find the two types and intermediates flying together.

*Maniola nurag* could well have evolved sympatrically with *jurtina* on Sardinia or it could have been the result of two waves of migration, the first having evolved specifically, before the second arrived.

Although this explanation assumes that there was access to the west and to the north of the Black Sea (possibly over the Caucasus) and also through Turkey, the Aegean Island area, Sicily, probably at a time when peninsular Italy did not exist, Sardinia, Corsica, north Africa, across the Strait of Gibraltar, to the Iberian Peninsula, France and Britain, it does largely follow the routes of the Siberian and Oriental migrations. The situation in Corsica introduces a problem as the island would have to have been connected to continental Europe and Sardinia, something about which morphogeologists disagree. However, morphological comparisons confirm these suggestions very well. I suggest that *nurag* is the furthest development of the *jurtina* ancestor. This is based on the fact that the valve is purely western in form, the fulvous on the upperside of the butterfly is very extensive and it was thought that it was the only *Maniola* species capable of producing a second brood, although only under artificial conditions (Simmons, 1930), but I successfully produced a brood of *jurtina* in February 1973, from eggs laid in August 1972, simply by providing the larvae with a continuous supply of their foodplant. This would also explain the similarities between the south-western races and those of Britain and support my claim that the British races are closer to each other than to the *jurtina* of the low Countries and Sweden.

## 5. NUMERICAL INTERPRETATION OF THE VALVE FORM

### Measurement of the valve

The necessity for finding an objective approach to comparing *jurtina* valves might not be obvious as, excepting a few intermediates, it is possible to say whether a specimen has a valve of the eastern or western type without much difficulty. The nature of the eastern, western and transitional distribution in western Europe is such that a much more intensive study of the structure's form could yield valuable information about each of these zones and their relationships to one another. It is important to remember that the valve of the species is unusually variable in shape, size and proportion. The overall size of the valve varies quite independently of the size of the insect of which it is part. Fig. 2 shows a diagrammatic version of the "typical" eastern and western types which roughly represent the two more widespread forms occurring in the species. The long "hairs" which are characteristic of the structure have been omitted for clarity. This outline is only a little different from what would be seen in a conventional genitalia mount, as the whole structure has been slightly flattened. Normally this distortion is uniform in all mounts made: abnormal distortion can be easily detected by the presence of cracking or overlap. For the purpose of this work various parts of the valve have been named and this is indicated on the figure. Also, conveniently abbreviated terms for the parameters from which measurements have been taken are given.

Measurements were taken across the narrowest part of the body from the dorsal edge to the ventral edge (N), also across the broadest part from the top of the dorsal process to the ventral edge (B). The method of determining the length of the dorsal process (L)



and its width (W) is described later. At first it was thought that the difference between B and N would give an accurate measurement of the length of the dorsal process, but it was soon realised that the occasional sample in which the valve was markedly tapering distally gave quite misleading figures. Neither N, nor B gave useful data on their own and were abandoned as part of the analysis. Similarly, the distal process, even within the same locality, was so variable that it was considered an unusable character.

The simple difference between the process length (L) and the process width (W) was by far the most useful algorithm giving consistent results, although it presented a problem of accurate measurement. For the most part it was a simple matter to measure W as the dorsal process usually "squares off" slightly at its extremity. However, the occasional specimen turned up in which it was so rounded that an educated guess was the only answer. Fortunately, this nearly always happened in the western type when the process was long and narrow and the effect of such individuals on the result can be considered negligible. More difficult to describe than to measure is the method by which the process length was determined. The edge from the distal process to the top of the dorsal process, which is basically concave, nearly always has a slightly convex part indicating the start of the dorsal process. A line is drawn at a tangent to the convex dorsal edge to this point. L is line. Occasionally no convex section can be detected in which case the line is drawn from mid-way between the distal and dorsal processes.

All figures given for the valve dimensions, are in millimeters, taken from an enlargement of twelve times. The actual size can, therefore, be simply calculated if comparisons are to be made between my figures and those taken from a magnification, different from that used throughout this work.

Extensive examination and measurement of the structure showed that the algorithm L-W gave in numerical terms an accurate representation of the nature of the valve.

When  $L - W > 0$  the valve is of the western type.

When  $L - W < 0$  the valve is of the eastern type.

The reason for taking a difference rather than a ratio was purely for convenience in working with smaller figures and positive and negative values, representing the western and eastern types, respectively. However, as will be seen later, the ratio  $\frac{L}{W}$  was used in the calculation of variability co-efficients.

#### Statistical

The following conventions are used:

F = L - W (i.e. the difference between the process length and the process width)

$$R = \frac{L}{W}$$

n = sample size

It was desirable to calculate from the data the following values for each sample:

- 1) the mean (M)
- 2) the range (r)
- 3) the standard deviation (sd) being the square root of the sum ( $\sum$ ) of the squared deviations (d) from the mean (m), divided by n

$$\text{i.e. } sd = \sqrt{\frac{\sum d^2}{n}}$$

- 4) the co-efficient of variability (cv) being the standard deviation expressed as a percentage of the mean. For this the ratio (R) was used

$$\text{i.e. } cv = \frac{\text{sd (of R)} \times 100}{m}$$

## 6. STATISTICAL STUDIES

### General distribution patterns (Map 2)

The measurement and analysis of resulting data from eighty-nine localities was not without its problems. Not least were the localities in which the values of F for the samples did not fit a developing pattern, or one which was anticipated. Such were places like Scholes (Yorkshire, England) (0.5), Coleraine (Co. Derry, Northern Ireland) (0.9) and Rabat (Morocco)(1.3) which gave remarkably low figures and Serignac (Gard, France)(2.5) and Cramond Island (Scotland)(2.3) which gave unusually high values. At first these results were suspected and in such cases checks were made with a larger sample which invariably confirmed the original figure. The presence of the rather low figures in the west can be explained as another manifestation of the relict theory which I proposed for the occurrence of relict types in the west. Admittedly, the rather high values present us with an anomaly.

The 1.8 recorded for Santander in north-west Spain might at first seem incongruous until one considers the geographical position of the area, cut off by the Cantabrian Mountains to the south. This area is inhabited by a number of species which have developed distinct characteristics. In the case of *jurina* the form there resembles that of south-east France more than anywhere else in Spain. This has been confirmed by the form of the genitalia.

In general, however, a remarkably clear pattern resulted and there was an extremely good correlation between the figures for adjacent localities. This was tested by comparing two samples from Surrey, one from Banstead Downs and the other from Ashted Heath. In the case of the Ashted sample the value of F was 1.1, while that of Banstead was only 0.2 different at 1.3. In general, the value of F increased to the south and west and decreased to the south and east, reiterating what was already observed in the broadening out of the transitional zone in the north, with a greater gap between the eastern and western forms in the south than in the north.

### West - east analysis and the nature of the transitional zone

To determine more accurately the nature of this east-west variation, a special sample study was made of the value of F in two series of selected sites, to relate the change in the mean value of longitudinal direction. In addition to the mean the standard deviation and range were used to build up a picture of the variation. In the south it was possible to use a set of eight samples from localities lying along a straight line from Santander to the Col du Tende ranging from 43 to 44 degrees north. In the north, the west - east line ran from Falais (Calvados) to Verbier, taking a southern turn at its eastern end and ranging from 49 to 46 degrees north. The necessity for using material from localities along this line was in spite of the fact that a special effort was made to collect samples for this purpose. It would have been desirable to continue the set of figures further into the

eastern range, particularly in the south, but material was not available.

The figures which resulted from the measurements and calculations are represented in the population range diagrams (Fig. 3 and 4). Therein can be seen the very real differences between the east-west transition in the north and south. Not least of these is the consistently higher variability in the north. Indeed this was so great that if one *sd* was represented on either side of the mean it would have extended beyond the range in some cases. Furthermore, the range itself was greater in the north, in some examples plummeting to a very low negative value. In the south the range never dropped below zero at the minimum end of the scale. More important, perhaps was the difference in the nature of the two sample series. The northern transition is characterised by an erratic but definite decrease in the mean west to east, accompanied by an increase in the standard deviation, while in the south there is virtually no change in the mean west to east, nor is there any real change in the *sd* from Santander to St. Valier, thereafter followed by a sudden drop in the mean and increase in the variability.

Another illustration of the broadening of the transition zone to the north can be seen if we relate the drop in mean to the west-east distance in both samples. Taking the distance from the most easterly western sample to the eastern limit of the transition zone, we find that in the north the drop from Feucherolles (Seine et Oise, France) to Besançon, a distance of 400 km is 1.0. This compares with the distance of 60 km from St. Valier to the Col du Tende where the drop in mean is 0.7. It is difficult to say whether or not there is an eastward decrease of the mean within the transition zone, but indications are that this is so. One single point of interest is the sudden drop in variability at Verbier, indicating the apparent isolation of the eastern type from even the transitional zone at this point. The *cv* at Verbier was only 20 which compares with between 30 and 40 for localities within the western range and 80 to 90 for the transitional localities. The *cv* of 123 in the Cretan samples was unexpected, however.

#### The effect of altitude

Adequate material to determine the effect of altitude on the valve was not available and only tentative remarks can be made from the samples examined. No two adjacent localities which varied significantly at altitude were studied. Verbier (1500 - 1750 m) and Ivrea (800 m) are more than a hundred kilometers apart and Cortina d'Ampezzo (1200 m) is half that distance from Bolzano (262 m). These were the closest localities from which any indication of the altitude effect could be obtained and from these it would seem that it had little or none. Rather than altitude having an effect on the valve's structure as such, it has probably acted more as a means by which certain primitive relict elements have been retained.

### 7. THE NATURE OF THE RACES OF *M. jurtina*

#### Isolating mechanisms

In spite of the widespread and largely continuous distribution of the larval foodplant of *Maniola jurtina* (*Poa* sp. and other grasses) over the greater part of its range, the insect forms very restricted populations often quite distinct from each other. *M. jurtina* is completely non-migratory, even on a local scale (Ford, 1945). Consequently, the geographical features creating isolation need not be substantial and often a short stretch

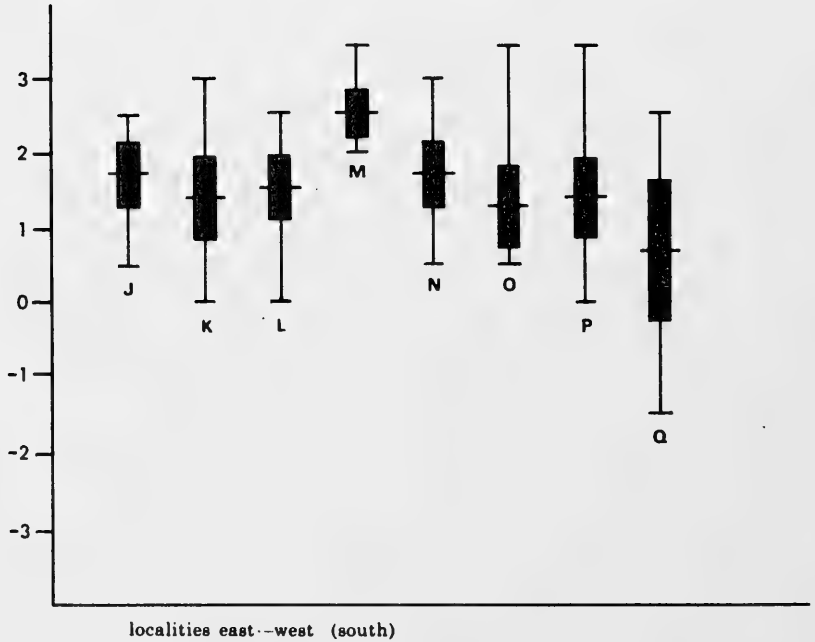
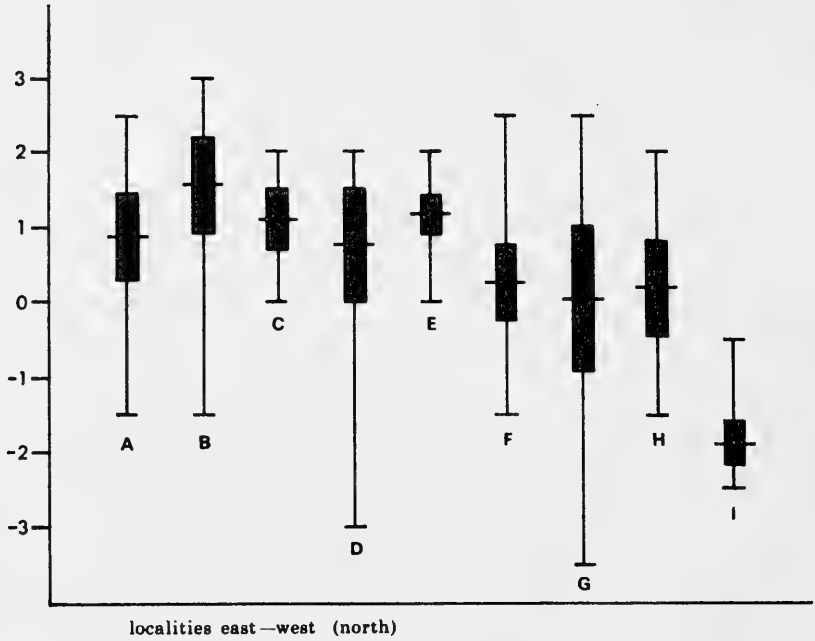


Fig. 3 and 4. Population range diagrams showing for each locality the range (thin vertical), 0.5 sd on each side of the mean (thick vertical) and the mean of F (horizontal). A. Falais, Calvados. B. Guernanville, Eure. C. Le Quesney, Seine Inférieure. D. Beauvais, Oise. E. Feucherolles, Seine et Oise. F. Chalôns s/Marne, Marne. G. Chaumont en B., Haute Marne. H. Besançon, Doubs. I. Verbier, Valais. J. Santander, Spain. K. Oloron, Basses Pyrénées. L. Brassac, Tarn. M. Serignac, Gard. N. Fountain de Vaucluse. O. Digne, Basses Alpes. P. St. Valier, Alpes Maritimes. Q. Col du Tende, Alpes Maritimes

of unsuitable terrain, wide rivers or estuaries are sufficient to provide these conditions.

As has been mentioned, *jurtina* in most of its range is a low to moderate altitude insect, being local over one thousand metres and very rare over fifteen hundred. This means that the Alps and Pyrenees completely cut off the vast number of populations which exist on either side of these great mountains. It is interesting to note, therefore, that the races to the north and the south of the Alps are far less different from each other than the races to the north and the south of the Pyrenees. However, as we have seen, the Alps, Jura, Vosges and to a lesser extent the Ardennes have played a major part in creating the conditions which have produced the eastern and western type ranges.

The evolution of distinct phenotypes as a result of geographical features is to be expected where conditions permit. The discovery of sympatric evolution — that is the development of a distinct local form or race without geographical isolation — by Ford (1964) introduces a whole new dimension into the study of *jurtina* races. So far this phenomenon has not been investigated fully and it is not possible at this stage to see what effect, if any, this could have had on the evolution of *jurtina* races. However, the dimorphic females which occur in some localities might be associated with this, although to suggest such a thing is pure speculation. Sympatric evolution in this butterfly is all the more remarkable in the light of the many records of *jurtina* found copulating with other species, not only those related to it, *Pyronia tithonus* (L.) and *Aphantopus hyperanthus* (L.), but also species of a different family, *Aglais urticae* (L.), or even superfamily, *Zygaena filipendulae* (L.). It causes one to wonder what are the factors creating the sympatric situation.

It was only recently that another phenomenon was discovered in *jurtina* (Thomson, 1971 and Dennis, 1971). This I called "temporal sub-speciation" and is the occurrence of what gives all indications of being bivoltinism in what is virtually certain to be a univoltine insect (Verity, 1953). In some parts of its range, notably in the south of France, Malta and a single locality on the Isle of Wight (England) *jurtina* emerges normally and has a more or less typical flight period followed, after a break, by a "second emergence" of fresh specimens. The late individuals display quite distinctive characteristics. They are usually smaller with a smaller apical eye spot in the female and both sexes have more extensive fulvous colour, particularly in the male. Most characteristic of these *jurtina* is the considerable darkening of the underside hindwing in the female, particularly with a concurrent increase in the striae. Since publication of my paper on the discovery of this almost unique situation [it has been noted in the moth *Deuteronomos erosaria* Schiff. (Bretherton, 1955)] I have had the opportunity of examining Maltese specimens of the late emergence and these confirm what had already been observed in the Isle of Wight and south of France. The evolutionary implications of this form of temporal sub-speciation are far reaching and it deserves very close study by evolutionists.

It is likely, therefore, that *jurtina* has been subjected to two main divisions by the Alps and the Pyrenees. The form resulting from this second break could well have penetrated the south-eastern part of France, largely replacing the phenotype which existed there. Over and above the main evolutionary sub-divisions are the individual forms which have resulted from more local isolating barriers. It would be naive to assume, as some entomologists do, that the phenotypes and their distribution will remain as they are today for an indefinite or very long period of time. Such changes could occur, if not overnight, in a relatively short time in species like *jurtina*, and the unstable nature of its races and the occurrence of the phenomena which I have mentioned must be kept in mind when studying this remarkable butterfly.

## Environmental effects: temperature/humidity

Two samples which I have examined from Iran perhaps give us some hint of the climatic effects on the wing markings of *jurtina*. One of these is from the hot, dry plateau just south of the main ridge of the Elburz Mountains. The other is from the more temperate and humid wooded northern watershed of that range. In the specimens from the northern region the underside hindwings of the female are very dark, with the medial band rather light whitish or silvery, the whole being covered with many dark striae. Those from the southern dry region have a very pale yellowish underside hindwing, with the medial band barely differentiated from the ground colour, except basally completely free from striae. From this it would appear that humid conditions would produce the dark striate markings, a conclusion which would concur with what is observed in the *jurtina* from north west Scotland and the Isles of Scilly. However, the variation must be genetic to a large extent, for such patterns do not prevail in maritime localities of western France or the Low Countries. A similar lack of consistency can be seen in the extent of the fulvous markings on the upperside of the butterfly throughout its range. Unjustified statements have been made that higher temperatures produce more fulvous on the wings, but this has now been proved wrong (Thomson, 1973). A high temperature, in fact, reduces the degree of fulvous on the female upperside, thus highlighting the genetic significance of the *bispulla* phenotype.

## The eastern and western phenotypes

Because of the genitalia differences in the two zones which have been defined in this paper, it becomes necessary to compare the phenotypes in the east and the west. The phenetic differences, although much more marked in the south than in the north, are present on either side of the transitional zone from Sweden to the Mediterranean. Possibly the most conspicuous difference is on the underside hindwing of the female which is in the east largely free from the strongly contrasting coloration of the medial band and similarly lacking it in the medial line of the forewing. In the west these patterns frequently approach a very dark, almost blackish sepia, while in the east the predominant tones are yellowish or reddish brown. The medial band on the hindwing is much more variable in the west, but it is far less frequently of the yellowish type than in the east. The fulvous markings are so variable that only general remarks can be made. However, in the east it is usually of a much duller colour than in the west. The wing shape too is variable, but contributes towards the more robust appearance of the western form.

The east-west distribution of the valve types would at first not seem to correspond very closely to the distribution of the known phenotypes of the species. A glance at the four maps (Maps 3 - 6) would tend to substantiate this. However, if we compare the geographical races which have been named, a strong correlation can be found. In the south of France the race *miscens* Verity is quite distinct from the north Italian *phormia* Fruh. and the differences between the so-called *fortunata* of Sicily and *prae-* and *emibispulla* Verity of south Italy have been recognised for some time. In the north the position is less clear, but the mainland British race has been separated from that of Sweden. Even the transitional race of Marstrand was observed to differ from that of the east of Sweden, before it was known that this could be confirmed by an examination of the genitalia. The fact that no *bispulla*-like race has evolved to the east of Sicily, should be evidence that, at least in the south, there is a strong link between structural characters and the wing

markings. No doubt old records of "*bispulla*" in the east arose from a lack of familiarity with the south-western races of the species which differ, not only in the nature of the underside hindwing and to a lesser extent the underside forewing, but also in the extent of the fulvous.

It is obvious that the main morphological differences are in the female which makes individual correlations between this and the male genitalia rather difficult. No east-west difference has so far been detected in the female genitalia, nor is there any individual correlation between the valve and the wing patterns.

#### Androconia

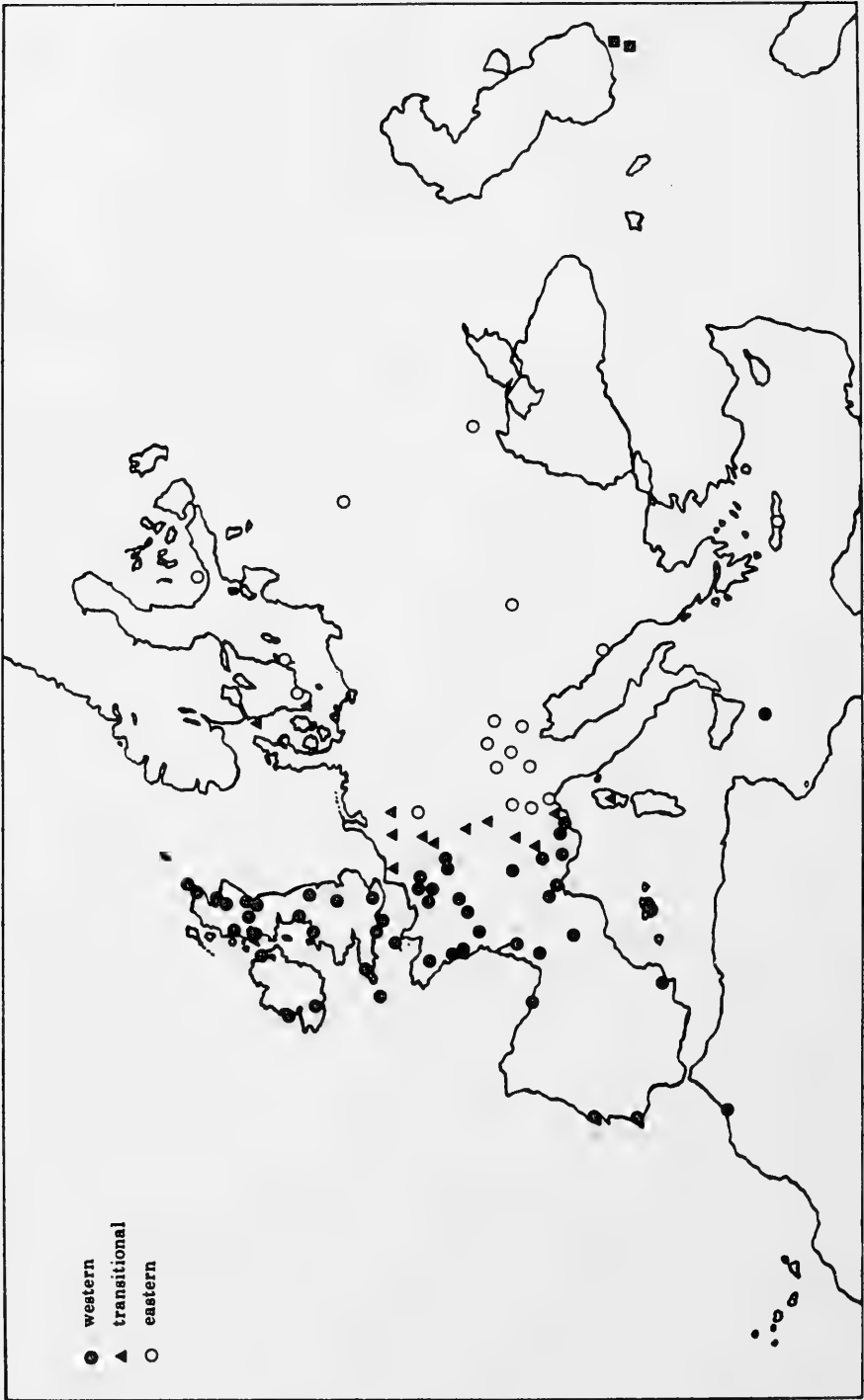
The androconial scales of *jurtina* are typical of a Satyrid being long and very narrow, tapering to almost nothing at the neck to which is attached a hair tuft. Although individually these scales vary quite a bit, extensive examination of those from different subspecies has failed to reveal any taxonomically useful character. Scales from north Africa, Crete and Iran are shown in Pl. 1 (Fig. 12-14).

On the other hand the androconial and itself is of some significance in terms of its form and variation. It has been said by some authors that *Maniola cypricola* differs from *jurtina* in that the androconial streak of the former extends beyond the third nervure, while in *jurtina* it does not (Seitz, 1908-28). Graves (1928) in his original description never claimed this, although he did comment that it was of a different shape. Even so, he acknowledged that some of the "*bispulla*" (?*fortunata*) had a similar brand. It should be noted that this is the androconial brand proper and not the dark scales which tend to extend much further. They are best detected by shining a strong light behind the specimen when the brand will show up standing out sharply as an opaque mark on a translucent ground. I have checked all of my specimens and find a most interesting situation. In the *jurtina* from Morocco and Malta the brand extends beyond the third nervure in all of the males. In Spain and Portugal the percentage with the extended brand is seventy-five (although at Santander it was zero). In the Pyrenees and Provence about a third had the brand extending beyond vein three, but this was not the case in Var and the Maritime Alps. Beyond this region and in the east the androconia never extended past the third nervure. The shape too is very variable, ranging from the broad scimitar shape described by Graves to a rather narrow and short streak in the north. In another direction it sometimes forms a rather broad blotch. Further investigations into this interesting variation would be worthwhile.

#### Species or subspecies

It must be considered at some point whether or not the genitalia types are indicative of distinct species. In the south where the morphological differences are so great and the border between the two zones so clear-cut, the suggestion is that the eastern and western types might well be. On the other hand in the north the morphological transition from west to east is so gradual that, with the allopatric distribution of the two types and the zone of contact being as it is, it would seem unlikely that this would be so. The genitalia variation such as is found in *jurtina* does not necessarily represent speciation: such structures are very useful diagnostically, but must never replace the true criterion for species differentiation.

The primitive type, however, poses a particular problem. Not only are the genitalia



Map. 1. The distribution of valve types in *Maniola jurtina*



differences consistent with apparently no intermediates, but the butterflies having this type of structure inhabit a rather different biotope. Unfortunately, distribution data are inadequate, but it would appear that there is an overlap between the *jurtina* populations with the primitive type valve and those with the eastern type. I am prepared to suggest that *ghilanica* could well prove to be a distinct species. This could be supported by the possible evolutionary development which I have already suggested. Certainly, other butterfly "species" have been separated on much less evidence. Until breeding and/or cytological studies or, in the case of the primitive forms, fuller distribution data prove otherwise, it is best to treat the genitalia types as representing sub-species, sub-species groups or races.

#### Race types and distribution

The taxonomic confusion, surrounding this species, stems mainly from the natural tendency to try to divide the species into neat and largely similar sections. This "pigeon hole" approach to the analysis of *jurtina* races soon leads to more problems than it can solve, as races and sub-species are more or less heterogeneous groups of distinct populations (Mayr, 1969). In *jurtina* this is particularly so.

The types of *jurtina* races fall into four main categories:

**h o m o g e n e o u s** — the simplest form of geographical race, but it is not found in many parts of the *jurtina* range. In it isolated populations do not show consistent differences over a large area (e.g. ssp. *ghilanica*). The term "homogeneous" is used relative to the nature of the species.

**c l i n a l** — in which we find a gradual change north to south or east to west or both. This is frequent not only in *jurtina* but also in other organisms (e.g. *janira*, *occidentalis*).

**h e t e r o g e n e o u s** — which consists of numerous local populations, each distinct from the other, but linked by one or more main characteristics. Problems arise when the line has to be drawn between certain components of this type of race and the next, or when they are linked to adjacent races by populations consisting of both races and intermediates (e.g. *splendida*, *miscens*).

**i n s u l a r** — in this context this type of race need not evolve on an island, but can equally well appear in an isolated continental situation. In either case the race consists of no more than a few similar populations (e.g. *cassiteridum*); insular races can be clinal, but the line of distinction is difficult to draw.

The apparent jumble of *jurtina* races with which we find ourselves, becomes much more logical when we examine the situation in the light of the material discussed throughout this paper. Indeed, the species is, in terms of geographical variation, manifestly typical. Firstly, we have the widespread race, ranging from the Baltic in the north to the Mediterranean in the south, to the Alps, Vosges and Jura in the west and to the Ural in the east. Within this race there is no more than a rather weak cline from north to south and from east to west. One part of the *jurtina* ancestor has produced a western form of the widespread race, a much more variable strain, evolving into numerous more or less distinct races. Around the perimeter of both the western and eastern widespread races has evolved the classic geographical isolate — four to the north west, possibly one or two to the south west, three to the south, at least three to the east and possibly one to the north (Map 7).

#### 8. TAXONOMY

Although it is reasonable to suppose that in the case of *jurtina* the nature and distribu-

tion of the geographical races is now fairly well understood, taxonomic problems arise. Because of the differences in the nature of these races, it is impossible to apply uniform standards throughout. The relatively extensive areas present no problem, but a decision has to be made where the line has to be drawn between these and the individual distinct populations (demes) in one instance and the two ends of a cline in another. My judgement in respect of the recognition of races has been made bearing in mind all the relevant factors — genitalia, wing markings, presence or absence of a cline and, only in a few instances, and in connection with morphological characters, the geographical position, relative to the whole species range.

In brief, I do not believe that the taxon for a race should be adopted in the case of a single distinct population, unless this be consistently and markedly distinct in more than one single character. Nor should various grades within a cline be recognised taxonomically, unless these are clearcut sections, each quite distinct from the other, with a zone of secondary intergradation between them in some instances. In most cases even the value of recognising the forms at either end of a cline is doubtful unless the differences are considerable.

Having placed the *jurtina* races within their appropriate taxa, the question of the use of terms for infra-specific categories remains. In selecting these I have tried to be objective, but in doing so, my decisions will inevitably be criticised for both “over-splitting” and “over-lumping” simultaneously! I have tried to take the reasonable middle course. Considering the zoogeography of the *jurtina* races I do not believe that many of the described races are unjustified. The list of species group names associated with the butterfly which I have accepted as such, compares favourably with those organisms with a widespread sub-species, surrounded by distinct races at the edge of their range. The use of three categories (four, if we include the group names) provides flexibility and goes some way towards organising a species which evades attempts at categorisation. The term “race” has often been used synonymously with “subspecies”, so it is important that I define these terms in the context of this paper and in respect to the species.

**sub-species:** “a geographically defined aggregate of local populations which differs taxonomically from other such divisions of the species” (Mayr, loc.cit.) occupying separate and often contiguous regions.

**race:** a geographically defined group of populations with distinctive characters, present in most or all of the individuals but not placed in the sub-species category because —

- (a) these characters are not significantly different from other geographical races, or
- (b) the populations comprising the race represent an intermediate stage in a long cline from one sub-species to another, or
- (c) insufficient material has been examined (i.e. cited by the describer), to justify recognition as a sub-species.

**form:** a potential race or sub-species, but not classified as such, because no justification for taxonomic separation has at this time been found, or a population (or group of populations) which has been described as a distinct race or sub-species, but which in my opinion is synonymous with a previously described race or sub-species, or barely distinct from it.

In the following account I have avoided irrelevant synonymy and the repetition of adequate descriptions which can be found elsewhere. Only a reference to the literature in which this can be found is given. However, where no description in detail has been made, or where the original description or subsequent descriptions are misleading, a redescription

has been made. This takes the form of a fairly general description of the main features of both sexes, followed by a statement of the variation trends. The average wingspan and that of the smallest and largest specimen is given as twice the distance from the centre of the thorax to the apex of the forewing. In the male the ground colour of fresh examples varies little throughout the range of the species. It is, when freshly emerged, a very dark brown-sepia, almost black basally. No mention is thus made of this character. In the female this varies from dark brown-sepia, though not as dark as the male, to a rather greyish brown-sepia. The first colour form I have referred to as "dark" and the second "light".

I have included an alphabetical list of all names associated with *jurtina*, including those which are infra-subspecific. The names coined by Leeds (1950), are excluded, unless these are known forms of the species and not hypothetical concepts or synonyms. The full bibliographic references to all but one of these names can be found in this or previous papers (Thomson, 1969 and 1970). The one omission is *anticoextensa* Leeds (*loc.cit.*, p. 106) which was inadvertently left out of my original list and is the form in which the apical eyespot of the forewings is elongated (but not downwards).

## MANIOLA Schrank, 1801: 152, 170

Type: *jurtina*

### GENITALIA WESTERN OR TRANSITIONAL

*jurtina* - group

#### *Maniola jurtina jurtina* (Linnaeus)

*Papilio jurtina* Linnaeus, 1758: 124.

Type locality. Europe and Africa — Linnaeus, 1758. North Africa — Verity, 1913: 184—185.

Genitalia: western (illustrated by Le Cerf, 1913)

Description. Male — 58.3 mm (smallest 54.0: largest 62.0); upperside: forewing fulvous scaling orange, suffuse and variable. Apical eyespot moderately large, rather diffuse but distinctly pupilled. Androconial band well defined, extending beyond vein three. Hindwing without fulvous scaling; underside: forewing basal and discal areas light reddish fulvous slightly darker than the submarginal, band with a distinct medial line. Outer margin and termen greyish, inwardly edged with dark grey-brown, lightly striate. Apical eyespot moderately large, usually single pupilled. Hindwing basal and discal areas and outer margin light greyish brown. Medial band greyish usually with three or four ocelli unpupilled and encircled with fulvous, wing lightly striate.

Female — 61.2 mm (smallest 60.0: largest 63.0); upperside: forewing fulvous scaling orange extending well into the discal area. Submarginal band extensive, strongly broken by the ground colour along the nervures. Apical eyespot large, usually bipupilled. Hindwing with submarginal fulvous band; underside: forewing basal and discal areas light reddish fulvous contrasting with the light fulvous submarginal band with a very dark medial line. Outer margin and termen greyish, inwardly edged with dark grey-brown, striate. Apical eyespot large, often bipupilled. Hindwing basal and discal areas and outer margin greyish or greyish fulvous. Medial band greyish, usually without ocelli and inwardly edged with a line of suffuse light fulvous, wing striate.

Variation consists mainly in the extension of the fulvous in the male which sometimes forms an indistinct band mixed with the ground colour. In the female the forewing discal fulvous can be more or less mixed with the ground colour and the submarginal band more or less broken by the nervures. The female underside hindwing varies towards a yellowish fulvous or light violet grey.

Diagnostic. The large size, the long androconial and in the male and submarginal band of the female upperside forewing broken by the nervures are distinctive features.

Range. Algeria, Tunisia and Morocco. Canary Islands as *f. fortunata*.

Discussion. The question of deciding upon the typical sub-species is certainly not free from controversy and largely depends on one's interpretation of who was the "first reviser" in respect of restricting the type locality. Lempke (1935: 182) was of the view that Linnaeus himself was instrumental in restricting the type locality to Sweden because the first mention of the species in a restricted locality was in Fauna Svecica (1761: 276). However, I would tend to agree with Mayr (1969: 403) that

"... in order to qualify as first reviser an author must give evidence of a choice between available alternatives". Verity was there the author who took the adequate action in restricting the type locality to north Africa (see Hemming, 1968: 185) even although I would not necessarily agree that his basis for doing so (the origin of the Linnean "type") was correct (Thomson, 1971: 92).

#### form *fortunata* *Alphéraky*

*Epinephele janira* var. *fortunata* Alphéraky, 1889: 222, pl. 11, fig. 4.

Type locality. Orotava, Teneriffe, Canary Islands - Alphéraky, 1889.

Genitalia. Western .

Description and diagnostic. The form *fortunata* appears to differ from *jurtina* from north Africa only in its slightly larger size, slightly darker ground colour and more concave costa of the female forewing. A recently received sample from Teneriffe were of a form with female underside markings much closer to the race from Malta than I have seen, although the uppersides retained the characters associated with *fortunata*. I suspect that these were exceptional.

Range. Canary Islands.

Discussion. Unfortunately I do not have sufficient material to determine whether or not there are significant differences between this form and the typical sub-species.

#### *Maniola jurtina hyperhispulla* subsp. nov.

Holotype. Male - Buskett, Malta. May 1971 (Anthony Valletta).

Paratypes. 2 males - "Malta, 1969", 1 female - Buskett, Malta. 3 September 1971 (Anthony Valletta). Holotype and paratypes in the author's collection.

Genitalia. Western.

Description. Form A (early).

Male - 55.1 mm (smallest 52.0; largest 58.0); upperside: forewing fulvous scaling orange forming a distinct band. Apical eyespot moderately large, well defined, distinctly pupilled. Androconial band well defined usually extending beyond vein 3. Hindwing without fulvous scaling; underside: forewing basal and discal areas light reddish fulvous, slightly darker than the submarginal band with an indistinct medial line. Outer margin

and termen greyish, inwardly edged with dark brown, lightly striate. Apical eyespot moderately large, usually single pupilled, surrounded by light fulvous. Hindwing basal and discal areas and outer margin greyish brown, medial band greyish, usually with three or four ocelli unpupilled and encircled by fulvous. Wing lightly striate.

Female - 57.6 mm (smallest 53.0: largest 60.0); upperside: forewing fulvous scaling orange, largely covering the discal and basal areas. Submarginal band extensive, not separated from the discal fulvous, nor broken by the ground colour along the nervures. Apical eyespot large, usually pupilled. Hindwing with a submarginal fulvous band occasionally extending basally; underside: forewing basal and discal areas light reddish fulvous contrasting with the lighter submarginal band, with a distinct medial line. Outer margin and termen light greyish or light yellowish grey, inwardly edged by dark brown, striate. Apical eyespot large, often bipupilled. Hindwing basal and discal areas and outer margin grey brown. Medial band greyish or silvery usually without ocelli, inwardly edged with a very distinct band of bright fulvous.

Variation consists of the lightening or darkening of the underside hindwing in the female, giving the effect of greater or lesser contrast with the medial band.

Form B (late).

Male - none available for study.

Female - 57.9 mm (smallest 54.0: largest 60.0); upperside: forewing fulvous scaling orange, extending well into and occasionally largely covering the discal and basal areas. Submarginal band extensive, not broken by the ground colour along the nervures. Apical eyespot large, usually bipupilled. Hindwing with a submarginal fulvous band occasionally extending basally; underside: forewing basal and discal areas light reddish fulvous contrasting with the fulvous of the lighter submarginal band with a distinct medial line. Outer margin and termen dark greyish fulvous strongly striate and inwardly edged with dark grey brown. Apical eyespot large and often bipupilled. Hindwing basal and discal areas and outer margin dark greyish fulvous. Medial band greyish fulvous with no, one, or two ocelli, occasionally pupilled and encircled with fulvous, inwardly edged by a very indistinct fulvous suffusion. Wing strongly striate.

Variation consists mainly in the extent of fulvous in the discal area of the upperside forewing and the enlargement of the apical eyespot.

Diagnostic. By the extent of fulvous in both sexes and the conspicuous fulvous edging of the female underside hindwing medial band, this sub-species differs from *M. jurtina jurtina* and *M. jurtina hispulla*, although the smaller *hispulla* male occasionally has a bright submarginal fulvous suffusion on the upperside forewing.

Range. Known only from Malta.

Discussion. The differences between the early and late forms are interesting. The later specimens are rather more variable than the early ones. It is unfortunate that late males were not available for comparison.

### *Maniola jurtina hispulla* Esper

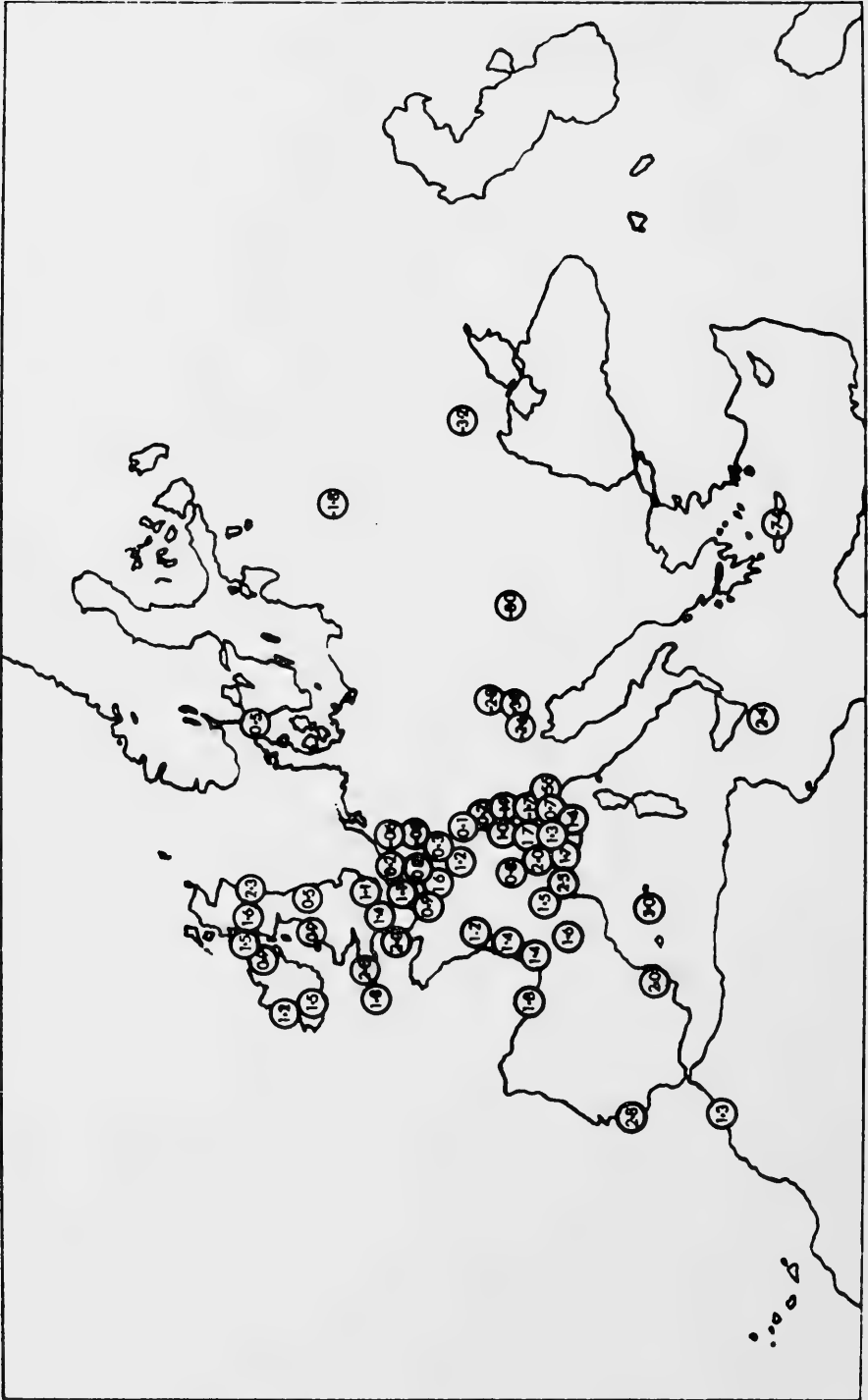
*Papilio Hispulla* Esper, 1805: II, pl. CXIX.

*Papilio Hispulla* Hübner, 1805: 27, figs. 593—596.

Type locality. Lisbon - Esper, 1805.

Genitalia. Western.

Description. Male - 52.0 mm (smallest 48.0; largest 58.0); upperside: forewing



Map. 2. The distribution of the value of F in *Maniola jurtina*.

fulvous scaling orange suffuse and variable. Apical eyespot rather small, but sometimes moderately large, diffuse, indistinctly pupilled. Androconial brand well defined frequently extending beyond vein 3. Hindwing without fulvous scaling; underside: forewing basal and discal areas light yellowish or reddish fulvous, barely distinguishable from the submarginal band with an indistinct medial line. Outer margin and termen greyish or greyish brown almost without striae. Apical eyespot usually rather small, usually single pupilled, surrounded by light fulvous. Hindwing basal and discal areas and outer margin greyish or greyish brown. Medial band usually lighter, with two to four ocelli, unpupilled and encircled with fulvous. Wing almost without striae.

Female — 54.7 mm (smallest 52.0; largest 58.0); upperside, forewing fulvous scaling orange, extending well into the discal area. Submarginal band extensive occasionally broken by the ground colour along the nervures. Apical eyespot large usually bipupilled. Hindwing nearly always with a submarginal fulvous band; underside: forewing basal and discal areas reddish fulvous, contrasting strongly with the lighter submarginal band, with a distinct medial line. Outer margin and termen greyish or dark greyish yellow, darker inwardly, lightly striate. Apical eyespot large, often bipupilled surrounded by light fulvous. Hindwing basal and discal areas and outer margin greyish brown or dark greyish yellow. Medial band light greyish or greyish yellow, usually suffused with more or less distinct fulvous, usually with 0—2 unpupilled ocelli, encircled with fulvous. Wing lightly striate.

Diagnostic. Differs from *jurtina* in its much smaller size and less constant fulvous markings and from *hyperhispulla* in its smaller size and much less bright female underside.

Range. Spain and south-east France, north of the Cantabrian Mountains as race *cantabrica* and in south-east France as race *miscens*, the Balearic Islands and probably also Sardinia.

Discussion. The Spanish *hispulla* is an extremely variable creature and some populations— in northern and upland areas of the Iberian Peninsula would probably be applicable to *cantabrica* or *miscens*. More work is necessary on the species in central Spain.

#### race *cantabrica* Agenjo

*Epinephele jurtina cantabrica* Agenjo, 1934: 313.

Type locality. Camargo, Santander, Spain — Agenjo, 1934.

Genitalia. Western. Rarely a relict transitional type occurs.

Description. Agenjo, 1934. Male — 51.0 mm (smallest 50.0; largest 52.0); upperside: forewing fulvous scaling suffuse and variable. Apical eyespot moderately large, rather diffuse and distinctly pupilled. Androconial brand fairly well defined, not extending beyond vein three. Hindwing without fulvous scaling; underside: forewing basal and discal areas reddish fulvous, contrasting with the lighter submarginal band, with a distinct medial line. Outer margin and termen greyish brown lightly striate, darker inwardly. Apical eyespot rather large, usually single pupilled, but not infrequently unpupilled. Hindwing basal and discal areas and outer margin greyish brown. Medial band lighter with two to three ocelli, unpupilled and encircled with fulvous. Wings lightly striate;

Female — 56.2 mm (smallest 51.0; largest 58.0); upperside: fulvous scaling orange, present as a suffuse patch in the discal area. Submarginal band well developed, frequently broken by the ground colour along the nervures. Apical eyespot usually bipupilled. Hind-

wings with occasional submarginal fulvous; underside: forewing basal and discal areas reddish fulvous, contrasting with the lighter submarginal band with a distinct medial line. Outer margin and termen greyish brown or brown rather heavily striate. Apical eyespot large often bipupilled. Hindwing basal and discal areas and outer margin dark yellowish grey or brown. Medial band greyish yellow or greyish fulvous usually with 0—2 ocelli. Wing rather strongly striate.

Variation is principally in the size of the apical eyespot, the greater or lesser encroachment of the ground colour into the fulvous areas and the coloration of the underside hindwing in the female.

Diagnostic. Differs from *bispulla* in the indistinct discal and hindwing, fulvous of the female upperside and the dark underside forewing, fulvous in the two sexes.

Range. Spain north of the Cantabrian Mountains.

Discussion. The number of individuals which fly with *cantabrica* but which are to all intents and purposes indistinguishable from *bispulla*, varies from year to year, occasionally forming a very large minority of the population.

#### race *miscens* Verity

*Maniola jurtina* race *miscens* Verity, 1953: 268.

Type locality. St. Barnabé, Nice, Alpes Maritimes — Verity, 1953.

Genitalia. Western with (rarely) relict transitional types.

Description. Male — 52.4 mm (smallest 46.0: largest 59.0); upperside: forewing fulvous scaling orange, occasionally yellowish suffuse and variable occasionally forming a band below the apical eyespot or extending basally. Apical eyespot moderately large distinctly pupilled with white. Androconial brand fairly well defined rarely extending beyond vein three; underside: forewing basal and discal areas light fulvous, barely distinguishable from the submarginal band, with no medial line. Outer margin and termen greyish, usually almost without striae. Apical eyespot moderately large, usually single pupilled. Hindwing basal and discal areas and outer margin greyish or light greyish-brown, medial band a little lighter, usually with two to four ocelli, encircled with fulvous. Wing almost without striae; female — 56.7 mm (smallest 50.0: largest 61.0); upperside: forewing fulvous scaling orange, occasionally yellowish, present as a suffuse patch or extending well into the discal area. Submarginal band well developed, occasionally broken by the ground colour along the nervures. Apical eyespot moderately large, sometimes bipupilled. Hindwing almost always with a submarginal fulvous or light or extensive suffusion; underside: forewing basal and discal areas light fulvous or light reddish fulvous, slightly darker than the submarginal band, with a distinct medial line. Outer margin and termen greyish, light greyish brown or greyish yellow, lightly striate. Apical eyespot moderately large, often bipupilled. Hindwing basal and discal areas and outer margin greyish, light greyish brown or greyish yellow. Medial band light greyish or greyish yellow, often without ocelli. Wing lightly striate.

Variation is in the extent of the fulvous and the size of the apical eyespot in both sexes, although only rarely does the female upperside marking approach that of *ssp. occidentalis*.

Diagnostic. Differs from *bispulla* in the colour of the underside hindwing of the female and in being generally less brightly and more inconsistently marked with fulvous.

Range. South-east France in the Department of Alpes Maritimes, Var, Basses Alpes,



Hautes Alpes, Bouches du Rhône, Vaucluse, Drôme, Gard and possibly also Ardèche, Hérault, Aude and Pyrénées Orientales.

*mirtyllus*-group

*Maniola jurtina mirtyllus* Fourcroy

*Papilio mirtyllus* Fourcroy, 1785: 239.

Type locality. Not specified. Fourcroy's description appeared in a work on the Lepidoptera of the Paris region. It is best, therefore, to consider the type locality of the ssp. *mirtyllus* as north-east France.

Genitalia. Transitional with both western and (in the eastern part of its range) eastern types.

Description. Male — 46.8 mm (smallest 43.0: largest 50.0); upperside: forewing fulvous scaling orange suffuse and variable. Apical eyespot rather small, diffuse, indistinctly pupilled. Androconial brand suffuse, not extending beyond vein three. Hindwing without fulvous; underside: forewing basal and discal areas light fulvous, barely darker than the submarginal band, without medial line. Outer margin and termen greyish, without striae. Apical eyespot rather small, usually single pupilled. Hindwing basal and discal areas and outer margin greyish. Medial band slightly lighter, usually with two or three ocelli, unpupilled and encircled with fulvous. Wing lightly striate; female — 51.7 mm (smallest 45.0: largest 57.0); upperside: forewing fulvous, scaling yellowish or orange, present as a suffuse patch in the discal area. Submarginal band well developed, not broken by the ground colour along the nervures. Apical eyespot moderately large, usually single pupilled. Hindwing usually without fulvous; underside: forewing basal and discal areas light reddish fulvous, barely contrasting with the lighter submarginal band, with a distinct medial line. Outer margin and termen yellowish grey or greyish brown, lightly striate. Apical eyespot moderately large, usually single pupilled. Hindwing basal and discal areas and outer margin yellowish grey or greyish brown. Medial band light yellowish grey or greyish, usually without ocelli. Wing lightly striate; variation is usually in the female upperside forewing fulvous which is also occasionally present in the building. The apical eyespot in both sexes varies a lot in size.

Diagnostic. In addition to the genitalia this sub-species differs from *insularis* in the more uniform underside of both sexes by the usual lack of the medial line on the underside forewing of the male and from *miscens* in its smaller size and less extensive female fulvous.

Range. South west Sweden, (Norway), Denmark, Netherlands, Belgium and France, roughly north and east of a line from Pas de Calais to the Franco-Italian border. See map 1 for distribution of genitalia types.

Discussion. The ssp. *mirtyllus* form a north to south cline, the limits of which are very different from each other. In the north the small dark race from southwest Sweden blends into the comparatively constant central form which is found in the Low Countries and most of northeast France. At its southern end we find a singularly large race with rather extensive fulvous in some parts of Haute Savoie. The dimensions given are for the central part of the cline (Belgium). The figures for populations to the north and south are:

southwest Sweden	— male	45.0 mm (smallest 39.0: largest 50.0)
	female	47.6 mm (smallest 44.0: largest 52.0)
Hautes Savoie	— male	49.0 mm (smallest 46.0: largest 51.0)
	female	53.8 mm (smallest 52.0: largest 58.0)

Some transitional populations in the Alpes Maritimes (e.g. Col du Tende) are probably more applicable to ssp. *emibispulla*.

### *Maniola jurtina occidentalis* Pionneau

*Epinephele janira* ab.*occidentalis* Pionneau, 1924: 58.

*Epinephele janira* ab.*meridionalis* Pionneau, 1924: 58.

Type locality. West France — Pionneau, 1924.

Genitalia. Western, with the occasional relict transitional type.

Description. Male — 50.1 mm (smallest 46.0: largest 55.0); upperside: forewing fulvous scaling orange, suffuse and variable, but usually confined to a ring around the eyespot. Apical eyespot rather small, diffuse and indistinctly pupilled. Androconial brand suffuse, not extending beyond vein three. Hindwing without fulvous; underside: forewing basal and discal areas fulvous or light fulvous, barely darker than the submarginal band, usually with no medial line. Outer margin and termen greybrown, lightly striate. Apical eyespot rather small, usually single pupilled. Hindwing basal and discal areas and outer margin grey-brown. Medial band slightly lighter, usually with two or three ocelli, unpupilled and encircled with fulvous. Female — 54.5 mm (smallest 50.0: largest 60.0); upperside: fulvous scaling yellowish or orange present as a suffuse patch in the discal area. Submarginal band usually well defined, frequently broken by the ground colour along the nervures. Apical eyespot moderately large, often bipupilled. Hindwing usually with a submarginal fulvous suffusion or “point”; underside: forewing basal and discal areas reddish fulvous, dark fulvous or fulvous, darker than the submarginal band usually with a distinct or rather dark medial line. Outer margin and termen light greyish, dark greyish-brown or dark yellowish fulvous moderately, or rather heavily striate. Hindwing basal and discal areas and outer margin greyish brown, dark grey-brown, or dark yellowish fulvous. Medial band greyish, light greyish or yellowish with 0—2 ocelli unpupilled. Wing moderately or rather heavily striate.

Variation is in the female upperside forewing submarginal fulvous band and in the fulvous of the hindwing which is more or less extensive. The various colour forms of the female underside hindwing are confusing, tending towards a rather monochrome grey on the one hand to a fairly bright yellow fulvous on the other.

Diagnostic. Differs from *miscens* in its smaller size and considerably less extensive fulvous in the female, also by the smaller and more suffuse apical eyespot of the male.

Range. France south and west of the range of ssp. *mirtyllus* and north and west of the range of race *miscens*.

Discussion. Pionneau wrote of var. *meridionalis* (1936): “Dans le Sud-Ouest de la France, en Gironde, on ne rencontre pour ainsi dire que cette race.”

Also his original description of “ab. *meridionalis*” is decidedly vague: “... qui est d’une manière générale d’un brun très foncé dans le midi de la France.”

One cannot draw any useful conclusion from such a misleading description. I have examined a number of representative series from Gironde, Dordogne and Loire Inferieure

and find that there is no justification for separating them as a distinct race — nor even for recognising Pionneau's *meridionalis* as a form.

The northeastern region in which this sub-species merges with *mirtyllus* is complex. The characters of *occidentalis* may be found in populations with transitional type genitalia and those of *mirtyllus* with western type genitalia.

*splendida*-group

***Maniola jurtina splendida* Buchanan White**

*Epinephele janira* var. *splendida* Buchanan White, 1871: 200.

The locality. Longa Island, Ross-shire, Scotland — Bunchanan White, 1871.

Genitalia. Western.

Description. Graves, 1930: 50. Thomson, 1969: 56—57 (includes a distribution map). Thomson, 1970: 261—268.

For the range of variation in this race, see Thomson, 1970 (l.c.) in which will be found an account of the various forms which the sub-species takes.

Diagnostic. Best distinguished by the very dark underside (particularly the hindwing) of the male, the dark striate ground colour of the underside hindwing of the female, with "Hübner's mark" present in most individuals; also by the extensive and rather dark fulvous of both sexes.

Range. Throughout the Western Isles, on Orkney, northwest Scotland to south of the Caledonian Canal forming a cline further south and east with ssp. *insularis* in which both sub-species and intermediates are found.

Discussion. Buchanan White's original description mentions that he had seen specimens of "var. *splendida*" from Nice. What he had seen, would probably have been *miscens*, an example of which still exists in his depleted collection, housed in the Perth County Museum.

***Maniola jurtina cassiteridum* Graves**

*Maniola jurtina cassiteridum* Graves, 1930: 75, pl. 1, fig. 7, 8, 9.

Type locality. Isles of Scilly (England) — Graves, 1930.

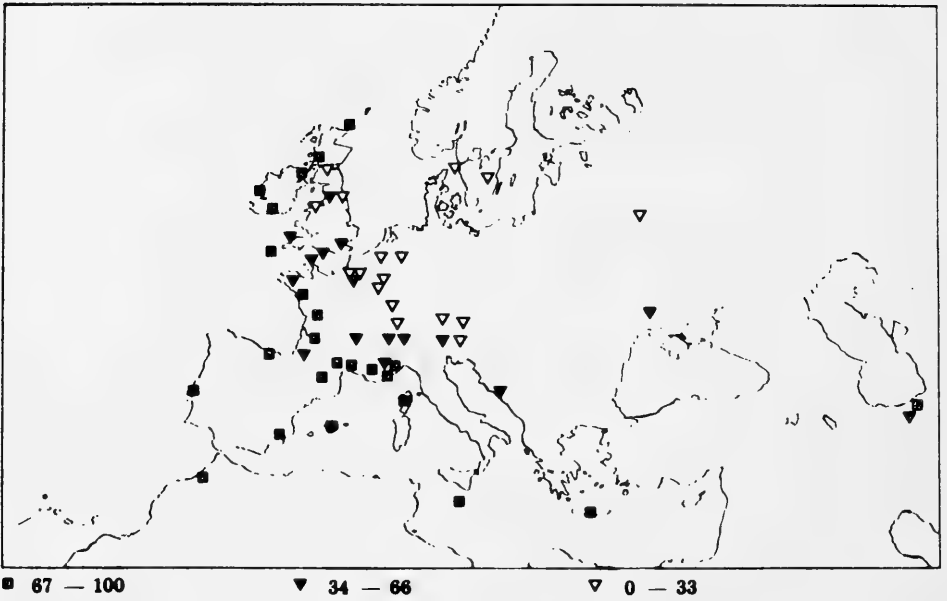
Genitalia. Western.

Description. Graves, 1930.

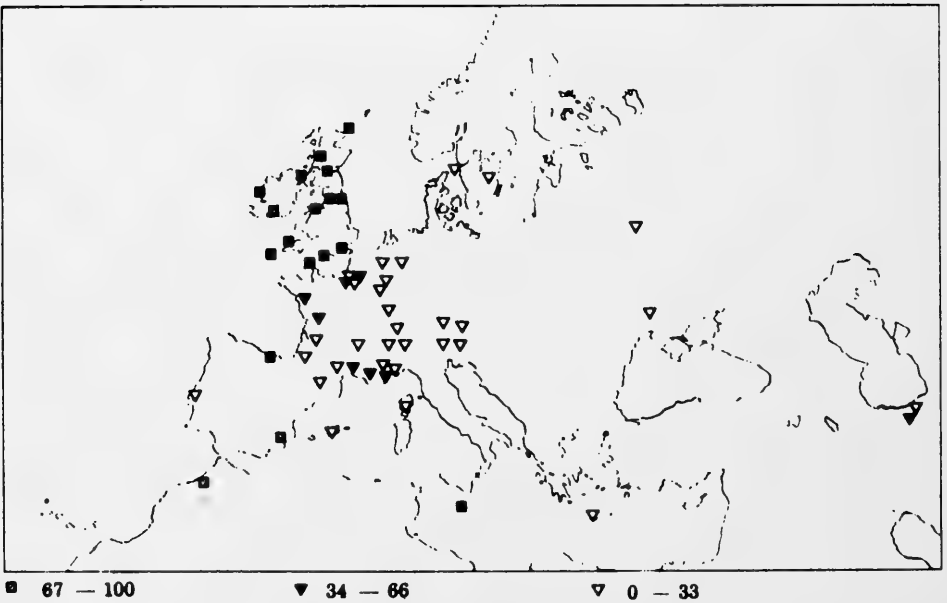
Diagnostic. The most distinctive feature of this race is the remarkable underside of the female hindwing which has the heavy striae and strongly contrasting light medial band. This is also a feature of the male but this sex is more easily distinguished by the large, often white pupilled, orange ringed ocelli on the underside hindwing.

Range. The Isles of Scilly and (with characters less pronounced) Lundy Island and Alderney (Channel Islands).

Discussion. A remarkable and probably significant fact is that the late *jurtina* on the Isle of Wight (see page 14) resembles this race to some extent on the underside of both sexes. Furthermore, *cassiteridum* is on the wing (sometimes fresh) throughout September, when the *jurtina* on the adjacent Cornish Peninsula are over, or almost so. Some of the females on Lundy Island tend towards the Irish *iernes*.

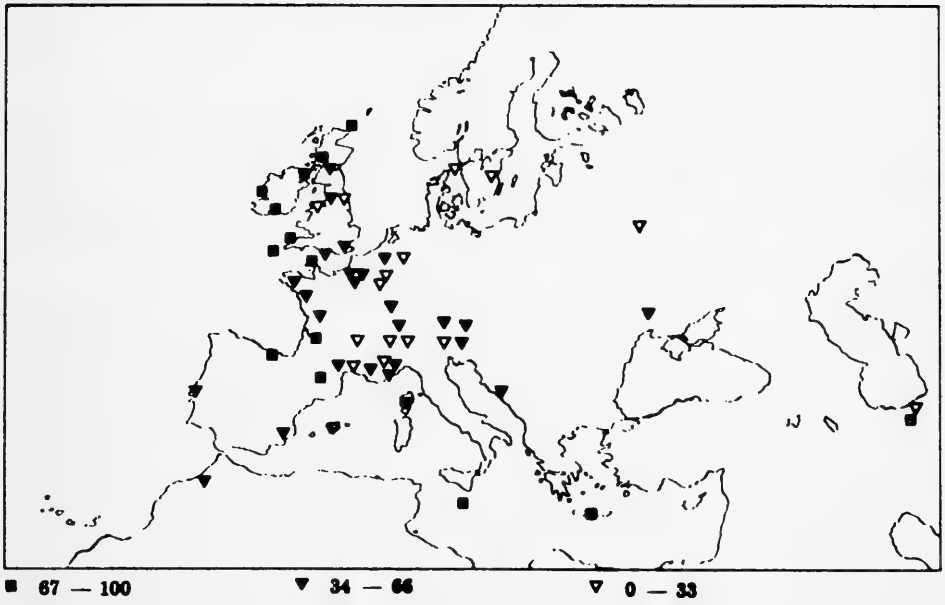


Map 3

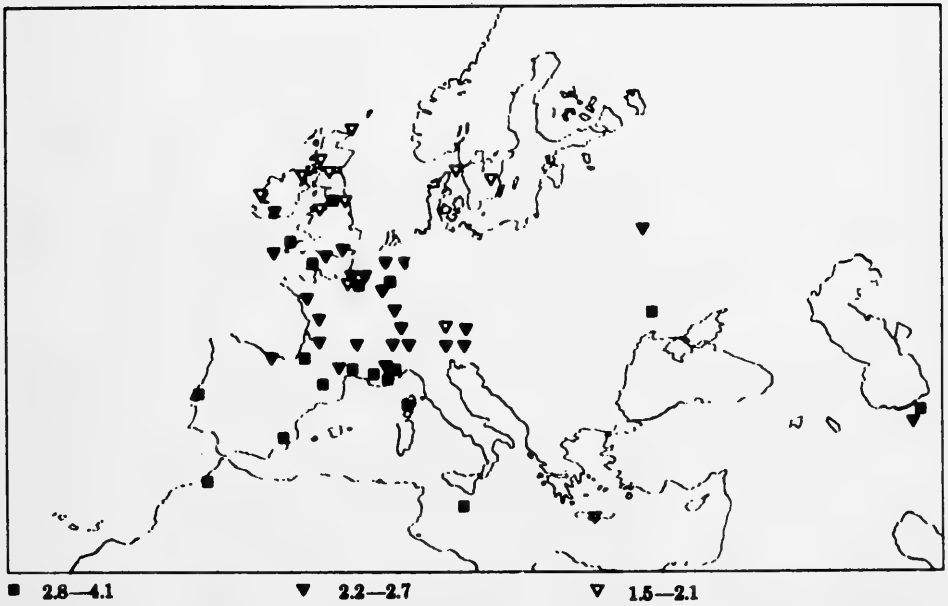


Map 4

Maps 3—6. The distribution of morphological characters in *Maniola jurtina*. 1. females with fulvous on the upperside hindwing; 2. males with a medial line on the underside forewing; 3. females with the apical eyespot bipupilled on either surface; 4. male average spotting on the underside hindwing



Map 5



Map 6

**Maniola jurtina iernes** Graves

*Maniola jurtina iernes* Graves, 1930.

Type locality. Co. Kerry, Eire (Ireland) — Graves, 1930.

Genitalia. Western with the very occasional relict transitional type structure.

Description. Graves, 1930.

Diagnostic. The very large gynaikotropic males, with extensive fulvous markings and even larger females, with brilliantly coloured undersides, are easily distinguished from any other race.

Range. Ireland, with characters less distinct in parts of the north, Isle of Man.

Discussion. In the north of Ireland (e.g. Coleraine) a percentage of the females are virtually indistinguishable from bright maritime *insularis* and some rather diminutive males also turn up. The race on the Isle of Man agrees in every respect with *iernes* from southern Ireland, except that it is considerably smaller, 45.2 mm in the male and 48.9 mm in the female (see Thomson, 1971).

**Maniola jurtina insularis** Thomson

*Maniola jurtina insularis* Thomson, 1969: 53—55, pl. 1, fig. 1—4, 6—8, 11—12.

Type locality. Isle of Wight, England — Thomson, 1969.

Genitalia. Western, with the very occasional relict transitional type.

Description. Thomson, 1969. (*loc.cit.*)

Diagnostic. The contrasting underside forewing of the male, with the well marked dark medial line, is distinctive, as is the bright contrasting underside of the female. The fulvous is generally fairly extensive in the female — particularly on the forewing.

Range. England, Wales, Scotland to the Clyde in the west and Aberdeen in the east forming a cline further north and west with ssp. *splendida* in which both sub-species are found with intermediates.

Discussion. The mainland British *insularis* is a remarkably heterogeneous sub-species with populations of adjacent localities, consisting of quite different phenotypes. A close approach to ssp. *mirtyllus* can be found in some localities in Surrey and there are localities in North Wales in which the characteristics of the race are not well developed.

## GENITALIA EASTERN

*janira* - group**Maniola jurtina janira** Linnaeus

*Papilio janira* Linnaeus, 1758: 475.

*Papilio monoculus* Goeze, 1779: 285.

Type locality. Europe — Linnaeus, 1758. Central Europe — Verity, 1913: 184—185. Because of the differences in the genitalia the restriction of the type locality by Verity is inadequate. Action is necessary, to avoid confusion between the type locality of *janira* (ssp. of *jurtina* L.) and the western sub-species *mirtyllus* and *occidentalis*. SOUTH GERMANY is therefore made the new restricted type locality of the sub-species *janira*.

Genitalia. Eastern.

Description. Male — 48.2 mm (smallest 44.0; largest 55.0); upperside: forewing fulvous orange, confined to a ring around the eyespot. Apical eyespot rather small, diffuse, indistinctly pupilled. Androconial band suffuse, not extending beyond vein three. Underside: forewing basal and discal areas light reddish fulvous, barely distinguishable from the submarginal band with no medial line. Outer margin and termen greyish or greyish brown without striae. Apical eyespot rather small, usually single pupilled, sometimes surrounded by light fulvous. Hindwing basal and discal area and outer margin greyish or greyish brown. Medial band slightly lighter usually with two or three ocelli, unpupilled and encircled with fulvous. Wing very lightly striate. Female — 51.4 mm (smallest 47.0; largest 56.0); upperside: forewing fulvous scaling yellowish or orange present as a suffuse patch in the discal area. Submarginal band very variable, fairly well defined, occasionally broken by the ground colour along the nervures. Apical eyespot moderately large usually single pupilled. Hindwing usually without fulvous; underside: forewing basal and discal areas light reddish fulvous slightly darker than the submarginal band usually with an indistinct medial line. Outer margin and termen yellowish grey or greyish brown lightly striate. Apical eyespot moderately large usually single pupilled but not infrequently bipupilled. Hindwing basal and discal areas and outer margin yellowish grey or greyish brown. Medial band light yellowish grey or greyish usually without ocelli. Wing lightly striate.

Variation is considerable in the extent and form of the female upperside fulvous markings, but they rarely approach that of the races found further south. The apical eyespot can be rather large or small.

Diagnostic. Differs from all other eastern races by the small size and inextensive fulvous of the female upperside.

Range. Finland, northeast U.S.S.R., Germany, Switzerland, Austria and the far north of Italy, and eastwards probably as far as Czechoslovakia and Hungary. Further south it is found as the races *phormia* and *praehispulla*, further eastward as the race *strandiana* and possibly also *megala* and *maraschi*.

Discussion. The eastern and south eastern limits of *janira* are not well known, particularly in its transition to *strandiana* and in Turkey, where it possibly flies with *telmessia*. I have not included southwest Sweden within the range of the sub-species. The specimens I have with eastern genitalia from that region differ markedly from the widespread *janira* in their small size, very pale female underside and blind apical eyespot on the upperside of both sexes. Unfortunately I do not have sufficient material on which to base a fuller description, but these specimens will probably represent another case of a *jurtina* race, developing at the edge of the species range.

#### race *megala* Oberthür

*Epinephele janira* race *megala* Oberthür, 1909: 387.

Type locality. Akbès — Oberthür, 1909.

Genitalia. Two specimens dissected by Bernardi were thought to be of the eastern type *a* but the work of Tauber (1970) indicates that these and others found since in southern Turkey were of a quite distinct type. Examination of the Turkish populations using adequate sampling techniques is essential before conclusions can be made regarding the situation in this area.

Description. Oberthür's original description reads:

"... La plus grande forme géographique de *janira* que je connaisse est celle d'Akbès. Elle est plus grande que *fortunata*, Alphéraky ... Outre sa taille, elle se distingue par la profonde dentelure de ses ailes inférieures, par le coloris gris ou jaune brun du dessous des ailes inférieures qui, chez la ♀, est généralement assez sombre, c'est-à-dire très peu coloré de jaune en dessus et aussi par le développement de la tache noire subapicale ocellée, aux ailes supérieures. Je possède 7 ♂ et 9 ♀; un des ♂ a 5 taches noires cerclées de jaune, dont 4 pupillées de blanc, sur les ailes inférieures, en dessous. Il lui manque le 3e ocelle pour équivaloir au n° 429 d'Herrich-Schaeffer, mentionné ci-dessus, et dont la localité m'est restée inconnue. J'ai donné à la belle race géographique d'Akbès le nom *megala* ..."

Diagnostic. Presumably the very large size of this race should identify it.

Range. Akbès and according to Graves (1933: 179) Shar Dewesy on the Turco-Syrian borderland and Marmarice.

Discussion. Material was not available to supplement Oberthür's rather inadequate description.

#### form *antalyana* Tauber

*Maniola megala antalyana* Tauber, 1970: 109—111.

Type locality. Bay Dagliari, Yazir westl. Antalya, c. 1000 m — Tauber, 1970.

Genitalia. Of the type called "*megala*" by Tauber.

Description. Tauber, 1970.

Range. So far only in the type locality.

Discussion. Described as a subspecies of "the species *megala*" this form representing a single population in a remote part of Turkey and described from a very small sample must be studied more fully before being recognised as a subspecies or even a race.

#### race *maraschi* Pfeiffer

*Epinephele jurtina maraschi* Pfeiffer, 1932: 24.

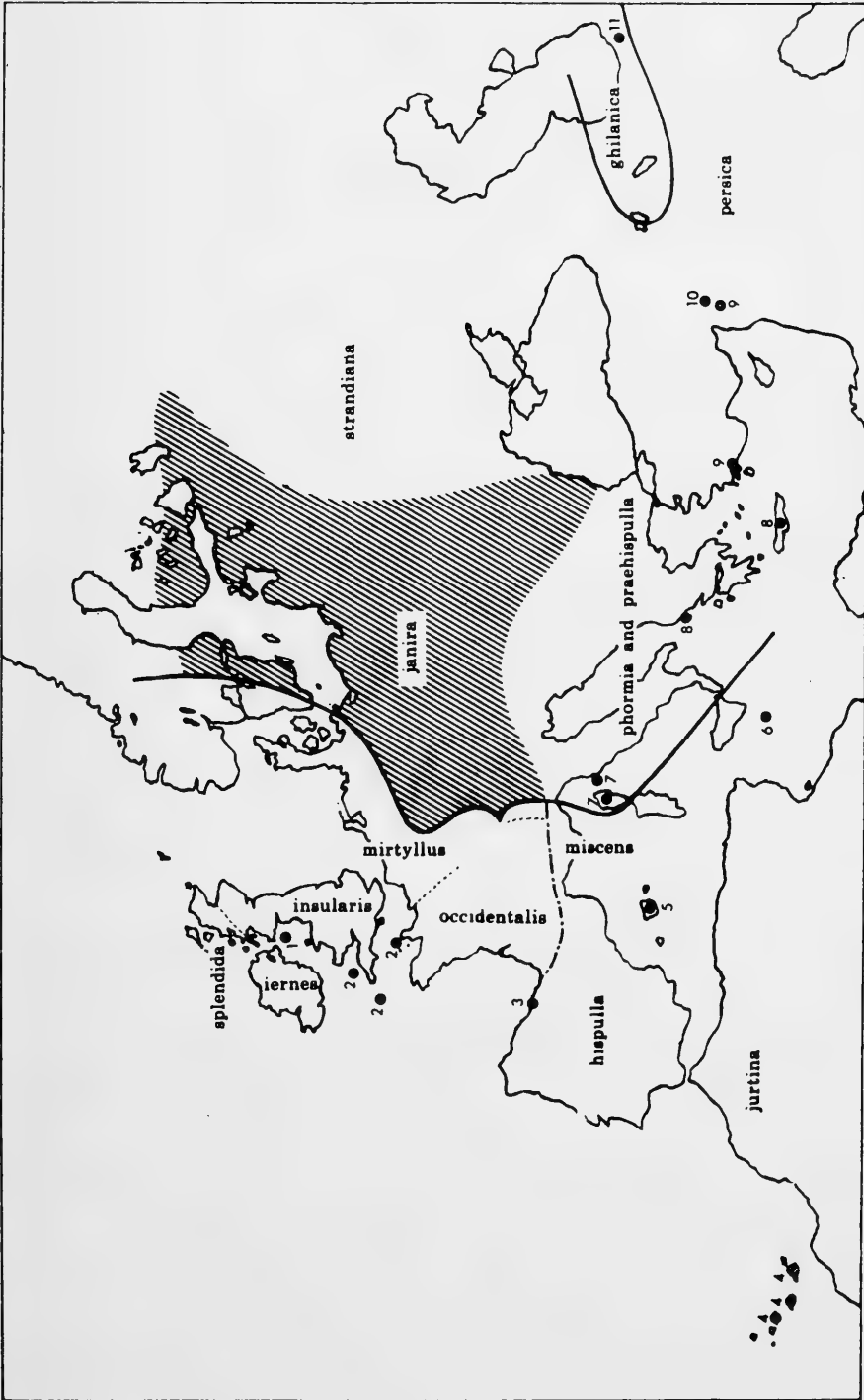
Type locality. Marasch — Pfeiffer, 1932.

Genitalia. Tauber (1970) found the "*megala*-type" in this race but further study is required.

Description. Pfeiffer's original description reads:

"... Die Art dürfte hier ihre Südgrenze in einer grossen, auffallend breitflügeligen Rasse erreichen. Das ♂ gleicht oseits am besten Riviera Stücken, nur dass das Apicalauge stets deutlich weiss gekernt ist. Die Vlf. — Us. zeigt ein mattes Braungelb mit sehr schmalem Randfeld. Die Hfl. — Us. ist erdbraun mit kaum sichtbarer Mittellinie. 4 bis 5 gelbbraun umzogene Augen sind stets vorhanden. Beim ♀ sind auf der Os. die leuchtend gelbbraunen Flecke breit angelegt und um das auffallend grosse Apicalauge stark gelblich aufgehellt. Die Ausdehnung der gelbbraunen Flecke entspricht ungefähr der ssp. *hispulla* Hbn. Die Grf. der Vfl. — Us. entspricht der Os. Ein zweites ungekerntes Apicalauge tritt daselbst einzeln auf. Die Grf. der Hfl. ist schokoladebraun mit violetter Einschlag (feilbraun). Unmittelbar nach der schwarzbraun abgesetzten Mittellinie liegen gelbliche Schuppenpartien, denen dann eine breite hellviolettbraune Binde folgt. Die Randbinde ist wiederum gleich dem Innenteil. Die Punktaugen sind sehr klein und schwankt deren Zahl von 0—3. Ein ♀ linksseitig asymmetrisch stark verdunkelt. ♂ u. ♀





Map. 7. The geographical forms, races and sub-species of *Maniola jurtina*. 1. *iernea*; 2. *cassitevidum*; 3. *cantabrica*; 4. *fortunata*; 5. *bispulla*; 6. *by-perbispulla*; 7. *emibispulla*; 8. *corfiobispulla*; 9. *megala*; 10. *marasebi*; 11. *iranica*

50—55 mm. Mit der ssp. *megala* Obth. aus dem südlichen Amanus die Marasform nichts gemein."

Diagnostic. The extension of the female upperside fulvous being "closest to *hispulla*" puts this race on its own in the east.

Range. Known only from Marasch.

Discussion. The very restricted locality of *maraschi* and the fact, that no further contribution to its distribution, variation or nature has been made in the literature, as far as I can trace, makes assessment of this race difficult. It is placed as a subspecies of *megala* by Tauber (1970).

#### race *strandiana* Obratzsov

*Maniola jurtina strandiana* Obratzsov, 1936: 638—639.

Type locality. Funduklejevka, Kiev, U.S.S.R.

Genitalia. Eastern.

Description. Obratzsov, 1936.

Diagnostic. Larger and fulvous more extensive than the more northern *janira* with which it forms a cline.

Range. Southern Russia — Kiev, Kherson, Crimea, Podolia and Bessarabia, probably Transsylvania: also in east Russia (Vjatka, Malmyzh) and possibly other regions south and west to the Caucasus, forming a cline in Estonia and Novgorod.

Discussion. The differences between *strandiana* and the southern races with eastern type genitalia further west (*prae-* and *emibispulla*) are not too clear and require further investigation.

#### race *phormia* Fruhstorfer

*Epinephele jurtina phormia* Fruhstorfer, 1909: 121.

Type locality. Meran, South Tyrol — Fruhstorfer, 1909.

Genitalia. Eastern.

Description. Verity, 1953: 270.

Diagnostic. Differs from *janira* in its larger size and rather more extensive fulvous on the female upperside.

Range. Northern and central Italy from 1.000—1.300 meters. Probably similar forms occur in the Balkan Peninsula and western Turkey.

Discussion. The race *phormia* is the first stage in a cline to the southern forms *prae-hispulla* and *emibispulla*. The differences between this race and *janira* are not great or consistent.

#### race *praehispulla* Verity

*Epinephele jurtina* race *praehispulla* Verity, 1921: 210.

Type locality. Florence — Verity, 1921.

Genitalia. Eastern.

Description. Verity, 1921.

Diagnostic. The larger size and fairly consistent fulvous suffusion on the female upperside hindwing are the only distinguishing features of this race.

Discussion. This race represents no more than a development of race *phormia*. Whether such minor distinctions are worth recognising is open to question.

#### form *parvula* Stauder

*Epinephele jurtina hispulla* f. *parvula* Stauder, 1915: 1, pl. 2, fig. 16.

Type locality. Monte Fiato and S. Angelo — Stauder, 1915.

Genitalia. Presumably eastern.

Description. Stauder, 1915.

Range. Found by Stauder only at Monte Fiato and St. Angelo (800—1300 m).

Discussion. Although it is feasible that there exists in this part of Italy a race consisting of dwarf *jurtina*, I would think it more likely, that the sample taken (only four males) in (?) 1914 were characteristic of that year only. Races of very small size of *jurtina* are known (Isle of Man; southwest Sweden).

#### form *schweigeri* Tauber

*Maniola jurtina schweigeri* Tauber, 1970: 111—112.

Type locality. Ulu Dag, Bursa, c. 1800 m.

Genitalia. Eastern type *a* (from few specimens).

Description. Tauber, 1970.

Range. Only in the type locality.

Discussion. This race is described on the evidence of the male genitalia. No females were found or examined. As has been stated the eastern type *a* valve has been found in various scattered localities as far apart as north Italy, Crete and U.S.S.R. Consequently, I do not believe that *schweigeri* should be recognised as a geographical race.

#### *Maniola jurtina emihispulla* Verity

*Epinephele jurtina* race *emihispulla* Verity, 1919: 124.

Type locality. Poggio, Elba — Verity, 1919.

Genitalia. Eastern with some transitional forms.

Description. Verity, 1953: 269.

Diagnostic. The fairly extensive female fulvous on the upperside is distinctive.

Range. Elba, Corsica and perhaps the far south of Italy. The form in some localities in the Maritime Alps (e.g. Col du Tende) is probably best placed with this sub-species.

Discussion. This is the only race with eastern type genitalia which makes any real approach to the fulvous marking found in *hispulla*. Even this is, however, not consistent and the underside medial line on the forewing is characteristically eastern.

#### *Maniola jurtina corfiothispulla* Graves

*Maniola jurtina corfiothispulla* Graves, 1933: 180.

Type locality. Corfu — Graves, 1933.

Genitalia. Eastern.

Description. Graves, 1933.

Diagnostic. The large size of both sexes, dully coloured upperside of the male and

peculiar fulvous colour in the female, serve to distinguish this race.

Range. Known only from Corfu and Crete.

Discussion. It is likely that *corfiothispulla* will be found on other Greek islands, where conditions have favoured its evolution.

### *Maniola jurtina persica* Le Cerf

*Epinephele jurtina* var. *persica* Le Cerf, 1912: 227.

Type locality. Iran (Tidar, Cazevin, Hamadan, Kohroud) — Le Cerf, 1912.

Genitalia. Eastern.

Description. Le Cerf, 1912: 227 (illustrated by Le Cerf, 1913: pl. II, figs. 16, 17).

Diagnostic. See Le Cerf, 1913: 42—43.

Range. Plateau of Iran, Kurdistan and northeast Turkey.

Discussion. The differences between *persica*, *strandiana* and other eastern races require to be defined much more clearly.

### *ghilanica*-group

### *Maniola jurtina ghilanica* Le Cerf

*Epinephele jurtina* var. *persica* Le Cerf, 1912: 227.

Type locality. Ghilan: Seilan-Kelahé, Seng-e-Serek, Sia-Khâni — Le Cerf, 1913.

Genitalia. Primitive.

Description. Le Cerf, 1913. Male — 50.3 mm (smallest 49.0: largest 52.0); upperside: forewing fulvous scaling orange suffuse and variable usually confined to a ring around the apical eyespot. Apical eyespot moderately large and well defined distinctly pupilled. Androconial band well defined not extending beyond vein three. Hindwing without fulvous scaling; underside: forewing basal and discal areas light fulvous barely distinguishable from the submarginal band usually with no medial line. Outer margin and termen greyish almost without striae. Apical eyespot moderately large single pupilled. Hindwing basal and discal areas greyish brown. Medial band very slightly lighter, usually with two to four ocelli, unpupilled and encircled with fulvous. Wing almost without striae;

Female — 56.3 mm (smallest 55.0: largest 58.0); upperside: ground colour dark. Forewing fulvous scaling orange present as a suffuse patch in the discal area. Submarginal band fairly extensive, not broken by the ground colour along the nervures. Apical eyespot rather small, sometimes bipupilled. Hindwing with occasional submarginal fulvous; underside: forewing basal and discal areas light reddish fulvous, contrasting with the lighter submarginal band with an indistinct medial line. Outer margin and termen greyish brown fulvous, darker basally, fairly strongly striate. Apical eyespot moderately large, sometimes bipupilled. Hindwing basal and discal areas outer margin rather dark grey or brown fulvous. Medial band silvery or violet grey without ocelli. Wing rather strongly striate.

Variation is largely confined to the extent of fulvous in both sexes and the size of the female apical eyespot. The underside of the female is remarkably constant.

Diagnostic. By the smaller size and colouration of the underside in both sexes, this sub-species differs from the only other sub-species with primitive genitalia.

Range. The northern watershed of the Elburz Mountains, Iran, at least as far west as Cala-dagli in the far east of Turkey.

Diagnostic. By the smaller size and coloration of the underside in both sexes, this indeed it would indicate that my series belonged to a different race. However, the original description was based on only four males and one female. It is possible that in this region, at the edge of the *jurtina* range, the populations are so isolated, that some have evolved their own characteristics, in spite of the fact that these populations are probably more homogeneous than *jurtina* anywhere in the west.

*Maniola jurtina iranica* subsp. nov.

Holotype. Male — Ab-e-Ali, Teheran, Iran (2200 m) 4 July, 1970, J. H. Robert. Paratypes. 1 male — data as holotype, 4 females — data as holotype. Holotype and paratypes in the author's collection.

Genitalia. Primitive.

Description. Male — 54.5 mm (smallest 54.0: largest 55.0); upperside: forewing fulvous scaling yellowish confined to a ring around the eyespot. Apical eyespot moderately large, fairly well defined and distinctly pupilled. Androconial band rather well defined, not extending beyond vein three. Hindwing without fulvous scaling; underside: forewing basal and discal areas light fulvous, almost indistinguishable from the submarginal band, with a very indistinct medial line. Outer margin and termen light greyish without striae. Apical eyespot moderately large, single pupilled. Hindwing basal and discal areas and outer margin light greyish, medial band barely lighter, usually with two unpupilled ocelli, encircled with fulvous. Wing without striae. Female — 59.6 mm (smallest 58.0: largest 62.0); upperside: ground colour light. Fulvous scaling yellowish, present as a suffuse patch in the discal area. Submarginal band well defined, occasionally broken by the ground colour along the nervures. Apical eyespot large, often bipupilled. Hindwings with occasional suffuse submarginal fulvous. Underside: forewing basal and discal areas light fulvous, contrasting with the lighter submarginal band, with a very indistinct medial line. Outer margin and termen light yellowish grey, darker inwardly without striae. Apical eyespot rather large, often bipupilled. Hindwing basal and discal areas and outer margin light yellowish grey. Medial band lighter, with 0—3 very small unpupilled ocelli. Wing without striae.

Variation is in the extent and form of the female upperside fulvous which may be broken, or not by the ground colour along the nervures and the size of the apical eyespot which is occasionally very large. The female underside is virtually constant.

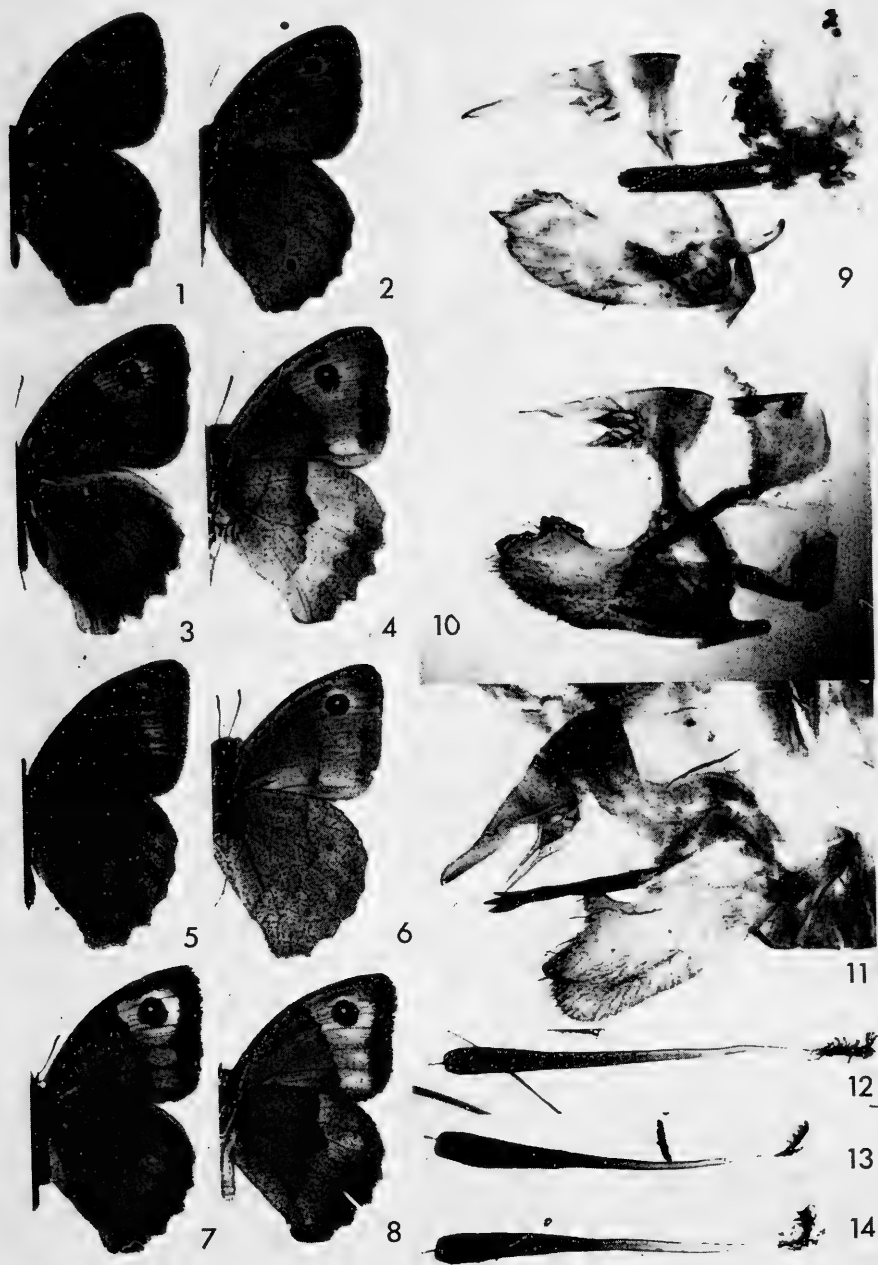
Diagnostic. Differs from *ghilanica* in its large size and by the pale light fulvous of the underside forewing and pale coloration of the hindwing in the female.

Range. The dry southern slopes of the Elburz Mountains and probably reaching across north Iran to north east Turkey.

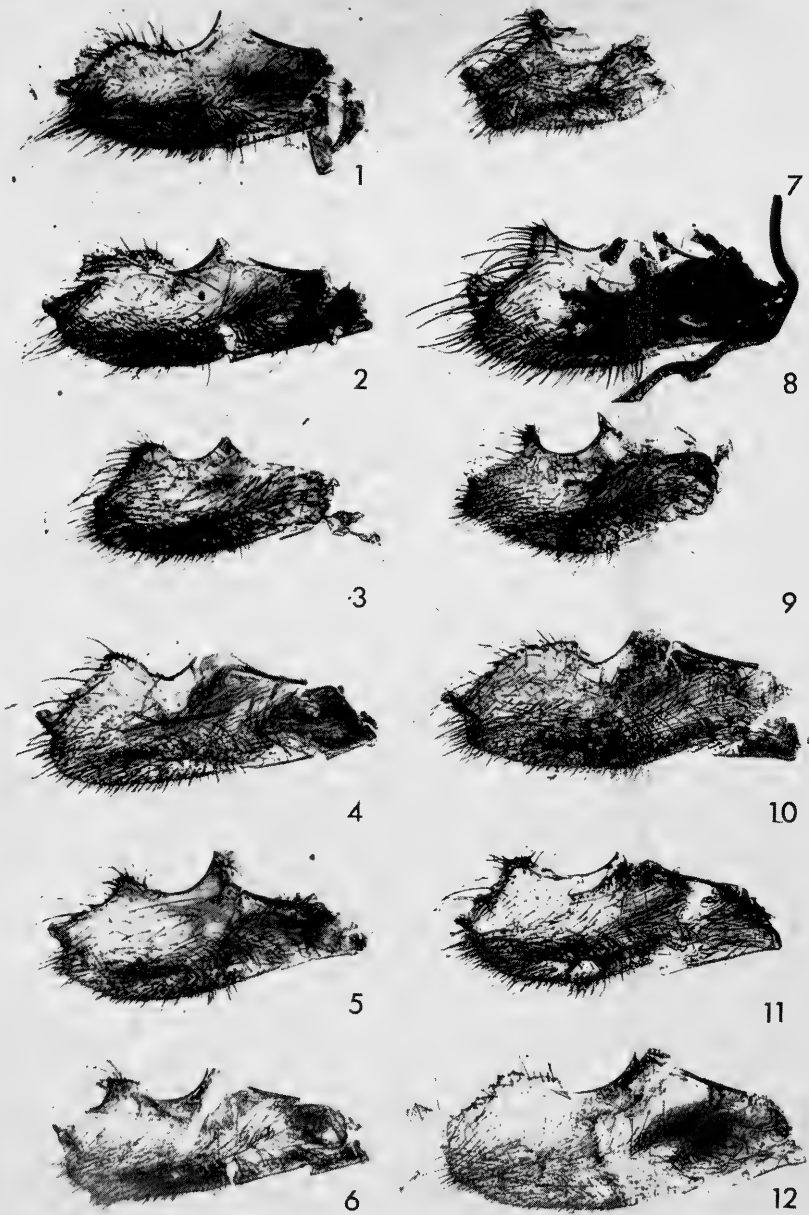
Discussion. The report by De Lattin (1950: 318) of ssp. *persica* at Van, Tatvan, Rasa-diye and Sasan-daglari in northeast Turkey probably refers to this race. The markings of *iranica* are possibly closer to *persica* than *ghilanica*.

LIST OF NAMES ASSOCIATED WITH *Maniola jurtina* L.

<i>addenda</i> Mousley	<i>fulvopincta</i> Heinrich	<i>nana</i> Stephen
<i>alba</i> Blackie	<i>ghilanica</i> Le Cerf	<i>nigrianira</i> Forsyth-Johnstone
<i>antalyana</i> Tauber	<i>glabrata</i> Leeds	<i>nigro-rubra</i> Lambillion
<i>anticrassipuncta</i> Leeds	<i>grisea</i> Tutt	<i>nuragiformis</i> Verity
<i>antifulva</i> Leeds	<i>grisea-argentacea</i> Oberthür	<i>obliterans</i> Seitz
<i>antiparvipunctata</i> Leeds	<i>bertha</i> Heinrich	<i>obliiiscens</i> Schultz
<i>antipluripunctata</i> Leeds	<i>bispulla</i> Esper	<i>occidentalis</i> Pionneau
<i>antirufa</i> Leeds	<i>bispulla</i> Hübner	<i>ocellata</i> Tutt
<i>antiultrafulvescens</i> Leeds	<i>buenei</i> Krulikovsky	<i>pallens</i> Thiery-Mieg
<i>anomala</i> Rebel	<i>hyperanthoides</i> Thomson	<i>pallidus</i> Frohawk
<i>anommata</i> Verity	<i>hyperbispulla</i> Thomson	<i>pamphilus</i> Hoefnagel
<i>apicoextensa</i> Leeds	<i>iernes</i> Graves	<i>parafeminea</i> Thomson
<i>biocellata</i> Lempke	<i>ierniformis</i> Graves	<i>parvula</i> Stauder
<i>biocellata</i> Tutt	<i>illuminata</i> Krulikovsky	<i>pauper</i> Verity
<i>biocullata</i> Rebel	<i>illustris</i> Jachontoff	<i>persica</i> Le Cerf
<i>brevipennis</i> Lempke	<i>infraimpunctata</i> Leeds	<i>phormia</i> Verity
<i>brigitta</i> Ljunch	<i>infrapupillata</i> Lempke	<i>postexcessa</i> Leeds
<i>caeca</i> Ksenschopolski	<i>infrareticulata</i> Lempke	<i>praebispulla</i> Verity
<i>caeca</i> Rebel	<i>inocellata</i> Kiss	<i>pseudomas</i> Cockerell
<i>caecoides</i> Strand	<i>insularis</i> Thomson	<i>radiata</i> Frohawk
<i>cantabrica</i> Agenjo	<i>intermedia</i> Blackie	<i>rectoformis</i> Thomson
<i>cassiteridum</i> Graves	<i>iranica</i> Thomson	<i>rufocincta</i> Fuchs
<i>cervinus</i> Frohawk	<i>janira</i> Linnaeus	<i>schweigeri</i> Tauber
<i>cinerascens</i> Fuchs	<i>janirus</i> Herbst	<i>semialba</i> Brand
<i>cinerea</i> Cosmovici	<i>jurtina</i> Linnaeus	<i>semi-intermedia</i> Lempke
<i>coeca</i> Rocci	<i>latimargo</i> Peerdeman	<i>splendida</i> Buchanan White
<i>commacula</i> Leeds	<i>lemur</i> Schrank	<i>strandiana</i> Obraztsov
<i>concolorata</i> Thomson	<i>leucothoë</i> Cabeau	<i>subbispulla</i> Strand
<i>corfiothispulla</i> Graves	<i>luigionii</i> Rostagno	<i>subtus-albida</i> Silbernagel
<i>costa-cava</i> Cabeau	<i>major</i> Leeds	<i>suffusa</i> Tutt
<i>dextro-albescens</i> Tutt	<i>maraschi</i> Pfeiffer	<i>telmessiaeformis</i> Verity
<i>emibispulla</i> Verity	<i>marginata</i> Thomson	<i>testacea</i> Schille
<i>erymanthea</i> Esper	<i>marmorea</i> Lambillion	<i>tincta</i> Blackie
<i>erymanthoides</i> Strand	<i>megala</i> Oberthür	<i>tithoniformis</i> Verity
<i>feminea</i> Graves	<i>meridionalis</i> Pionneau	<i>ubryki</i> Aigner
<i>fortunata</i> Alpheraky	<i>mirtyllus</i> Fourcroy	<i>violacea</i> Wheeler
<i>fracta</i> Zweigelt	<i>miscens</i> Verity	<i>wautieri</i> Lambillion
<i>frohawki</i> Blackie	<i>monoculus</i> Goeze	



Pl. 1. Fig. 1, 2 — *Maniola jurtina iranica*, male holotype. Fig. 3, 4 — *Maniola jurtina iranica*, female paratype. Fig. 5, 6 — *Maniola jurtina hyperbispulla*, male holotype. Fig. 7, 8 — *Maniola jurtina hyperbispulla*, female paratype. Fig. 9 — male genitalia, primitive type (Iran). Fig. 10 — male genitalia, eastern type (U.S.S.R.). Fig. 11 — male genitalia, western type (Spain). Fig. 12 — androconial scale, Morocco. Fig. 13 — androconial scale, Crete. Fig. 14 — androconial scale, Iran. (Fig. 1—8 Slightly reduced, Fig. 9—11  $\times 15$ , Fig. 12—14 greatly magnified)



Pl. 2. *Maniola jurtina* — male valve. Fig. 1, primitive, idem, Iran; Fig. 2, relict primitive, Cortina d'Ampezzo; Fig. 3, relict transitional type *a*, Surrey, England; Fig. 4, relict transitional type *a*, Chaumont, France; Fig. 5, relict transitional type *b*, Besançon, France; Fig. 6, secondary transitional, Chalons, France; Fig. 7, western type *b*, Isles of Scilly, U.K.; Fig. 8, western type *a*, Alicante, Spain; Fig. 9, western type *b*, Surrey, England; Fig. 10, eastern type *a*, north Italy; Fig. 11, eastern type *b*, Verbier, Switzerland; Fig. 12, eastern type *c*, Anexzar, Crete. All figures  $\times 16$ .

G. THOMSON: *Variation of Maniola jurtina*



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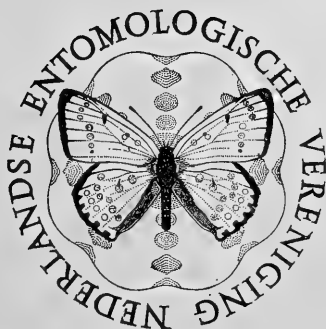
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# TIJDSCHRIFT VOOR ENTOMOLOGIE

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DE NEDERLANDSE ENTOMOLOGISCHE VERENIGING



## INHOUD

F. KASY. — Beitrag zur Kenntnis der Familie Stathmopodidae Meyrick, 1913 (Lepidoptera, Gelechioidea), p. 227—299.



# BEITRAG ZUR KENNTNIS DER FAMILIE STATHMOPODIDAE MEYRICK, 1913 (LEPIDOPTERA, GELECHIOIDEA)

von

FRITZ KASY

*Naturhistorisches Museum, Wien*

## SYNOPSIS

Aus der Familie Chrysoesthiidae (= Heliodinidae) werden zehn Genera, drei von ihnen als neue Synonyme, zur Familie Stathmopodidae gestellt und diese Familie wird charakterisiert. Von 45 Arten werden die Genitalien dargestellt, von den Gattungstypen auch das Geäder. 16 Arten werden neu synonymisiert, vier neu kombiniert, eine zu einer Subspecies reduziert und drei neu beschrieben. Die in der Paläarktis vorkommenden Arten werden ausführlicher behandelt.

Die vorliegende Studie nahm ihren Ausgang von einer Revision der wenigen im paläarktischen Raum vorkommenden Arten der Gattungen *Stathmopoda* Herrich-Schäffer und *Tortilia* Chrétien. Ein Aufenthalt am British Museum (Natural History) im Jahre 1968 ermöglichte die Ausdehnung dieser Untersuchungen auf andere Faunengebiete. Wegen der Fülle des Materials mußte ich mich dabei aber zunächst auf die Arten beschränken, die mit den paläarktischen näher verwandt zu sein schienen oder ihnen so ähnlich sind, daß sie als Synonyme in Frage kamen. Ferner wurde eine Anzahl jener Arten untersucht, die die Typen von Gattungen darstellen, die seinerzeit zu den Heliodinidae gestellt worden waren. Damit sollte geklärt werden, welche von ihnen zum *Stathmopoda*-Komplex gehören. Schließlich konnte auch noch ein erheblicher Teil der aus Südostasien beschriebenen *Stathmopoda*-Arten in die Untersuchungen mit einbezogen werden.

Der *Stathmopoda*-Komplex, der seine Hauptverbreitung in der indo-australischen Region hat, wird hier als eigene Familie innerhalb der Gelechioidea aufgefaßt. Allerdings ist dies als ein Provisorium zu werten, weil gründlichere Untersuchungen weiterer bisher bei den Heliodinidae, aber auch in anderen Familien untergebrachten Gattungen vielleicht doch noch Übergänge zu anderen Verwandtschaftsgruppen aufzeigen werden. Nach dem derzeitigen Stand unserer Kenntnisse kann man sich jedenfalls der Ansicht Gaedikes (1967) anschließen, daß *Stathmopoda* Herrich-Schäffer nicht mit *Chrysoesthia* Hübner (der jetzt gültige Name für *Heliodines* Stainton) in einer Familie Chrysoesthiidae (= Heliodinidae) vereinigt werden kann, ebenso, daß es nicht gut möglich ist, *Stathmopoda* und verwandte Gattungen bei einer der schon bestehenden Familien unterzubringen. Riedl (1969), der nur *Stathmopoda pedella* untersucht hat, stellt diese zwar wieder zu den Momphinae, bezeichnet dies aber selbst als ein Provisorium. Die Familienbezeichnung Stathmopodidae wurde übrigens schon von Meyrick (1913b: 310) gebraucht, indem er einige Arten unter diesem Namen beschrieb, aber keine Definition der Familie gab. Auch Janse (1917: 190) stellte den Familiennamen Stathmopodidae in einer Liste über eine Reihe von Arten und Gattungen aus Südafrika.

Die Familie Stathmopodidae kann wie folgt charakterisiert werden:

Kopf glatt, Augen normal, Ocellen fehlend. Meyrick gibt zwar für einige Gattungen Ocellen an (z.B. 1914b), doch konnten bei Überprüfung der Gattungstypen keine gefunden werden. Fühler kürzer als die Vfl., meist von etwa  $\frac{3}{4}$  ihrer Länge, mehr oder weniger fadenförmig, bei den Männchen von *Stathmopoda* und *Hieromantis* auffallend lang bewimpert. Scapus ohne Kamm oder einzelne Borste, meist zwei- bis dreimal so lang wie breit, manchmal aber zu einem Augendeckel verbreitert. Labialpalpen verhältnismäßig lang (meist etwa dreimal so lang wie der große Augendurchmesser), anliegend beschuppt, aufgebogen, Endglied etwa so lang wie das Mittelglied, spitz. Rüssel gut ausgebildet, wie bei den anderen Gelechioidea an der Basis beschuppt.

Hintertibien, besonders auf der Oberseite, stark behaart oder beborstet, Borsten insbesondere auch in der Umgebung der Sporen in Form von Wirbeln oder Büscheln, aber auch an den distalen Enden der basalen Tarsenglieder. Diese besondere Ausbildung der

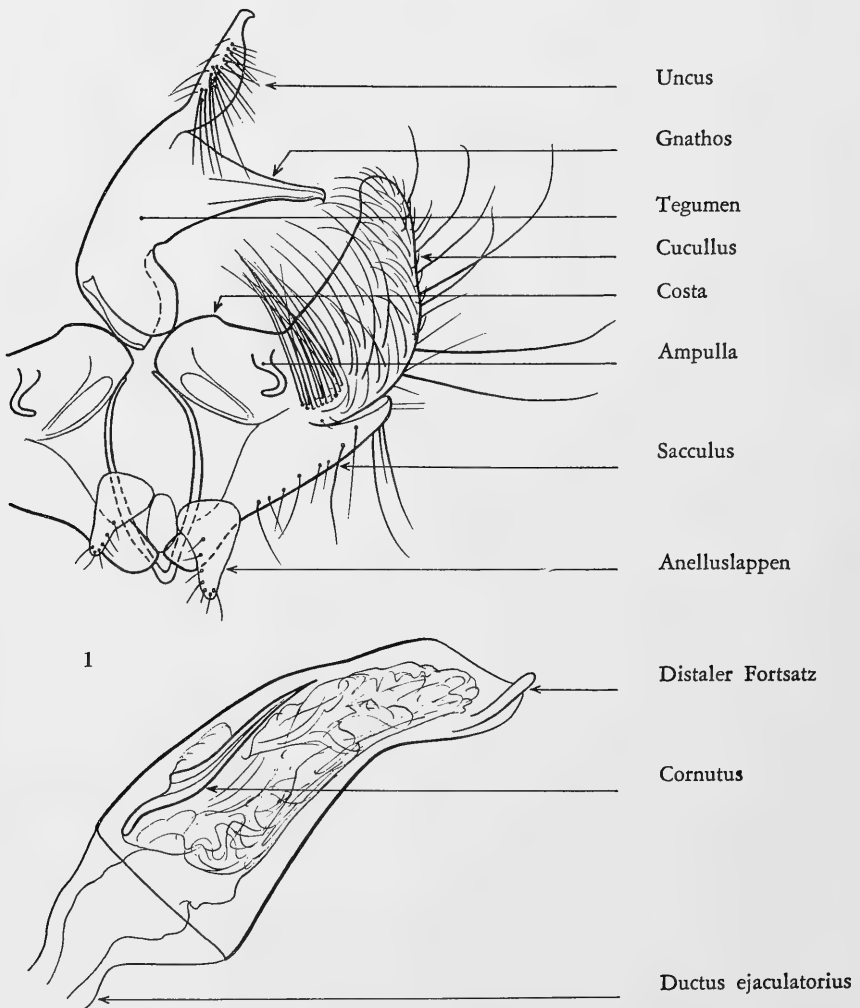


Abb. 1. Männliche Genitalarmatur einer Stathmopodide. Aedeagus herausgelöst



Hinterbeine steht offenbar im Zusammenhang damit, daß sie in der Ruhestellung des Falters nach den Seiten weggestreckt oder sogar über den Körper erhoben werden (siehe z. B. Hofmann & Spuler 1907: 10, t. 89, f. 73b).

Flügel schmal bis sehr schmal, spitz. Vfl.: r aus 4 oder 5 Ästen bestehend,  $r_1$  stets nach der Mitte, meist sogar erst weit nach der Mitte aus der Zelle entspringend. Geäder im Bereich  $m_1$  bis  $cu_2$  vollständig oder mehr oder weniger reduziert. Äußere Zellschlußadern oft nur schwach ausgebildet, besonders bei kleinen Formen. Hfl.: Zelle zwischen  $m_1$  und  $m_2$  stets offen. Geäder im Bereich  $m_1$  bis  $cu_2$  meist vollständig. Die Vfl. sind bei den meisten Arten bunt, vielfach gelb mit bräunlicher Zeichnung, auch die Thoraxoberseite ist oft bunt gefärbt und nicht selten gemustert.

Abdomen: Die Tergite auf den Segmenten 2—7 (bei den meisten Männchen) bzw. 2—6 (bei den Weibchen und manchen Männchen) mit Stacheln, meist in unregelmäßigen Reihen an den Caudalrändern, manchmal aber auch in anderer Anordnung. Manche *Stathmopoda*-Männchen haben auf der Ventralseite des 8. Segmentes ein Paar Coremata (Abb. 69 und Bradley, 1961: 151, t. 17, f. 6), andere auf der Dorsalseite vor dem Tegumen ein Büschel Duft(?) -Schuppen, bei einer Art wurde ein solches auf der Ventralseite in der Gegend des Saccus festgestellt.

Genitalien ♂ (Abb. 1)\*): Tegumen caudad gebogen, Uncus und Gnathos immer vorhanden, beide etwa gleich lang, im Querschnitt rinnenförmig. Valven einfach gebaut, dem Grundtyp der Schmetterlingsvalven entsprechend. Costa relativ kurz, in der Nähe ihres distalen Endes oft ein kurzer, nach unten oder innen gerichteter Fortsatz, der im folgenden als Ampulla bezeichnet wird. Er kann ziemlich grazil und länger sein, in diesem Falle ist er mehr oder weniger hakenförmig gebogen, oder er ist nur als Höcker oder stumpfer Zapfen ausgebildet, vielfach ist er auch ganz reduziert. Sacculus mehr oder weniger kräftig, von unterschiedlicher Länge, distal oft mehr oder weniger vortretend. Cucullus flach, an der Innenseite stark behaart, von unterschiedlicher Form. Aedoeagus ohne deutliches Coecum, relativ plump, mehr oder weniger walzenförmig oder distal verjüngt, vielfach schwach gekrümmt, auf einer Seite mit einem distalen Fortsatz endend. Dieser ist meist haken-, spatel- oder bandförmig oder, bei sich stark verjüngendem Aedoeagus, als sklerotisierte Spitze desselben ausgebildet. Bei der Mehrzahl der Arten keine Cornuti oder nur eine größere Zahl winziger Stacheln vorhanden, bei manchen Arten aber auch kräftige Cornuti ausgebildet.

Genitalien ♀ (Abb. 2)\*): Ostium bursae meist am Caudalrand, breit. Fast immer ein vom Ductus bursae deutlich abgesetztes, breites, im Querschnitt flaches Antrum vorhanden, manchmal mit winzigen Stacheln, manchmal mit Falten, aber nie stärker sklerotisiert. Ductus bursae weichhäutig, bei einigen Arten nach dem Antrum auf jeder Seite ein sklerotisiertes Stäbchen in der Wand, bei manchen Arten im Ductus bursae eine kropfförmige Auftreibung, die Falten und Wandverdickungen aufweist. Corpus bursae immer zweiteilig, der erste Abschnitt blasenförmig, mit ein oder zwei Signa, meist in Form sklerotisierter Falten mit schwach gesägten Rändern, manchmal eines mit einem schräg abstehenden Zahn. Am Übergang zum zweiten Abschnitt des Corpus bursae und in diesem oft dörnchenähnliche Sklerite, manchmal auch Stachelfelder. Der zweite Abschnitt des Corpus bursae, der vom ersten meist schon am Übergang zum Ductus bursae abzweigt, ist im allgemeinen mehr oder weniger schlauchförmig, manchmal sehr lang, oft

\*) In der vorliegenden Publikation werden die ♂-Genitalien stets doppelt so stark vergrößert dargestellt wie die ♀-Genitalien.

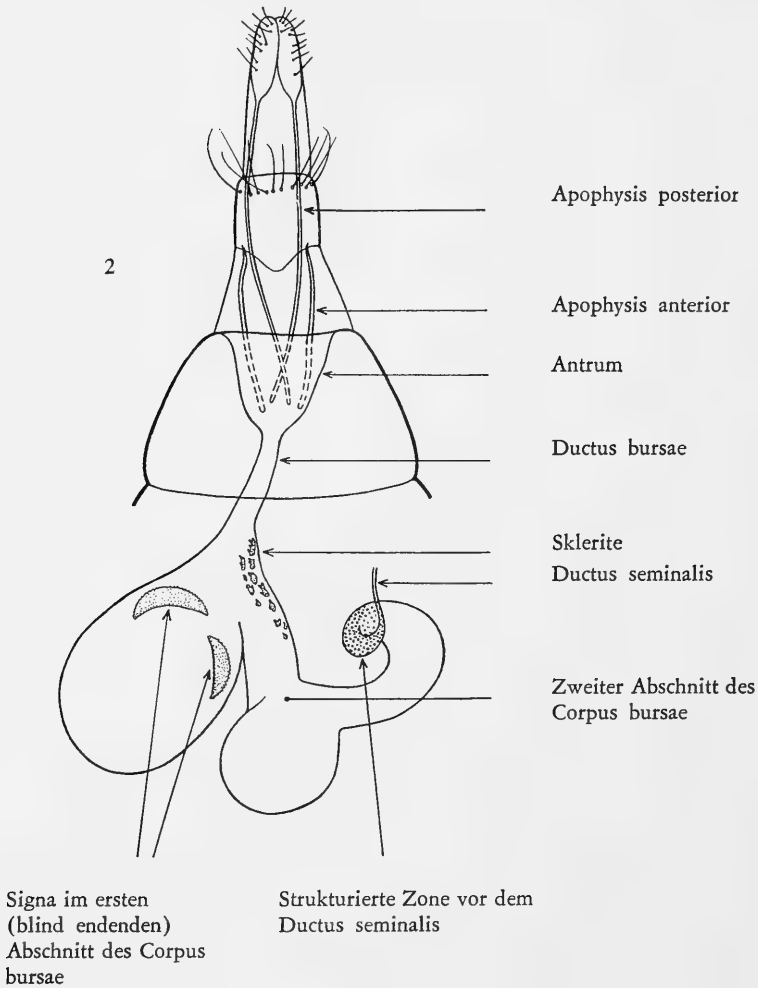


Abb. 2. Weibliche Genitalarmatur einer Stathmopodide

mit blasenartigen Auftreibungen, bei einigen Arten ist er aber zu einem zipfelförmigen Anhang reduziert. Er verjüngt sich schließlich zum Ductus seminalis, vor diesem ist seine Wand meist mehr oder weniger deutlich strukturiert, weil sie winzige Körnchen oder Dörnchen enthält; die Zone mit dieser Wandstruktur ist unterschiedlich lang. Die Ausbildung des zweiten Abschnittes des Corpus bursae ist artcharakteristisch, weshalb er bei der Anfertigung der Genitalpräparate sorgfältig herauspräpariert werden muß. Ovipositor nicht stärker sklerotisiert, Apophyses anteriores von ca.  $\frac{1}{2}$  bis  $\frac{2}{3}$  der Länge der Apophyses posteriores.

Sowohl die männlichen wie die weiblichen Genitalien sind innerhalb der ganzen Familie so einheitlich ausgebildet, daß sie kaum zur Trennung von Gattungen dienen können.

Erste Stände und Ökologie: Nur von wenigen Arten bekannt. Von diesen leben die Raupen teils an bzw. in Früchten und Blüten, manche an Sporangien von Farnen, teils an abgestorbenen Pflanzenteilen, andere aber — vermutlich räuberisch — in Kolonien

von Schildläusen; auch in Pflanzengallen sollen welche leben. Die Raupen einiger Arten wurden schädlich an Feigen- bzw. Kaki-Früchten, an *Ceratonia*-Schoten, an getrockneten *Cassia*-Blättern (Senna) und an getrockneten Orangenschalen gefunden? Auch aus den Beeren des Kaffeestrauches wurde eine *Stathmopoda*-Art gezüchtet (Meyrick 1936 : 618). Während die meisten Stathmopodidae-Raupen nicht an frischen Blättern zu leben scheinen, gibt Fletcher (1933: 20) ein Schadauftreten der Raupen von *Hieromantis ioxysta* Meyrick an dem Baum *Schleichera trijuga* (inzwischen als Synonym von *Cupania lessertiana* erkannt, Fam. Sapindaceae) an.

Verbreitung: Hauptsächlich indo-australisch, aber auch in anderen tropischen und subtropischen Gebieten der Alten Welt vorkommend, daher sicher erst ein Bruchteil der Arten bekannt, in Amerika anscheinend schwach vertreten, in Europa nur eine Art.

Die Untersuchungen am *Stathmopoda*-Komplex wurden durch die Bereitstellung von Material und sonstige Hilfe durch folgende Herren in dankenswerter Weise unterstützt: H. G. Amsel, Landessammlungen für Naturkunde, Karlsruhe; St. Bleszynski, zuletzt Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn; A. Diakonoff, Rijksmuseum van Natuurlijke Historie, Leiden; W. Dierl, Zoologische Sammlung des Bayerischen Staates, München; M. I. Falkovitsh, Zoologicheskii Institut Akademii Nauk USSR, Leningrad; F. Hartig, Instituto di Entomologia, Bozen; S. Moriuti, Entomological Laboratory, College of Agriculture, University of Osaka Prefecture, Sakai; K. Sattler, British Museum (Natural History), London; L. Vári, Transvaal Museum, Pretoria; P. Viette, Muséum national d'Histoire naturelle, Paris. Mein ganz besonderer Dank gilt der Deutschen Forschungsgemeinschaft, die mir durch ein Stipendium einen zweimonatigen Studienaufenthalt am British Museum (Natural History) ermöglichte, sowie den Herren in den dortigen Lepidopteren-sammlungen, insbesondere P. E. S. Whalley und J. D. Bradley für die freundliche Aufnahme und vielseitige Unterstützung. Die gewissenhafte Anfertigung der Zeichnungen verdanke ich wieder meinem Mitarbeiter Herrn Richard Imb.

Für die immer wiederkehrende Bezeichnung "Coll. British Museum (Natural History), London" wird im folgenden die Abkürzung (BM), für "Coll. Naturhistorisches Museum Wien", die Abkürzung (Mus. Vind.) verwendet. Die Abkürzungen im Literaturverzeichnis entsprechen denen der "List of Serial Publications in the British Museum (Natural History) Library", London 1968.

Liste und Reihenfolge der im folgenden behandelten Stathmopodidae-Gattungen und -Arten <sup>1)</sup>.

1) ♂-Fühler nicht gewimpert.

*Tortilia* Chrétien. Synonyma: *Diadoxastis* Meyrick syn. n., *Apertodiscus* Amsel.

*Tortilia flavella* Chrétien. Synonyma: *Isorrhhoa sidiota* Meyrick syn. n., *Stathmopoda trigonella* Zerny

<sup>1)</sup> Über die von mir untersuchten, nicht zu den Stathmopodidae gehörenden Gattungen wird eine eigene Publikation erscheinen.

*Tortilia hemitorna* (Meyrick) comb. n.

*Tortilia charadritis* (Meyrick) comb. n. Synonyma: *Stathmopoda stupenda* Turati syn. n., *Tortilia viatrix* Busck syn. n., *Tortilia zernyi* (Amsel) syn. n., *Stathmopoda trissorrhiza* Meyrick syn. n.

*Tortilia parathicta* (Meyrick) comb. n. Synonymum: *Labdia cholerotha* Meyrick syn. n.

*Tortilia pallidella* sp. n.

*Calicotis* Meyrick

*Calicotis crucifera* Meyrick

*Thylacosceles* Meyrick

*Thylacosceles acridomima* Meyrick

*Pachyrhabda* Meyrick

*Pachyrhabda steropodes* Meyrick

*Aeoloscelis* Meyrick

*Aeoloscelis hipparcha* Meyrick

*Aeoloscelis tripodae* Meyrick

2) ♂ -Fühler lang bewimpert.

*Stathmopoda* Herrich-Schäffer. Synonyma: *Boocara* Butler, *Placostola* Meyrick, *Erineda* Busck, *Agrioscelis* Meyrick syn. n., *Kakivoria* Nagano syn. n.

*Stathmopoda skelloni* (Butler)

*Stathmopoda anticyma* Meyrick

*Stathmopoda auriferella* (Walker). Synonyma: *Stathmopoda divisa* Walsingham syn. n., *Stathmopoda ischnotis* Meyrick syn. n., *Stathmopoda crocophanes* Meyrick syn. n., *Stathmopoda theoris* (Meyrick) syn. n., *Stathmopoda tharsalea* Meyrick syn. n.,

*Stathmopoda adulatrix* Meyrick syn. n., *Stathmopoda cirrhaspis* Meyrick syn. n.

*Stathmopoda diakonoffi* nom. nov. für *Stathmopoda divisa* Diakonoff

*Stathmopoda callichrysa* Lower

*Stathmopoda balanarcha* Meyrick

*Stathmopoda biclavis* Meyrick

*Stathmopoda diplaspis* (Meyrick). Synonymum: *Stathmopoda ovigera* Meyrick

*Stathmopoda placida* Meyrick. Synonymum: *Stathmopoda isoleuca* Meyrick

*Stathmopoda plinthiota* Meyrick

*Stathmopoda opticaspis* Meyrick

*Stathmopoda moriutiella* sp. n.

*Stathmopoda dicitra* Meyrick

*Stathmopoda nitida* Meyrick

*Stathmopoda dactylis* Meyrick

*Stathmopoda cissota* Meyrick

*Stathmopoda callopis* Meyrick

*Stathmopoda iners* Meyrick

*Stathmopoda tetrarma* Meyrick

*Stathmopoda triloba* Meyrick

*Stathmopoda commoda* Meyrick

*Stathmopoda leptoclista* Meyrick

*Stathmopoda sycastis* Meyrick

*Stathmopoda astricta* Meyrick

*Stathmopoda aprica* Meyrick

- Stathmopoda sycophaga* Meyrick  
*Stathmopoda ignominiosa* Meyrick  
*Stathmopoda ficivora* sp. n.  
*Stathmopoda pedella* (Linnaeus). Synonyma: *Tinea angustipennella* Hübner, *Oecophora fastuosella* Costa  
*Stathmopoda hexatyla* Meyrick  
*Stathmopoda hexatyla informis* (Meyrick) stat. n.  
*Stathmopoda stimulata* Meyrick  
*Stathmopoda monobathra* Meyrick  
*Stathmopoda balanistis* Meyrick  
*Stathmopoda horrida* Meyrick  
*Stathmopoda haematosema* Meyrick  
*Stathmopoda masinissa* Meyrick. Synonyma: *Kakivoria flavofasciata* Nagano syn. n.,  
*Stathmopoda albidorsis* Meyrick syn. n.  
*Stathmopoda tacita* (Meyrick) comb. n.  
*Hieromantis* Meyrick  
*Hieromantis ephodophora* Meyrick



3



4

Abb. 3. *Tortilia flavella* Chrétien, Geäder, Flügelpräg.—3619—Mus. Vind. Abb. 4. *T. parathicta* (Meyrick), Holotypus von *Diadoxastis parathicta* Meyrick, Geäder, Flügelpräg.—15191—BM

### Tortilia Chrétien

*Tortilia* Chrétien, 1908: 201. — Meyrick, 1914b: 5. — Busck, 1934: 68. — Amsel, 1955: 62 (*Apertodiscus* Amsel, Synonym).

*Diadoxastis* Meyrick, 1913a: 78. — 1914b: 5.

*Apertodiscus* Amsel, 1935a: 303.

*Tortilia* Chrétien: Typus: *Tortilia flavella* Chrétien (festgelegt in der Urbeschreibung, monotypisch).

*Diadoxastis* Meyrick: Typus: *Diadoxastis parathicta* Meyrick (festgelegt in der Urbeschreibung, monotypisch). **Syn. nov.**

*Apertodiscus* Amsel: Typus: *Apertodiscus zernyi* Amsel (festgelegt in der Urbeschreibung, monotypisch).

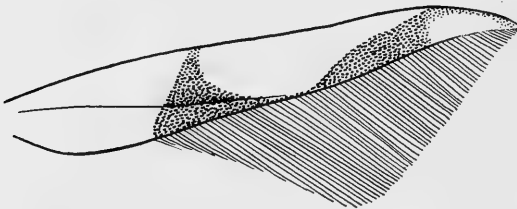
Diagnose: Chrétien (1908), Meyrick (1914b), Busck (1934).

Ergänzungen: Geäder (Abb. 3, 17): im Vfl. r nur aus 4 Ästen bestehend (vermutlich  $r_1$  mit  $r_2$  verschmolzen).

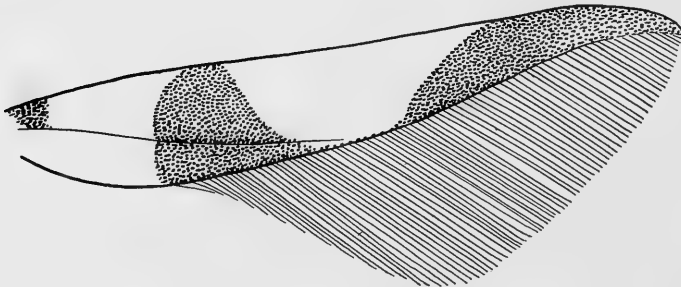
Genitalien ♂: Ohne für die Gattung typische Merkmale, vielleicht mit Ausnahme des distalen Fortsatzes am Aedoeagus, der stets hakenförmig ausgebildet ist.

Genitalien ♀: Nur ein Signum vorhanden, aber im zweiten Abschnitt des Corpus bursae Stachelfelder. Antrum oft undeutlich.

Bemerkungen: Meyrick gibt für *Diadoxastis* das Vorhandensein von Ocellen an, was einen Unterschied zu *Tortilia* bedeuten würde. Sein Befund konnte durch eigene Untersuchungen jedoch nicht bestätigt werden. Im Geäder unterscheidet sich *Diadoxastis parathicta* Meyrick von *Tortilia flavella* Chrétien nur dadurch, daß bei ihr  $m_1$  von  $r_5$  getrennt ist (Abb. 4), während bei letzterer (Abb. 3) diese Ader aus  $r_5$  entspringt. In den Genitalien bestehen aber so gute Übereinstimmungen, daß man diesen Geäderunterschied nicht als gattungstrennendes Merkmal bewerten sollte, umso mehr als innerhalb der Gattung *Statbmopoda*, wie noch gezeigt werden wird, viel größere Geäderunterschiede vorkommen.



5



6

Abb. 5. *Tortilia flavella* Chrétien, Vfl. des Lectotypus, Algerien: Biskra. Abb. 6. Ditto, Vfl. Iran: Derband bei Teheran

**Tortilia flavella** Chrétien

*Tortilia flavella* Chrétien, 1908: 202. — 1916: 491. — Amsel, 1955: 62 (*trigonella* Zerny, Synonym). — 1961: 52.

*Isorrhhoa sidiota* Meyrick, 1917: 61. — 1924: 96.

*Stathmopoda trigonella* Zerny, 1935: 149, t. 2, f. 48 (Falter, phot.).

*Tortilia flavella* Chrétien: Locus typicus: Algerien: Biskra. Lectotypus ♂ (hier festgelegt): "Gommier fleurs, B 4.8.07" "Type" [dieser Zettel wurde erst von Viette angebracht] "*flavella*". GU-3764 ♂ — Mus. Vind. Coll. Paris Mus.

*Isorrhhoa sidiota* Meyrick: Locus typicus: Westpakistan: Abbottabad. Holotypus ♂: "Holotype" "Abbottabad, N.W. India, TBF. .6.16" "*Isorrhhoa sidiota* Meyr., 2/2. E. Meyrick det., in Meyrick Coll." "Meyrick Coll. B.M. 1938—290" "*sidiota* Meyr." GU—15190—BM (BM). Syn. nov.

*Stathmopoda trigonella* Zerny: Locus typicus: Marokko: Ijjoukak (südwestl. Marakesch). Lectotypus ♂ (hier festgelegt): "Marokko, Gr. Atlas, Goundafa, 1200 m. 21. — 29. VI. 33. Zerny" "*Stathmopoda trigonella* Zerny, Typus ♂" "Orig. Fig." "Lectotypus ♂, *Stathmopoda trigonella* Zerny, 1935. teste F. Kasy, 1968". GU—3635 ♂ — Mus. Vind. (Mus. Vind.).

Diagnose (Untersucht 18 ♂, 12 ♀). Exp. 9,0—11,0 mm. Fühler hell, Scapus gelblich, distal an der Oberseite oft bräunlich. Labialpalpen ca. 2,5; Endglied etwas

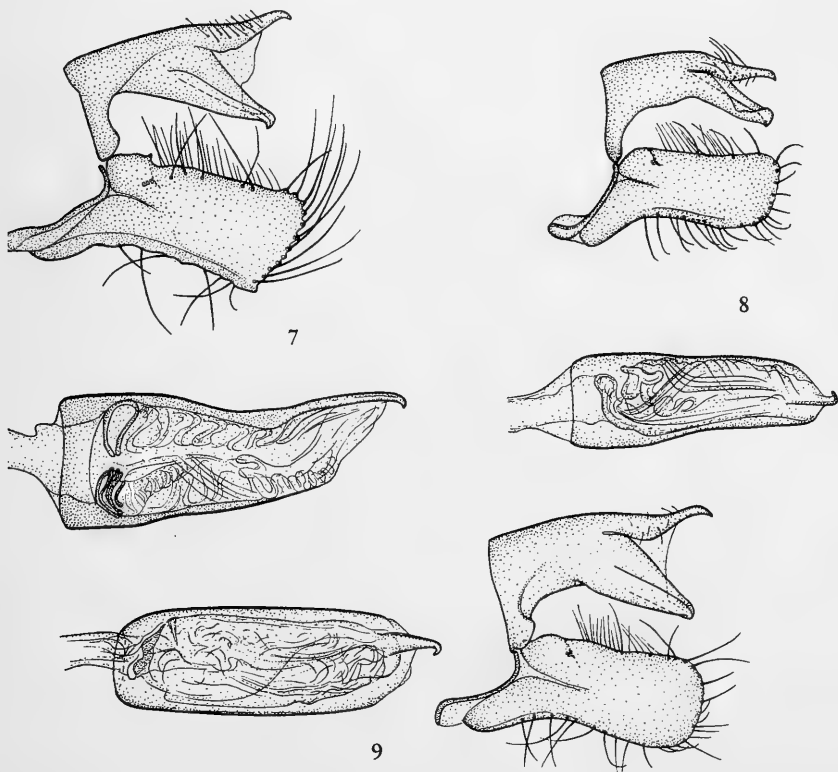


Abb. 7. *Tortilia flavella* Chrétien, ♂-Genitalien, GU—3622—Mus. Vind. Abb. 8. *T. hemitorna* (Meyrick), ♂-Genitalien, GU—15077—BM. Abb. 9. *T. charadritis* (Meyrick), Paratypus von *T. viatrix* Busck, ♂-Genitalien, GU—15146—BM

kürzer als das Mittelglied; gelblich, an den Spitzen manchmal bräunlich. Stirn weißlich bis gelblich, glänzend. Patagia gelb bis bräunlich, manchmal auch dunkler braun. Thorax gelb, manchmal hinter dem Kopf ein brauner Fleck, Schulterdecken gelb, manchmal an der Basis braun. Beine hell, gelblich, eventuell bräunlich gefleckt. Abdomen hell, gelblichgrau. Vfl. (Abb. 5 und 6) hell ockergelb mit dunkler, graubrauner bis schokoladenbrauner Zeichnung in folgender Anordnung: An der Wurzel am Vorderrand ein länglicher eckiger Fleck (nur bei den 2 Ex., die mir aus Algerien vorliegen, also auch bei dem Lectotypus von *flavella*, fehlend, vergl. Abb. 5), oft auch am Hinterrand ein kleiner, mehr grauer Gegenfleck vorhanden; nach  $\frac{1}{3}$  eine Querbinde, die am Hinterrand wesentlich breiter als am Vorderrand ist, sie ist manchmal trapezförmig, manchmal aber auch unregelmäßiger geformt, insbesondere oft am Hinterrand nach distal mehr oder weniger vorgezogen; apikaler Teil des Flügels ebenfalls dunkel, dieses Feld nach innen schräg

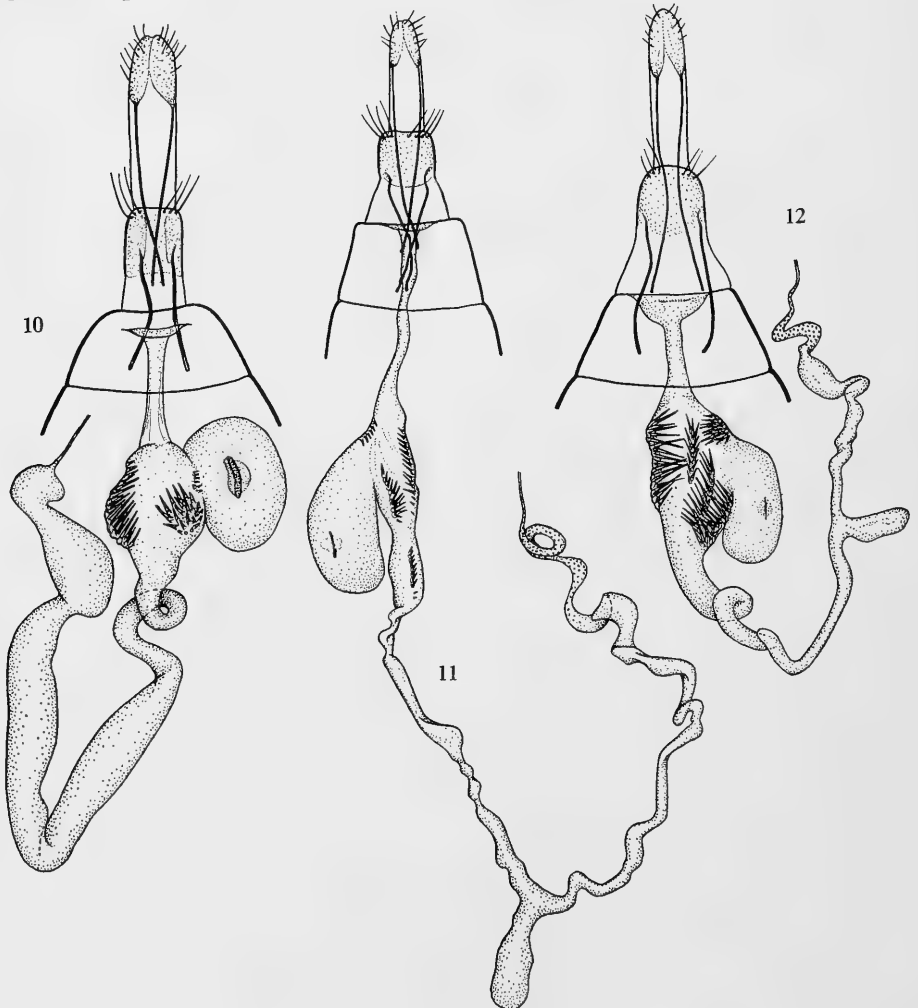


Abb. 10. *Tortilia flavella* Chrétien, ♀-Genitalien, GU—3626—Mus. Vind. Abb. 11. *T. hemitorna* (Meyrick), ♂-Genitalien, GU—15142—BM. Abb. 12. *T. charadritis* (Meyrick), Paratypus von *Apertodiscus zernyi* Amsel, ♀-Genitalien, GU—4254—Amsel



begrenzt. In diesem dunklen Apikalfeld bei den Exemplaren aus Algerien und Marokko, aber auch dem einzigen mir aus SW-Arabien vorliegenden Stück, ein länglicher Fleck von der gelben Flügelgrundfarbe (Abb. 5), bei allen anderen Exemplaren jedoch nicht einmal eine Aufhellung an dieser Stelle vorhanden. Fransen grau bis graubraun, die des Apex dunkler. Hfl. einschließlich der Fransen gelblichgrau, am Apex manchmal dunkler.

Genitalien ♂ (Abb. 7) (untersucht 14 Ex.): Tegumen mit Uncus und Gnathos etwas kürzer als die Valven. Bei letzteren Dorsal- und Ventralrand etwa parallel zueinander, Sacculus nicht vorspringend, aber bis zum Valvenende reichend, Caudalrand ziemlich gerade, nur dorsal etwas gerundet, Costa kurz, nur wenig vorspringend, Ampulla klein, zapfenförmig. Aedoeagus ziemlich plump, distal sich etwas verjüngend, ohne Cornuti, aber im basalen Abschnitt einige unregelmäßig geformte, stärker sklerotisierte Gebilde. Distaler Fortsatz ziemlich lang und grazil, mit gekrümmter Spitze.

Genitalien ♀ (Abb. 10) (untersucht 9 Ex.): Ostium bursae breit, Antrum kurz und nicht deutlich vom Ductus bursae abgesetzt. Signum groß, mit komplizierten Faltenbildungen, im zweiten Abschnitt des Corpus bursae normalerweise zwei große Felder kräftiger Stacheln, von denen das kleinere an der dem blind endenden Abschnitt zugekehrten Seite liegt, wo sich überdies noch einige kleine Stacheln befinden. Bei den zwei mir aus dem Elbursgebirge vorliegenden Weibchen sind die Stacheln in drei länglichen Feldern angeordnet und bei einem von ihnen ist noch ein viertes Feld von geringer Ausdehnung und aus kleinen Stacheln bestehend vorhanden. Bei dem einzigen mir aus Syrien vorliegenden ♀ sind die zwei Stachelfelder sozusagen zweiteilig, weil die Stacheln in Form eines U bzw. V (mit jeweils ungleich langen Schenkeln) angeordnet sind. Ob diese Unterschiede geographisch bedingt sind oder es sich vielleicht überhaupt um mehrere Arten handelt, wird erst nach Vorliegen umfangreichen Materials entschieden werden können. Der schlauchförmige Abschnitt des Corpus bursae weist zunächst einige Windungen auf und erweitert sich dann zu einem längeren mehr oder weniger blasenförmig aufgetriebenen Abschnitt, der in den eigentlichen Ductus seminalis übergeht.

Erste Stände und Ökologie: Chrétien (1908) gibt als Nahrungssubstrat der Raupe Blüten und Früchte einer Gummi liefernden *Acacia*-Art an, 1916: 491 berichtet er, daß er die Art aus an den Bäumen hängen gebliebenen, vertrockneten vorjährigen Granatäpfeln gezüchtet hat. Die Falter wurden vom Juni bis August gefangen, Chrétien vermutet zwei Generationen.

Verbreitung: Marokko: Großer Atlas: Goundafa; Algerien: Biskra, Ben Mosa; Südarabien: Aden; Syrien: Ladikije (= Lattakia); Iran: Derbend bei Teheran, ca. 2000 m; Afghanistan: Paghmangebirge WNW von Kabul, 2500 m, Nuristan: nördl. Barikot, 1200 m, Petschtal, ca. 1100 m; Westpakistan: Abbottabad; Indien: Kaschmir: Srinagar.

Bemerkungen: Die Variabilität der Art (vielleicht auch die im ♀-Genital) dürfte z. Tl. geographisch bedingt sein, was erst nach Vorliegen umfangreicheren Materials geklärt werden kann.

### *Tortilia hemitorna* (Meyrick) comb. nov.

*Stathmopoda hemitorna* Meyrick, 1913a: 37 (Diagnose!).

Locus typicus: Iidien: Madras: Ootacamund. Holotypus (Monotypus) ♀: "Holotype" "Ootacamund, India, TBF. 7400' 15. 9. 12" "*Stathmopoda hemitorna* Meyr., 4/7. E. Meyrick det., in Meyrick Coll." "Meyrick Coll. B.M. 1938—290" "*hemitorna* Meyr." GU—15141—BM (BM).

Diagnose: Die Art sieht wie eine winzige *Tortilia flavella* Chrétien aus (Exp. ca. 7 mm).

Genitalien ♂ (Abb. 8) (untersucht 3 Ex.): Kaum von denen der *flavella* verschieden, Cucullus vielleicht etwas mehr gerundet.

Genitalien ♀ (Abb. 11) (untersucht 4 Ex.): Von denen der *flavella* gut zu unterscheiden. Die Stachelfelder im Corpus bursae sind langgestreckt, ein Unterschied gegenüber *flavella* ist das Vorhandensein eines solchen am Übergang zum schlauchförmigen Fortsatz des Corpus bursae; das Signum im blind endenden Abschnitt des Corpus bursae ist viel kleiner und einfacher gebaut, nur als sklerotisierte Falte ausgebildet, der schlauchförmige Teil des Corpus bursae ist viel länger als bei *flavella*, mit einer auffälligen seitlichen Aussackung, der Abschnitt vor dem Ductus seminalis besitzt Körnchen in der Wand, wie sie auch sonst bei den Stathmopodidae an dieser Stelle meist auftreten, aber gerade bei *flavella* fehlen.

### *Tortilia charadritis* (Meyrick) comb. nov.

*Isorrhhoa charadritis* Meyrick, 1924: 65.

*Stathmopoda stupenda* Turati, 1927: 341, f. 8 (Falter, phot.).

*Tortilia viatrix* Busck, 1934: 69, t. 12, f. 1, 2 (Falter), f. 3 (Geäder), f. 4, 5 (Genit. ♂), f. 6 (Genit. ♀).

*Apertodiscus zernyi* Amsel, 1935a: 303, t. 12, f. 157 (Falter, phot., unkenntlich), t. 17, f. 64 (Genit. ♂, ohne Aedoeagus), f. 65 (Geäder Vfl., unrichtig). — 1935b: 211. — 1935c: 269.

*Apertodiscus cernyi* Amsel: Zacher 1934: 107 (lapsus calami!).

*Stathmopoda trissorrhiza* Meyrick, 1939: 58.

*Isorrhhoa charadritis* Meyrick: Locus typicus: Oberägypten: Assuan. Holotypus (Monotypus) ♂: "Holotype" "Aswan, Egypt, KJH. 5. 5. 21" "*Isorrhhoa charadritis* Meyrick, 1/1. E. Meyrick det., in Meyrick Coll." "Meyrick Coll. B.M. 1938—290" "*charadritis* Meyr.". GU—15177—BM (BM).

*Stathmopoda stupenda* Turati: Locus typicus: Libyen: Cyrenaica: Giarabub. Holotypus (Monotypus) ♂: "Typ." "VII. 26, Cyrenaica, R. U. Agrario 2272, Geo. C. Krüger". GU—3917—Mus. Vind., Coll. Hartig, Bozen. Syn. nov.

*Tortilia viatrix* Busck: Locus typicus: U.S.A.: New Jersey: Hoboken, eingeschleppt aus dem Sudan. Syn. nov. — Zur Untersuchung stand mir eine Serie Paratypen aus dem (BM) zur Verfügung.

*Apertodiscus zernyi* Amsel: Locus typicus: Palästina: Jericho. Holotypus ♀: "Georgsklost., Wadi el Kelt, 21. 5. 1930. Lichtfang" "Palästina Expedition 18. 2. — 4. 6. 30. H. Amsel" "Typus, leg. H. Amsel. *Apertodiscus zernyi*". GU—4256—Amsel. Coll. Amsel, Karlsruhe. Syn. nov.

*Stathmopoda trissorrhiza* Meyrick: Locus typicus: Westpakistan: Lyallpur. Lectotypus ♂ (hier festgelegt): "Lectotype" "Lyallpur, Punjab, 18.IV.1936. G. Singh." "dried fruits Zizyphus sp." "*Stathmopoda trissorrhiza* Meyr., Type, E. Meyrick det." "*Stathmopoda trissorrhiza* n. sp." "Lectotypus ♂, *Stathmopoda trissorrhiza* Meyrick, 1939. teste F. Kasy, 1968". GU—15305—BM (BM). Syn. nov. Der Lectotypus wurde aus den zwei Cotypen des (BM) ausgewählt, die beide ♂ sind. Da Meyrick ♂ und ♀ angibt, ohne deren Zahl zu nennen, wäre es möglich, daß er entweder (wie auch in anderen Fällen) das Geschlecht nicht richtig bestimmt oder daß die Typenserie ursprünglich aus mehr als zwei Exemplaren bestanden hat.

Diagnose (untersucht 6 ♂, 10 ♀): Exp. 7,2—9,2 mm. Fühler hell, bräunlich, Scapus bräunlich, an der Basis und distal heller, gelblich. Labialpalpen ca. 2,5, Endglied etwas

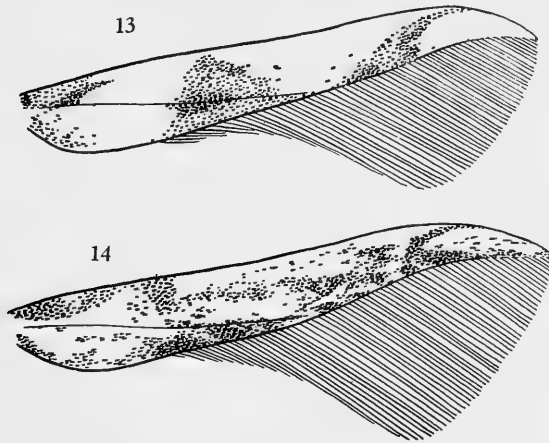


Abb. 13. *Tortilia charadriis* (Meyrick), Paratypus von *Apertodiscus zernyi* Amsel, Vfl. Abb. 14 Ditto, Vfl. ä. 20 km südl. Quetta, Westpakistan

kürzer als das Mittelglied, gelblich, Mittelglied außen mit einem bräunlichen Streifen, Endglied an der Spitze meist bräunlich. Stirn gelblichweiß, glänzend. Thorax braun, Schulterdecken gelblich, basal braun. Beine hell, gelblich, die distalen Teile bräunlich, am ersten Beinpaar auch die basalen Abschnitte, aber nur an den Außenseiten. Abdomen gelblichgrau. Vfl. (Abb. 13) hell ockergelb mit dunkelbrauner Zeichnung und Sprenkelung; an der Wurzel entlang des Vorderrandes ein brauner Streifen, bei dunklen Stücken mit der Mittelbinde verschmolzen, am Hinterrand an der Wurzel braune Beschuppung, in der Flügelmitte eine breite Querbinde, die zum Vorderrand meist schmaler wird, sie ist manchmal trapezförmig oder dreieckig geformt, meist aber sehr unscharf und unregelmäßig begrenzt; vor dem Apex eine schräge, schmale, unscharfe Querbinde; auch die hellen Flügelteile mehr oder weniger dunkel beschuppt, insbesondere in der Falte. Bei einem bei Quetta (Westpakistan) gefangenen Stück ist die Flügelzeichnung vollkommen aufgelöst (Abb. 14). Hfl. einschließlich der Fransen bräunlichgrau. Fransen gelblichgrau. Geäder: wie bei *Tortilia flavella* Chrétien (cf. auch Busck, 1934, f. 3)  $r_4$  und  $m_1$  aber sehr schwach. In der Abb. bei Amsel (1935a, t. 17, f. 65) fehlen einige Adern.

Genitalien ♂ (Abb. 9) (untersucht 3 Ex.): Sehr ähnlich dem der beiden vorhergehenden *Tortilia*-Arten, aber der Cucullus stärker gerundet.

Genitalien ♀ (Abb. 12) (untersucht 4 Ex.): Rand des Ostium bursae dicht mit winzigen Stacheln besetzt (bei *Tortilia flavella* sind solche nur bei starker Vergrößerung zu sehende Stacheln ebenfalls vorhanden, aber schütterer angeordnet und noch kleiner, bei *hemitorna* Meyrick scheinen sie ganz zu fehlen). Das Genital ist sehr ähnlich dem von *hemitorna*, also mit kleinem Signum, blasenförmiger Aussackung am schlauchförmigen Abschnitt des Corpus bursae und deutlicher Wandstruktur am Übergang zum Ductus seminalis, jedoch durch andere Ausbildung und Lage der Stachelfelder im Corpus bursae unterschieden, charakteristisch ist ein kleines rundes Feld, das sich am Übergang des Ductus bursae in den blind endenden Abschnitt des Corpus bursae befindet. Bei *hemitorna* sind an dieser Stelle nur einige in einer Längsreihe angeordnete Stacheln vorhanden. Andererseits fehlt das für diese Art typische Stachelfeld am Übergang zum schlauchförmigen Abschnitt des Corpus bursae, auch sind bei *charadriis* die Stachelfelder viel kräftiger entwickelt.

Erste Stände und Ökologie: Die Raupe wurde nach Busck (1934: 69) an getrockneten *Cassia*-Blättern in Lagerräumen schädlich. Nach Meyrick (1939: 59) an getrockneten *Zizyphus*-Früchten. Nach Amsel (1935b: 211) bzw. Zacher (1934: 107) wurde die Raupe in Kairo an getrockneten Orangenschalen gefunden. Da die Bestimmung der Falter durch Amsel erfolgt war, in dessen Typenserie seiner *zernyi* sich auch eine *Stathmopoda auriferella* (Walker) befand, könnte es sich bei dem Material von Zacher aber auch um letztere Art gehandelt haben.

Nach Busck l.c. läßt der Falter in der Ruhestellung alle Beine an die Unterlage geschmiegt, im Gegensatz also zu vielen anderen Stathmopodidae, die in dieser die Hinterbeine meist über den Körper erheben. Die gefangenen Falter stammen vom IV. (NW-Pakistan), V. (Ägypten, Palästina, Westpakistan) und VII. (Libyen).

Verbreitung: Libyen: Cyrenaica: Giarabub; Ägypten: Assuan, Kairo (? , siehe obige Bemerkung); Sudan (ohne genauere Angabe, von dort in die U.S.A.: New Jersey und New York, eingeschleppt); Südpalästina: Jericho; Westpakistan: Quetta, Lyallpur.

Bemerkungen: Die Gattung *Isorrhhoa* Meyrick, in der *charadritis* von Meyrick beschrieben worden war, gehört, wie die Untersuchung des Gattungstypus ergeben hat, zu den Cosmopterigidae. Allerdings dürften außer *charadritis* noch andere zu den Stathmopodidae gehörende Arten irrtümlich zu *Isorrhhoa* gestellt worden sein.

#### *Tortilia parathicta* (Meyrick) comb. nov.

*Diadoxastis parathicta* Meyrick, 1913a: 79. — 1914b: 5, t. 1, f. 2 (Falter, farb.).

*Labdia cholerotha* Meyrick, 1928: 387.

*Diadoxastis parathicta* Meyrick: Locus typicus: Indien: Kanara: Pala. Holotypus

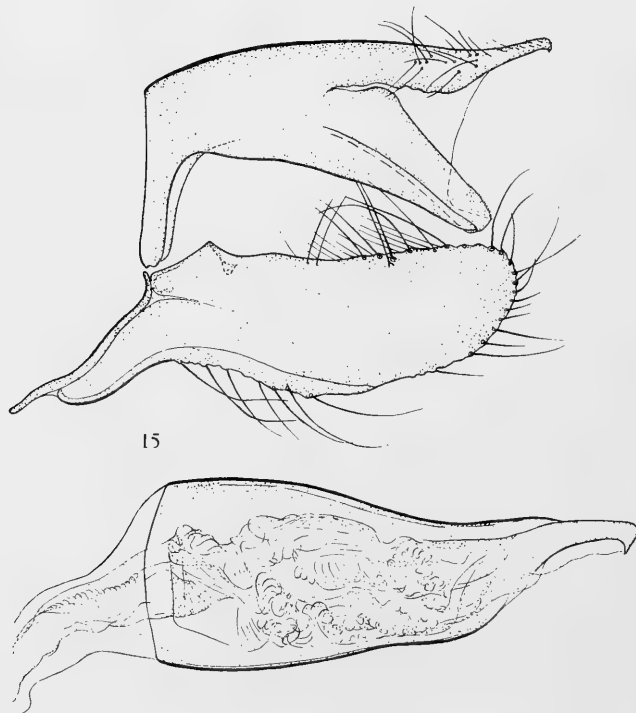
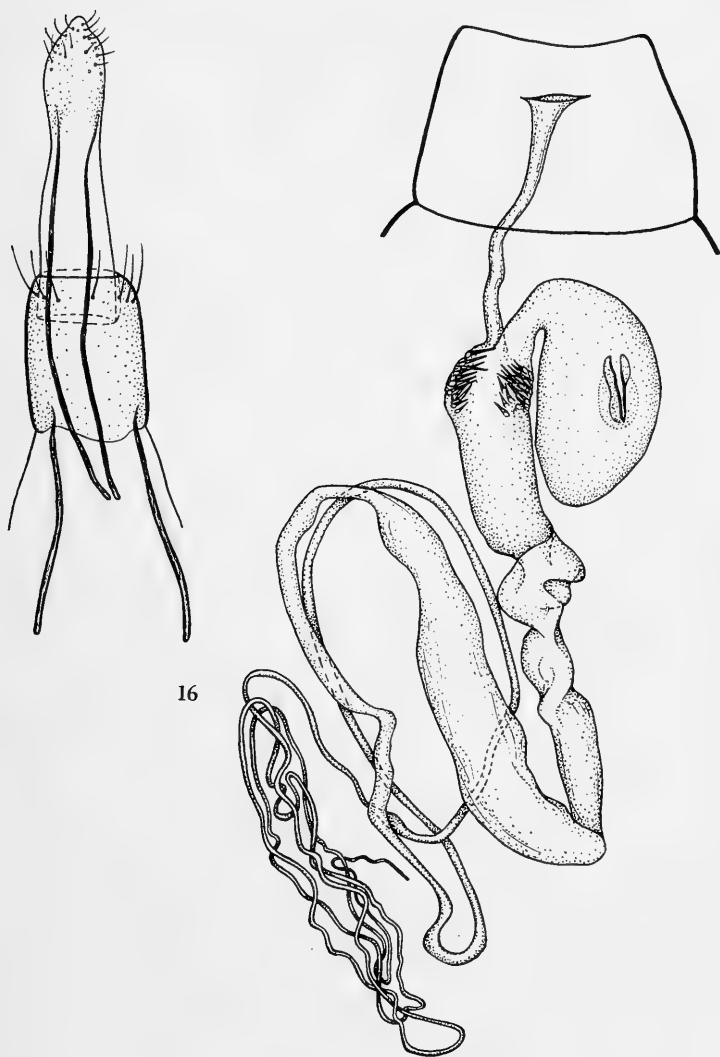


Abb. 15. *Tortilia parathicta* (Meyrick), comb. n., ♂-Genitalien, GU—15354—BM



16

Abb. 16. *Tortilia parathicta* (Meyrick) comb. n. Holotypus von *Diadoxastis parathicta* Meyrick. ♀-Genitalien, GU—15191—BM

(Monotypus) ♀: "Holotype" "Pala, Kanara, RM. 20. 10. 11" "*Diadoxastis parathicta* Meyr., 1/1. E. Meyrick det., in Meyrick Coll." "Meyrick Coll. B.M. 1938—290" "*parathicta* Meyr.". GU—15191—BM (BM).

*Labdia cholerotha* Meyrick: Locus typicus: Vorderindien: Nagpur. Lectotypus ♂ (hier festgelegt): "Lectotype" "At light, Nagpur, 17-1-1924, Fletcher coll." "5289". "Presented by R.L.E. Ford. B.M. 1949—487." "Cotype, *Labdia cholerotha*, M., Meyrick det. 1928" "*cholerotha* Meyr." "Lectotypus ♂, *Labdia cholerotha* Meyrick, 1928. teste F. Kasy, 1968". (BM). **Syn. nov.**

Diagnose: Meyrick (1913a und 1928).

Genitalien ♂ (Abb. 15) (untersucht 2 Ex.): Tegumen mit Uncus und Gnathos etwa so lang wie die Valven, diese verhältnismäßig schmal, Dorsalrand ziemlich gerade, Ven-

tralrand gebogen, Sacculus nicht vortretend, von ca.  $\frac{2}{3}$  der Valvenlänge, Costa kurz, Ampulla klein, höckerförmig. Aedeogagus distal sich verjüngend, ohne Cornuti, distaler Fortsatz kräftig, an der Spitze hakenförmig umgebogen.

Genitalien ♀ (Abb. 16) (untersucht 1 Ex.): Ohne deutlich abgesetztes Antrum, Signum groß, kompliziert gebaut, im zweiten Abschnitt des Corpus bursae zwei Stachelfelder, dieser Abschnitt in einen sehr langen schlauchförmigen Teil übergehend, der zunächst aber noch breit, blasenförmig ist.

Bemerkungen: Die zwei Typenexemplare von *Labdia cholerotha* Meyrick sind Männchen, der Monotypus von *parathicta* Meyrick ist ein Weibchen, weshalb die Synonymie nicht durch Vergleich der Genitalien bewiesen werden kann. Da die Tiere aber nicht nur gleich aussehen, sondern auch im Geäder übereinstimmen und überdies ihre Typenlokalitäten nur etwa 1000 km auseinander liegen, ist an der Synonymie wohl kaum zu zweifeln.

### *Tortilia pallidella* sp. n.

Locus typicus: Südiran: Bandar-Abbas. Holotypus ♀: "11. IV. 1972. S-Iran. 8 km östl. Bandar-Abbas. Exped. Mus. Vind.". GU—3935—Mus. Vind. (Mus. Vind.).

Diagnose (untersucht 54 ♂ und ♀): Exp. 6,3—8,9 mm. Kopf hell, gelblichgrau, glänzend; Patagia in der Mitte dunkelgelb, seitlich grau. Fühler hell, gelblichgrau, Scapus dunkel, graubraun. Labialpalpen ca. 2, Endglied etwas kürzer als das Mittelglied; hell, gelblichgrau. Thorax hell, gelblichgrau, in der Mitte aber, besonders seitlich, dunkelgelb beschuppt. Schulterdecken ebenfalls hell, gelblichgrau, an der Basis bleichgelb beschuppt. Beine hell, gelblichgrau, Hinterbeine distal dunkel gefleckt. Abdomen hell, gelblichgrau, die Segmente an der Basis bräunlich. Vfl. (Abb. 18): bleich, gelblichgrau

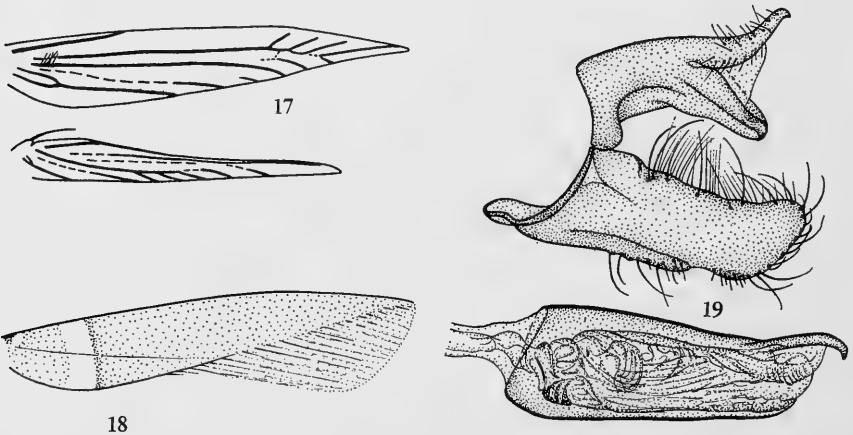


Abb. 17. *Tortilia pallidella* spec. nov., Geäder, Flügelpräp.—3919—Mus. Vind. Abb. 18. Ditto, Vfl. Abb. 19. Ditto, ♂-Genitalien, GU—3921—Mus. Vind

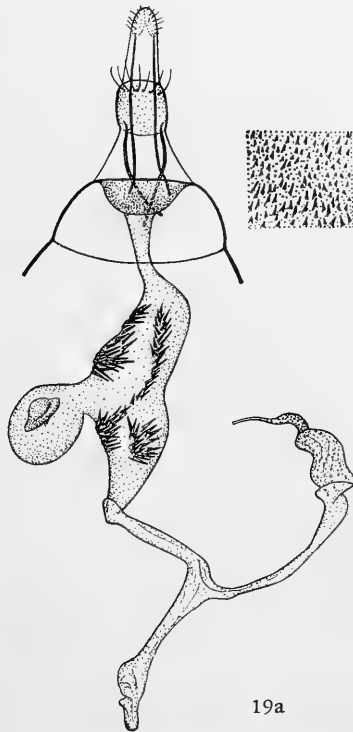
mit lila Schimmer, nahe der Wurzel eine bleichgelbe gebogene Querbinde, die sich zum Innenrand verbreitert und nach außen dunkler begrenzt ist. Bleichgelbe Beschuppung tritt auch ganz an der Wurzel auf, am Vorderrand aber ein dunkelbrauner Punkt. Fransen hell, gelblichgrau, die am Apex manchmal dunkler. Hfl. einschließlich der Fransen hell, gelblichgrau, am Apex oft mehr gelblich.

Genitalien ♂ (Abb. 19) (untersucht 2 Ex.): Tegumen mit Uncus und Gnathos nicht

ganz bis zum Valvenende reichend. Costa kurz, kaum vom Cucullus abgesetzt, Ampulla reduziert, Sacculus von ca.  $\frac{2}{3}$  der Valvenlänge, distal etwas als stumpfer Höcker vortretend; Cucullus distal etwas aufgebogen, sein Dorsalrand deshalb schwach konkav, Ventrocaudalrand breit gerundet. Aedoeagus wie bei den anderen *Tortilia*-Arten ausgebildet, also ohne Cornuti, mit kräftigem, am Ende hakenförmig gekrümmten distalen Fortsatz, Anelluslappen als ziemlich lange schmale Zipfel ausgebildet.

Genitalien ♀ (Abb. 19a) (untersucht 3 Ex.): Antrum breit, deutlich vom Ductus bursae abgesetzt, dicht mit feinen Stachelchen ausgekleidet und sich dadurch dunkler abhebend. Blind endender Abschnitt des Corpus bursae mit einem großen, kompliziert gebauten Signum, ähnlich dem von *Tortilia flavella* Chrétien. Im zweiten Abschnitt drei Stachelfelder, das mittlere langgestreckt, in der Mitte schmaler, am cephalen Ende stärker verbreitert als am caudalen; ersterem benachbart ein zweites, kleines, etwa kreisförmiges Stachelfeld, das dritte Stachelfeld wieder länglich, aber nur etwa halb so lang wie das mittlere. Schlauchförmiger Abschnitt des Corpus bursae stellenweise aufgetrieben, mit einer seitlichen Aussackung; Wandstruktur nur im Endteil. Das Genital unterscheidet sich von dem der anderen hier behandelten Arten durch die dichte, feine Bestachelung des Antrum, das bei der neuen Art auch deutlicher ausgebildet ist.

Erste Stände und Ökologie: unbekannt, bei Bandar-Abbas trat die Art in der ersten Aprilhälfte und zwar am häufigsten unter alten *Acacia*-Bäumen in einem z. Tl. kultivierten und bewässerten Gelände auf, bei Karachi wurde sie Ende Feber bis Anfang März gefangen, das einzige aus Israel vorliegende Stück stammt von Mitte August.



19a

Abb. 19a. *Tortilia pallidella* sp. n., ♀-Genitalien, rechts Ausschnitt aus der Wand des Antrum, stark vergrößert, GU—3934—Mus. Vind.

Verbreitung: Israel: Winget, Südiran: Bandar-Abbas, Westpakistan: Karachi.

Bemerkungen: Die neue Art hat mit den anderen bekannten *Tortilia*-Arten habituell keine Ähnlichkeit, sie gehört aber sowohl nach dem Geäder (Abb. 17) wie nach den Genitalien eindeutig in diese Gattung.

Paratypen: 2 ♂, 4 ♀, 8. 4. 1972, S-Iran, 8 km östl. Bandar-Abbas, Exped. Mus. Vind.; 11 ♂, 31 ♀, 11. 4. 1972, sonst gleiche Daten; 3 ♂, 10. 4. 1972, S-Iran, Dünen 17 km östl. Bandar-Abbas. Exped. Mus. Vind.; 1 ♂, 14. 4. 1972, S-Iran, 22 km nördl. Bandar-Abbas, Exped. Mus. Vind.; 1 ♂, Israel, Winget, 18. 8. 68; 1 ♂, 23. 2. - 9. 3. 1961, Umgbg. Flughafen Karachi, Pakistan, E. & A. Vartian leg.

### *Calicotis* Meyrick

Meyrick, 1889: 170. — 1914b: 7.

Typus: *Calicotis crucifera* Meyrick (festgelegt in der Urbeschreibung, monotypisch).

Diagnose: Meyrick (1889 und 1914b). Die Angabe, daß Ocellen vorhanden sind, konnte bei einer Überprüfung des Gattungstypus nicht bestätigt werden.

Ergänzungen: Geäder des Gattungstypus (Abb. 20) (untersucht 1 Vfl., 2 Hfl. verschiedener Exemplare): Im Vfl.  $r_1$  mit  $r_2$  gestielt. Im Bereich  $m_1$  bis  $cu_2$  eine Ader fehlend. Hfl. sehr schmal, Geäder stärker reduziert. Im Bereich  $m_1$  bis  $cu_2$  nur 3 Adern vorhanden,  $m_1$  erst nahe der Mitte zum Rand ziehend (wahrscheinlich handelt es sich bei dieser Ader um  $m_{1+2}$ , da ein Stück distalwärts am Flügelrand noch ein zweites Paar von Sinneskuppeln zu finden ist).

Genitalien ♂ und Genitalien ♀ ohne für die Gattung spezifische Merkmale.

Bemerkungen: Als für die Gattung typisch kann das Geäder angesehen werden (allerdings bei den anderen Arten von mir nicht untersucht) und das Vorhandensein der "Augendeckel". Mit *Patanotis* Meyrick, von der *Calicotis* nach Meyrick (1914b: 7) eine Weiterentwicklung darstellen soll, ist sie nicht verwandt. Wie eine Untersuchung des Gattungstypus ergeben hat, gehört *Patanotis* (die *Phalaritica* Meyrick nahesteht) zu den Blastodacnidae (bzw., wenn man diese nicht als eigene Familie auffaßt, zu den Momphidae). Auch zu *Licmocera* Meyrick, die wie *Calicotis* Augendeckel besitzt, besteht keine Verwandtschaft. Das gleiche gilt für *Vanicela* Walker.

### *Calicotis crucifera* Meyrick

Meyrick, 1889: 170 (Diagnose!). — 1914b: 7, t. 1, f. 5 (Falter, farb.).

Locus typicus: Neuseeland: Nordinsel: Taranaki. Lectotypus ♀ (hier festgelegt): "Lectotype" "Taranaki, New Zealand, 28/2/83" "*Calicotis crucifera* Meyr., 1/3. E. Meyrick det., in Meyrick Coll." "Meyrick Coll. B.M. 1938—290" "*crucifera* Meyr." "*Calicotis* Meyr." "Lectotypus ♀, *Calicotis crucifera* Meyr., 1889. teste F. Kasy, 1968" (BM).

Genitalien ♂ (Abb. 21) (untersucht 2 Ex.): Tegumen mit Uncus und Gnathos etwas kürzer als die Valven, distal einander genähert. Valven an der Basis breit, Cucullus aber ziemlich schmal, parallelrandig, distales Ende stark gerundet, Ampulla verhältnismäßig kräftig, fingerförmig, Sacculus etwa bis zur Valvenmitte reichend, distal etwas, aber stumpf vorspringend. Aedoeagus distalwärts nicht verjüngt, ohne Cornuti, distaler Fortsatz im Querschnitt flach, mit stumpfem Ende.

Genitalien ♀ (Abb. 22) (untersucht 2 Ex.): Antrum breit, mit einigen Längsfalten,



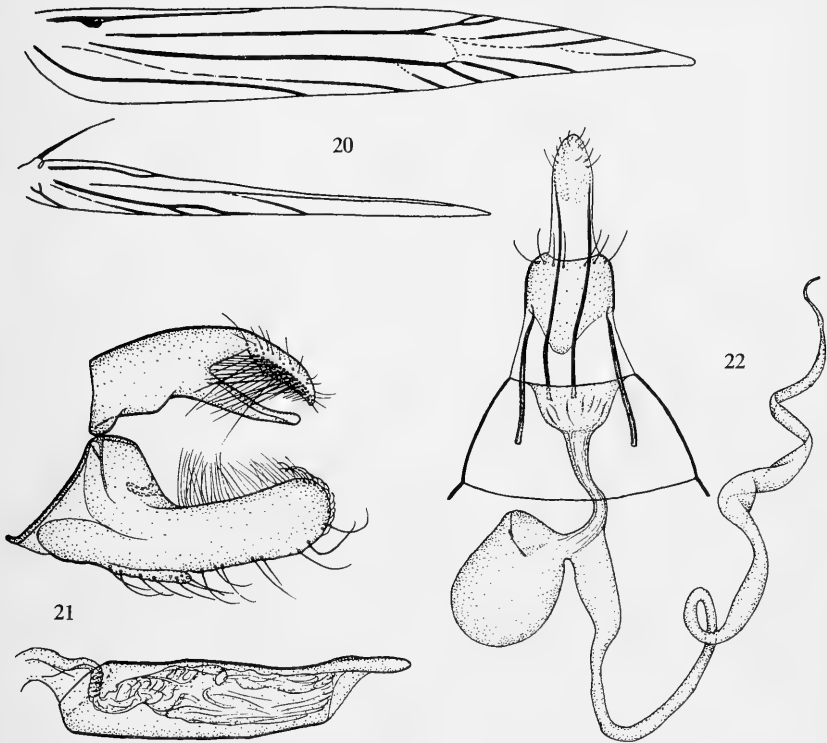


Abb. 20. *Calicotis crucifera* Meyrick, Geäder, Flügelpräp.—15115—BM. Abb. 21. Ditto, ♂-Genitalien, GU—15185—BM. Aedeogagus: GU—15110—BM. Abb. 22. Ditto, ♀-Genitalien, GU—15109—BM

nur ein Signum vorhanden (möglicherweise durch Verwachsung von zweien entstanden), zweiter Abschnitt des Corpus bursae in einen langen Schlauch übergehend.

Erste Stände und Ökologie: Meyrick (1889); die Raupe zwischen den fertilen Wedeln des Farnes *Platycerium grande*.

Verbreitung: Neuseeland: Taranaki und Palmerston, Australien: Sydney (Botanischer Garten, vielleicht eingeschleppt).

### *Thylacosceles* Meyrick

Meyrick, 1889: 171. — 1914b: 13.

Typus: *Thylacosceles acridomima* Meyrick (festgelegt in der Urbeschreibung, monotypisch).

Diagnose: Meyrick (1889 und 1914b).

Ergänzungen: Geäder (Abb. 23): Im Vfl. r aus 5 Ästen bestehend,  $r_1$  nahe  $r_2$ ;  $m_1$  fehlend.

Abdomen: Die Stachelreihen auf den Tergiten befinden sich nicht an deren Hinterrändern, sondern vor diesen im hinteren Drittel des Tergites, sie sind bogenförmig gekrümmt.

Genitalien ♂ (Abb. 24): Der Aedoeagus weicht in seiner Gestalt von dem sonst bei den Stathmopodidae üblichen Typ ab, da er seitlich einen höckerförmigen Vorsprung aufweist, auch besitzt er einen Cornutus von abweichender Form.

Genitalien ♀: Unbekannt.

Bemerkungen: Die Angabe Meyricks, daß Ocellen vorhanden sind, konnte nicht bestätigt werden. Zu den für die Gattung typischen Merkmalen kann außer der abweichenden Ausbildung des Aedoeagus auch die besondere Länge der Labialpalpen (ca. 4 × dem größten Augendurchmesser) gerechnet werden.

### *Thylacosceles acridomima* Meyrick

Meyrick, 1889: 171 (Diagnose!). — 1914b: 14, t. 2, f. 40 (Hinterbein).

Locus typicus: Neuseeland: Nordinsel: Wellington. Holotypus ♂: "Holotype" "Wellington, New Zealand, 1/1/80" "*Thylacosceles acridomima* Meyr., 1/4. E. Meyrick det., in Meyrick Coll." "Meyrick Coll. B.M. 1938—290" "*acridomima* Meyr." "*Thylacosceles* Meyr.". GU—15341—BM (BM).

Genitalien ♂ (Abb. 24) (untersucht 3 Ex.): Im Verhältnis zur Gesamtgröße des Tieres (vergleiche die Flügelabbildung) auffallend klein. Tegumen mit Uncus und Gnathos kürzer als die Valven, stark gekrümmt. Diese verhältnismäßig schmal, Costa kurz, nicht vortretend, Ampulla kurz, höckerförmig, Sacculus bis über die Valvenmitte reichend, distal stumpf vortretend, Cucullus gerundet, ventrocaudal schräg abgestutzt. Aedoeagus mit einem seitlichen, stumpfen, breiten Höcker und einem großen Cornutus, der in einer bestimmten Lage breit, löffelförmig erscheint.

Genitalien ♀: unbekannt.

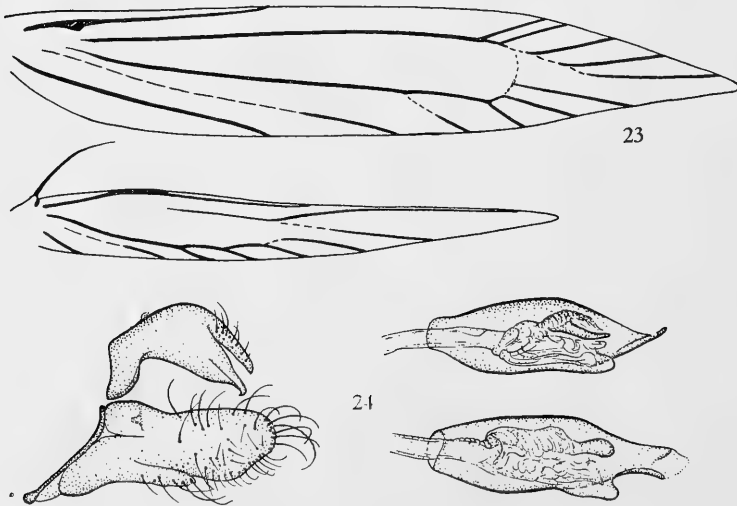


Abb. 23. *Thylacosceles acridomima* Meyrick, Geäder, Flügelpräp.—15113—BM. Abb. 24. Ditto, ♂-Genitalien, GU—15341—BM. (Aedoeagus in zwei verschiedenen Lagen)

**Pachyrhabda Meyrick**

Meyrick, 1897: 312. — 1914b: 13.

Typus: *Pachyrhabda steropodes* Meyrick (festgelegt in der Urbeschreibung, monotypisch).

Diagnose: Meyrick (1897 und 1914b).

Ergänzungen: Geäder (Abb. 25): Im Vfl. r aus 5 Ästen bestehend,  $m_1$  fehlend,  $m_2$  mit  $m_3$  aus einem Punkt. Im Hfl. das Geäder stärker reduziert (wie bei *Calicotis*).

Abdomen: Die Stachelfelder wie bei *Thylacosceles* nicht an den Tergiträndern, sondern vor diesen, in Form von Bögen.

Genitalien ♂ (Abb. 26): ohne für die Gattung typische Merkmale.

Genitalien ♀: Unbekannt.

**Pachyrhabda steropodes Meyrick**

Meyrick, 1897: 312 (Diagnose!).

Locus typicus: Australien: Victoria: Warragul. Lectotypus ♂ (hier festgelegt): "Lectotype" "Warragul, Victoria, 28/9/81" "*Pachyrhabda steropodes* Meyr., 1/5. E. Meyrick det., in Meyrick Coll." "Meyrick Coll. B.M. 1938—290" "*steropodes* Meyr." "Lectotypus ♂, *Pachyrhabda steropodes* Meyr., 1897. teste F. Kasy, 1968". (BM).

Genitalien ♂ (Abb. 26) (untersucht 2 Ex.): Tegumen mit Uncus und Gnathos fast so lang wie die Valve. Diese an der Basis am breitesten, Costa nicht vorspringend oder stärker abgesetzt, Ampulla als etwas gekrümmter Dorn ausgebildet, Sacculus bis etwa zur Valvenmitte reichend, distales Ende stumpf, nur wenig vortretend, Cucullus länglich, sein Distalrand breit gerundet. Aedoeagus ohne Cornuti, an einer Seite in einen stumpfen Fortsatz auslaufend, Anelluslappen fast kreisrund.

Genitalien ♀: unbekannt.

Verbreitung: Australien: Victoria: Warragul; Tasmanien: Mount Wellington.

**Aeoloscelis Meyrick**

Meyrick, 1897: 326. — 1914b: 16.

Typus: *Aeoloscelis hipparcha* Meyrick (festgelegt in der Urbeschreibung).

Diagnose: Meyrick (1897 und 1914b).

Ergänzungen: Geäder (Abb. 27): Wie bei vielen *Stathmopoda*-Arten. Im Vfl. r aus 5 Ästen bestehend,  $r_4$  mit  $r_5$  gestielt. Im Bereich  $m_1$  bis  $cu_2$  eine Ader fehlend.

Genitalien ♂ (Abb. 28): Ohne für die Gattung typische Merkmale.

Genitalien ♀ (Abb. 29): Beim Gattungstypus zwei Signa vorhanden, daneben auch Stachelfelder wie bei *Tortilia*.

Bemerkungen: abgesehen von der nur schwachen Bewimperung der ♂-Fühler und den zwei Stachelfeldern im Corpus bursae besitzt der Gattungstypus *Stathmopoda*-Merkmale.

**Aeoloscelis hipparcha Meyrick**

Meyrick, 1897: 328 (Diagnose!).

Locus typicus: Westaustralien: Geraldton. Lectotypus ♀ (hier festgelegt): "Lectotype" "Geraldton, W. Australia, 2/11/86" "*Aeoloscelis hipparcha* Meyr., 9/11. E. Meyrick

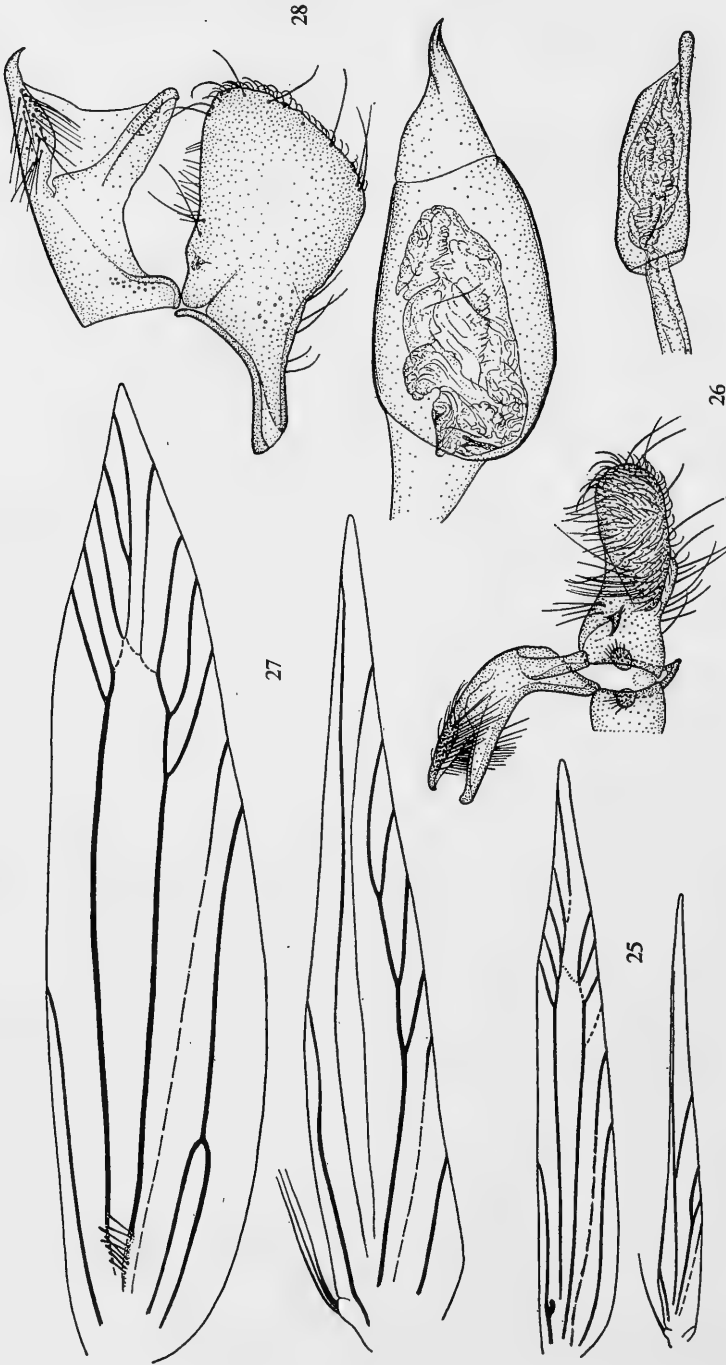


Abb. 25. *Pachyrbabada steropodes* Meyrick, Geäder, Flügelpräp.—16145—BM. Abb. 26. Ditto, ♂-Genitalien, GU—16146—BM. Aedeagus: GU—16145—BM. Abb. 27. *Aeolostelis hipparcha* Meyrick, Geäder, Flügelpräp.—15192—BM. Abb. 28. Ditto, ♂-Genitalien, GU—15193—BM

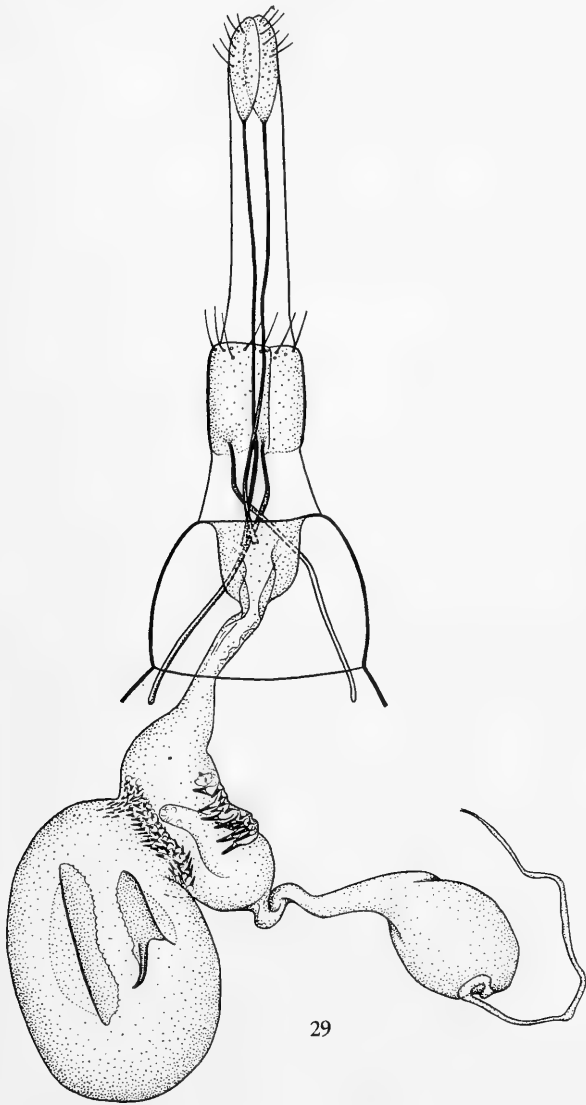


Abb. 29. *Aeoloscelis hipparcha* Meyrick, ♀-Genitalien, GU—15192—BM

det., in Meyrick Coll." "Meyrick Coll. B.M. 1938—290" "*hipparcha* Meyr." "Lectotypus ♀, *Aeoloscelis hipparcha* Meyrick, 1897. teste F. Kasy, 1968" (BM).

Genitalien ♂ (Abb. 28) (untersucht 2 Ex.): Tegumen mit Uncus und Gnathos etwa bis zur Valvenspitze reichend. Valve breit, distal sich etwas verbreiternd, Sacculus nicht vorspringend, Costa kurz, Ampulla kurz, lappenförmig. Aedoeagus im Verhältnis zum übrigen Genital sehr groß, plump, distal sich verjüngend, ohne Cornuti, distaler Fortsatz bandförmig, spitz endend.

Genitalien ♀ (Abb. 29) (untersucht 2 Ex.): Antrum vom Ductus bursae gut abge-

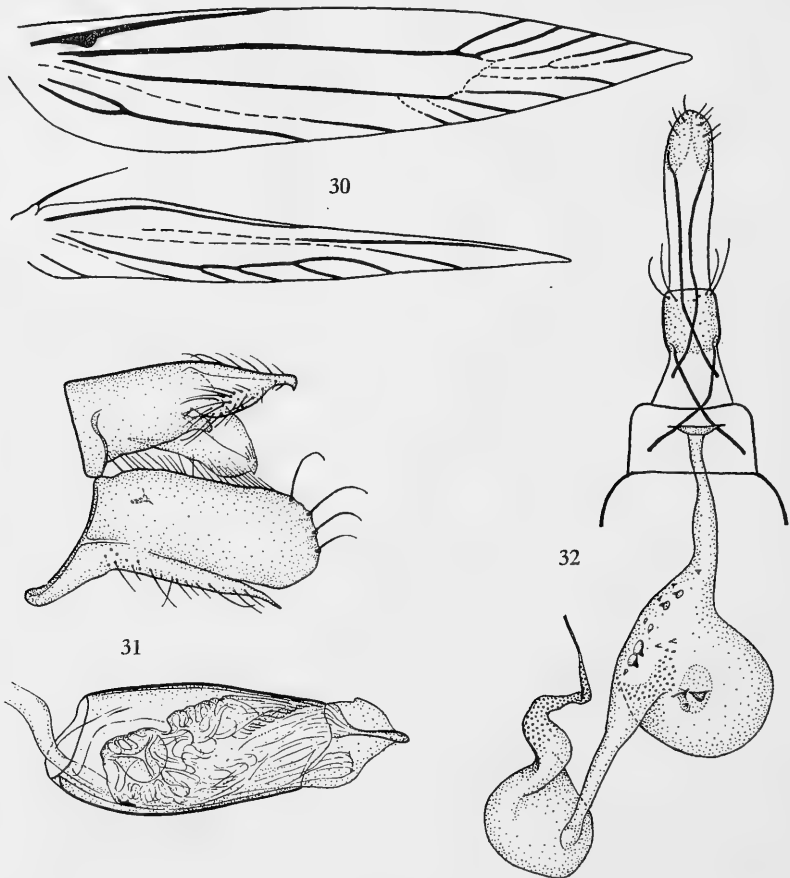


Abb. 30. *Aeoloscelis tripodae* Meyrick, Geäder, Flügelpräp.—15149—BM. Abb. 31. Ditto, ♂-Genitalien, GU—15149—BM. Abb. 32. Ditto, ♀-Genitalien, GU—15148—BM

setzt, etwa so lang wie breit, der blind endende Abschnitt des Corpus bursae mit zwei großen, ungleich ausgebildeten Signa, das größere etwa bandförmig, mit gesägtem Rand, das kleinere mit einem langen, im Querschnitt flachen, schräg wegstehenden Stachel. Der zweite Abschnitt des Corpus bursae mit zwei Stachelfeldern, von denen eines am Übergang zum blind endenden Abschnitt liegt, der ansetzende schlauchförmige Abschnitt kurz, in eine längliche Blase übergehend, an die der Ductus seminalis ansetzt.

### *Aeoloscelis tripodae* Meyrick

*Aeoloscelis tripodae* Meyrick, 1913b: 311 (Diagnose!).

*Isorrhhoa tripodae* Meyrick, 1914b: 6.

Locus typicus: S-Afrika: Transvaal: Barberton. Lectotypus ♀ (hier festgelegt): "Barberton, 17. XII. 1970, A. J. T. Janse" "*Aeoloscelis tripodae* Meyr., Type no. 241" "Lectotypus ♀, *Aeoloscelis tripodae* Meyrick, 1913. teste L. Vári, 1971". Coll. Transvaal Museum, Pretoria.

Genitalien ♂ (Abb. 31) (untersucht 1 Ex.): Tegumen mit Uncus und Gnathos kürzer als die Valven. Diese distal und basal etwa gleich breit, Distalrand gerundet, mit einigen kräftigen Borsten, Sacculus kräftig, fast so lang wie die Valve, distal spitz vortretend, Costa rückgebildet, Ampulla als kleiner fingerförmiger Fortsatz. Aedoeagus verhältnismäßig groß, etwas bauchig, ohne Cornuti, distaler Fortsatz an der Spitze verbreitert.

Genitalien ♀ (Abb. 32) (untersucht 1 Ex.): Antrum breit, nur ein Signum vorhanden, aus drei ungleich großen Höckern, die auf einer gemeinsamen Platte sitzen, bestehend, sonst kleinere und größere Dörnchen vorhanden, besonders am Übergang zum zweiten Abschnitt des Corpus bursae. Dieser besteht aus einem kurzen Schlauch, der in eine große Blase mündet, die sich zu einem Zipfel verjüngt, der in den Ductus seminalis übergeht.

Bemerkungen: Nach dem Geäder (Abb. 30) und der Form des ♀-Genitals paßt die Art gut zum Gattungstypus von *Aeoloscelis*, die Bewehrung des Corpus bursae weicht aber stärker ab. Die Überstellung in die Gattung *Isorrhoea* Meyrick, 1913, war zu Unrecht erfolgt.

### Stathmopoda Herrich-Schäffer

Herrich-Schäffer, [1853]: 54. — Stainton, 1854: 227. — Heinemann & Wocke, 1877: 426. — Meyrick, 1889: 167, 169 (*Boocara* Butler, Synonym). — 1897: 316. — Spuler, 1907—10: 389. — Meyrick, 1908: 397 (*Placostola* Meyrick, Synonym). — 1914b: 10 (*Erineda* Busck, Synonym). — Riedl, 1969: 713 (dort auch weitere Literatur).

*Boocara* Butler, 1880: 562.

*Placostola* Meyrick, 1887: 280.

*Erineda* Busck, 1909: 94.

*Agrioscelis* Meyrick, 1913a: 96.

*Kakivoria* Nagano, 1916: 136, t. 4, f. 1—18.

*Stathmopoda* Herrich-Schäffer: Typus: *Phalaena (Tinea) pedella* Linnaeus, 1761; durch sekundäre Monotypie, Herrich-Schäffer [1853]: 283.

*Boocara* Butler: Typus: *Boocara skelloni* Butler (festgelegt in der Urbeschreibung, monotypisch).

*Placostola* Meyrick: Typus: *Placostola diplaspis* Meyrick (festgelegt in der Urbeschreibung, die dort mit zur neuen Gattung gezogene *Gracilaria resplendens* Stainton gehört, wie Meyrick später selbst erkannt hat, nicht in die Verwandtschaft von *diplaspis*).

*Erineda* Busck: Typus: *Erineda elyella* Busck (festgelegt in der Urbeschreibung, monotypisch).

*Agrioscelis* Meyrick: Typus: *Agrioscelis tacita* Meyrick (festgelegt in der Urbeschreibung). **Syn. nov.**

*Kakivoria* Nagano: Typus: *Kakivoria flavofasciata* Nagano (festgelegt in der Urbeschreibung, monotypisch). **Syn. nov.**

Diagnose: Stainton (1854), Heinemann & Wocke (1877), Meyrick (1887) — (1914b), Spuler (1907—10), Riedl (1969).

Ergänzungen: Genitalien ♂: Ohne für die Gattung typische Merkmale. Aedoeagus meist ohne größere Cornuti. Ampulla gut ausgebildet bis fehlend. Einige Arten besitzen am 8. Abdominalsegment paarig ausgebildete Coremata, manche vor dem Tegumen ein Büschel Duft(?) -Schuppen.

Genitalien ♀: ebenfalls ohne für die Gattung charakteristische Merkmale. Ostium

bursae am Caudalrand des 7. Sternites, ein deutlich ausgebildetes Antrum vorhanden. Bei einigen Arten im Ductus bursae eine kropfförmige Auftreibung. Im blind endenden Abschnitt des Corpus bursae ein oder zwei Signa, diese mehr oder weniger in Form sklerotisierter Falten ausgebildet, manchmal eines davon mit einem schräg nach innen gerichteten stachelartigen Fortsatz. Daneben oft mehr oder weniger dornartige Sklerite am Übergang zum zweiten Abschnitt des Corpus bursae und in diesem selbst. Zweiter Abschnitt des Corpus bursae meist mehr oder weniger schlauchförmig, oft mit blasenartigen Auftreibungen, bei manchen Arten aber zu einem zipfelförmigen Anhang am ersten Abschnitt des Corpus bursae reduziert.

Bemerkungen: Als gattungstypisches Merkmal kann eigentlich nur die auffällige lange Bewimperung der ♂-Fühler angesehen werden, bei gleichzeitiger normaler Ausbildung des Scapus; im Gegensatz zur Gattung *Hieromantis*, bei der dieser zu einem Augendeckel verbreitert ist, die ♂-Fühler aber ebenfalls lang bewimpert sind. Die Ader r besteht im Vfl. fast immer aus 5 Ästen. Ansonsten ist das Geäder und auch die Flügelform sehr variabel, wie die Abbildungen 33—39 beweisen. Diese Unterschiede wurden

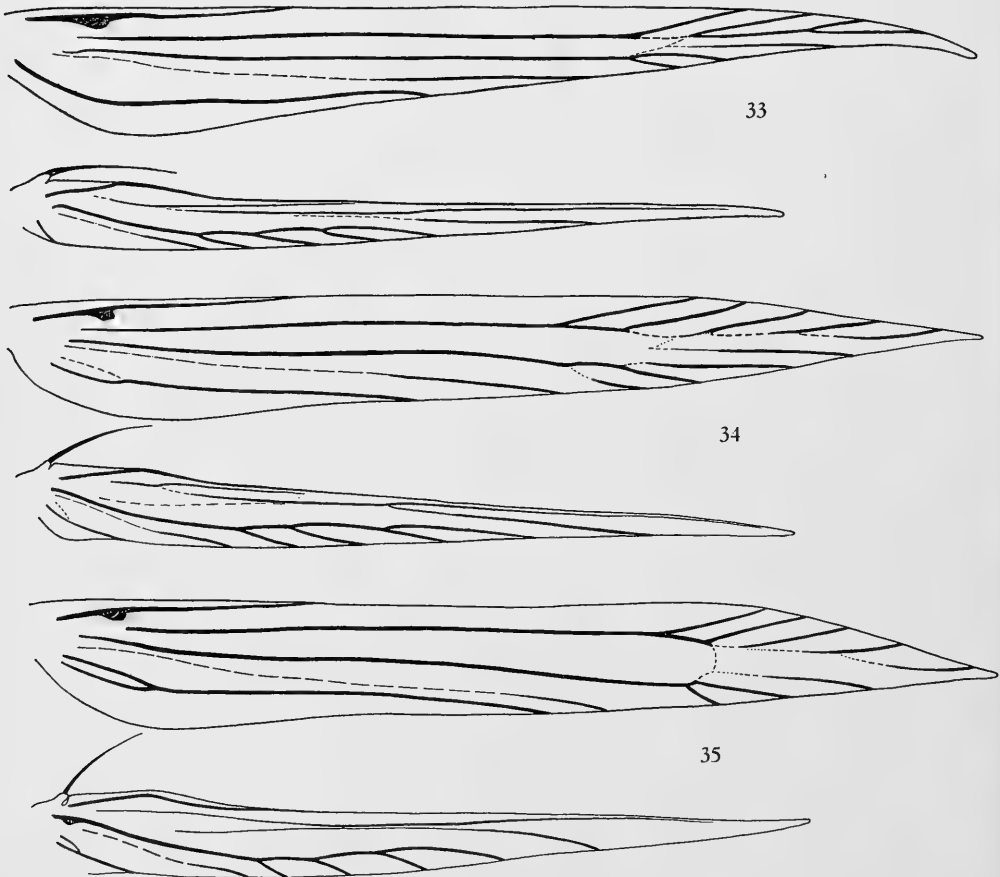


Abb. 33. *Stathmopoda sycastis* Meyrick, Geäder, Flügelpräp.—3614—Mus. Vind. Abb. 34. *S. pedella* (Linnaeus), Geäder, Flügelpräp.—3721—Mus. Vind. Abb. 35. *S. skelloni* (Butler), Geäder, Flügelpräp.—15108—BM



aber von Meyrick nicht als gattungstrennend aufgefaßt, obwohl er seine Gattungen nur nach äußeren Merkmalen und insbesondere auch nach dem Geäder unterschied. So wurde von ihm *Stathmopoda masinissa* Meyrick (= *Stathmopoda albidorsis* Meyrick) trotz der breiteren Flügel, des vollständigeren Geäders im Vfl. (Abb. 38) und der auffällig stark behaarten Hintertibien nicht in eine eigene Gattung gestellt. Andererseits wurde für diese Art (bzw. für ihr Synonym *flavofasciata*) von Nagano die Gattung *Kakivoria* errichtet, aber offenbar ohne Kenntnis ihrer Verwandtschaft mit *Stathmopoda*. Wie sich gezeigt hat, weicht die genannte Art auch in den Genitalien (Abb. 92, 93) vom Gattungstypus *Stathmopoda pedella* stärker ab (Abb. 79, 80), doch bilden andere *Stathmopoda*-Arten durch die Ausbildung ihrer Genitalapparate Übergänge. Es erscheint mir deshalb nicht zweckmäßig, gerade diese eine Art in einer eigenen Gattung unterzubringen. Aus dem gleichen Grunde ziehe ich hier auch *Agrioscelis* Meyrick als Synonym zu *Stathmopoda* ein. Nach dem Geäder (Abb. 39) und der Behaarung der Hintertibien könnte der von mir untersuchte Gattungstypus *tacita* Meyrick mit *Stathmopoda masinissa* (= *Kakivoria flavofasciata*) näher verwandt sein, der Bau der Genitalien (Abb. 94, 95) widerspricht aber einer solchen Annahme.

*Stathmopoda sycastis* Meyrick (und vermutlich auch die nach den Genitalien anscheinend verwandten Arten) hat in ihrem besonders schmalen distalen Teil des Vfl. das Geäder stärker reduziert als *Stathmopoda pedella* (Abb. 33). Sie weicht auch durch die Coremata beim ♂ von vielen anderen *Stathmopoda*-Arten ab. Vielleicht wäre hier die Aufstellung einer eigenen Gattung eher gerechtfertigt. Infolge des großen Artenreichtums wäre eine Aufteilung der Gattung *Stathmopoda* schon aus praktischen Gründen zweckmäßig. Dazu müßten aber noch weit mehr Arten und diese vor allem auch im Hinblick auf ihr Geäder untersucht werden. Überhaupt ist die Berechtigung bzw. Abgrenzung der derzeitigen Stathmopodidae-Gattungen problematisch. Man hat den Eindruck, daß es sich bei den Stathmopodidae um eine noch in voller Entwicklung befindliche, phyloge-

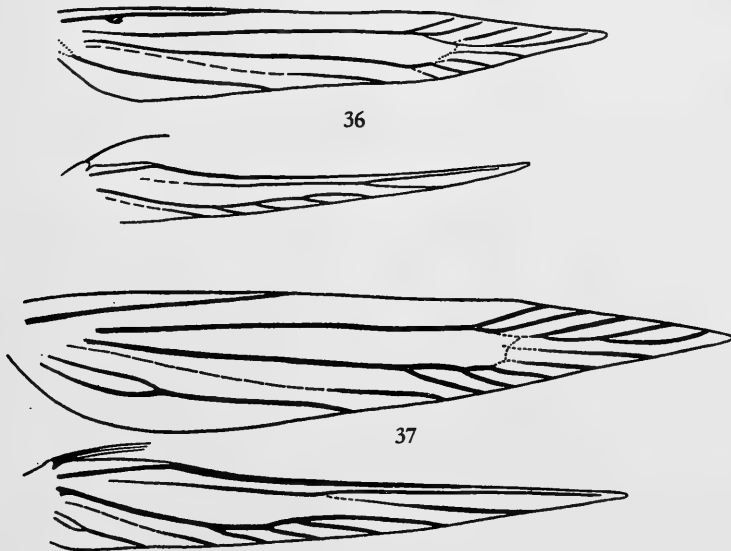


Abb. 36. *Stathmopoda diplaspis* (Meyrick), Geäder. Abb. 37. *S. auriferella* (Walker), Geäder, Flügelpräg.—3607—Mus. Vind.

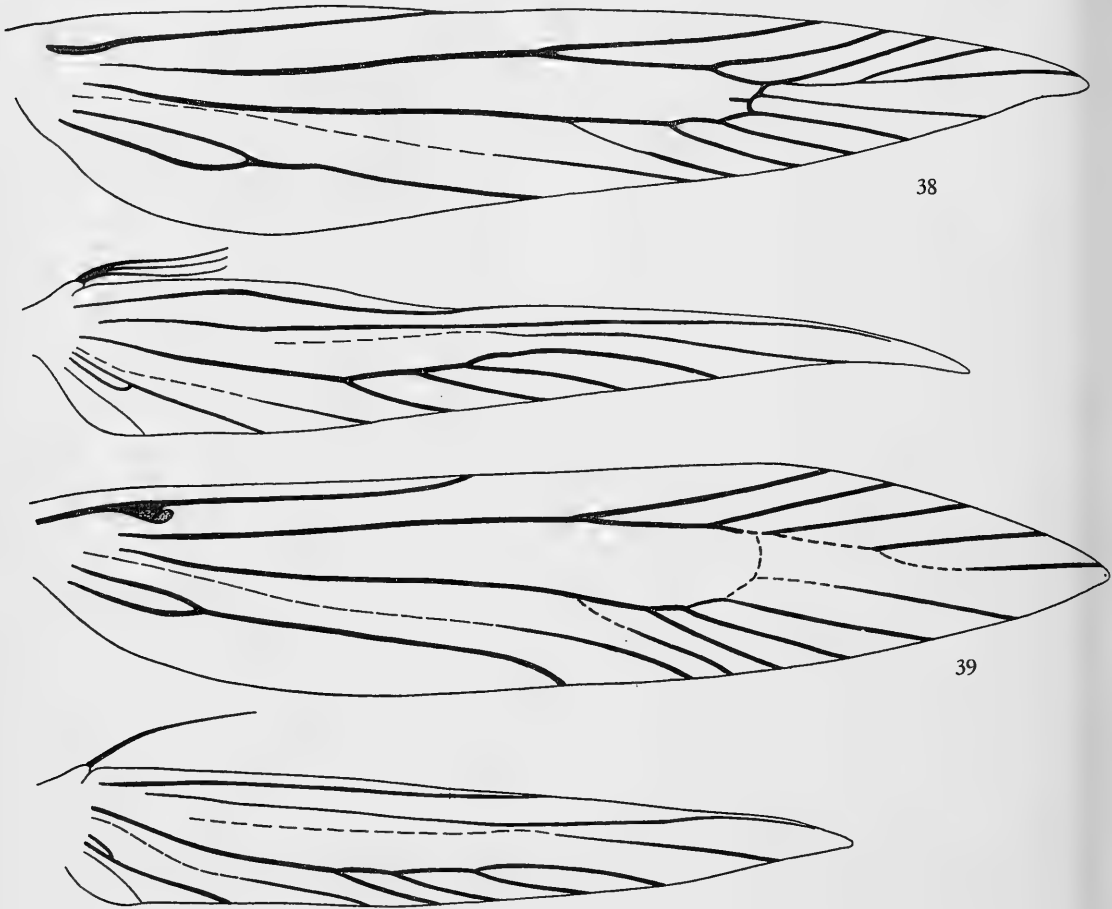


Abb. 38. *Stathmopoda masinissa* Meyrick, Geäder, Flügelpräp.—3922—Mus. Vind. Abb. 39. *S. tacita* (Meyrick), Geäder, Flügelpräp.—16142—BM

netisch junge Familie handelt, die sich noch nicht in gut voneinander zu trennende Verwandtschaftsgruppen differenziert hat. Für das geringe phylogenetische Alter könnte auch der Umstand sprechen, daß die in der indoaustralischen Region so artenreiche Familie in Südamerika keine Vertreter zu haben scheint.

Wie schon in der Einleitung betont wurde, hatten die Untersuchungen am *Stathmopoda*-Komplex primär die Aufgabe, die in der Paläarktis vorkommenden Arten zu klären. Im folgenden werden daher (wie übrigens schon bei den bisher besprochenen Gattungen) diese Arten gründlicher behandelt als die übrigen, von denen hauptsächlich die bisher unbekannt gewesenen Genitalien abgebildet und beschrieben werden. Die Anordnung der zahlreichen Arten wurde so gewählt, daß jeweils um eine aus der Paläarktis bekannte Art die mit ihr verwandten, aber auch bloß äußerlich ähnelnde, gruppiert werden. Die hier gegebene Reihenfolge ist also weit entfernt von einem natürlichen System, sie ist als bloßes Provisorium zu werten.

*Stathmopoda skelloni* (Butler)

*Boocara Skelloni* Butler, 1880: 562.

*Stathmopoda skelloni*: Meyrick, 1889: 169 (Diagnose!).

Locus typicus: Neuseeland: Südinsel: Marlborough-Provinz. Lectotypus ♀ (hier festgelegt): "Lectotype" "New Zeal., 80° 57" "*Boocara Skelloni* Butler... (unleserlich)" "*Boocara Skelloni* Butlr., Type ♂, N-Zeal. 80/57" "Lectotypus ♀, *Boocara Skelloni* Butler, 1880, teste F. Kasy, 1968". GU—15324—BM (BM). Von den drie der Beschreibung zugrundegelegten Exemplaren konnte nur eines im British Museum gefunden werden, dessen Geschlecht falsch bestimmt war.

Genitalien ♂ (Abb. 40) (untersucht 1 Ex.): Tegumen mit Uncus und Gnathos etwa so lang wie die Valven, gekrümmt. Diese kurz und breit, auch am distalen Ende, Costa kurz, Ampulla als ziemlich langer, graziler, gekrümmter Fortsatz ausgebildet, Sacculus fast bis zum Valvenende reichend, distal mit stumpfer Spitze etwas vortretend. Aedoeagus ohne auffällige Cornuti, aber mit zahlreichen winzigen Stacheln im Praeputialsack, distaler Fortsatz verhältnismäßig lang.

Genitalien ♀ (Abb. 41) (untersucht 2 Ex.): Antrum am Grunde stärker sklerotisiert. Zwei große Signa in Form ungleich großer, sklerotisierter Falten vorhanden; an den blind endenden Abschnitt des Corpus bursae schließt seitlich ein breiter schlauchförmiger Abschnitt an, der in eine Blase mündet, die sich allmählich wieder zu einem schlauchförmigen Abschnitt verjüngt, der nach einer Krümmung in den Ductus seminalis übergeht.

*Stathmopoda anticyma* Meyrick

Meyrick, 1927: 100 (Diagnose!).

Locus typicus: Samoa Inseln: Upolu: Apia. Lectotypus ♀ (hier festgelegt): "Lectotype" "20. Nov. 24. Apia, Upolu, Samoan Is. Buxton & Hopkins" "*Stathmopoda anticyma* Meyr. det.: E. Meyrick" "Brit. Mus. 1927—119" "*anticyma* Meyr.". GU—15304—BM (BM).

Genitalien ♂: unbekannt.

Genitalien ♀ (Abb. 42) (untersucht 2 Ex.): Antrum etwa so lang wie breit, am Anfang des Ductus bursae auf jeder Seite ein sklerotisiertes Stäbchen in der Wand. Die zwei Signa relativ klein, ihre Ränder auf einer Seite gesägt. Der zweite Abschnitt des Corpus bursae lang und schlauchförmig, nach einigen Windungen aber eine blasenförmige Auftreibung, an die wieder ein schlauchförmiger Abschnitt anschließt, der sich abermals zu einem blasenförmigen Gebilde erweitert, das dann in einen gedrehten Zipfel ausläuft. Dieser und der letzte Abschnitt der Blase mit Wandstruktur.

*Stathmopoda auriferella* (Walker)

*Gelechia? auriferella* Walker, 1864: 1022.

*Stathmopoda divisa* Walsingham, 1891: 121, t. 6, f. 61 (Falter, farb.). — Meyrick, 1911: 286.

*Stathmopoda ischmotis* Meyrick, 1897: 324.

*Stathmopoda crocophanes* Meyrick, 1897: 324.

*Aeoloscelis theoris* Meyrick, 1906: 410.

*Stathmopoda theoris*: Meyrick, 1907b: 983. — 1911: 286. — 1914b: 12, t. 2, f. 32 (Geäder). —

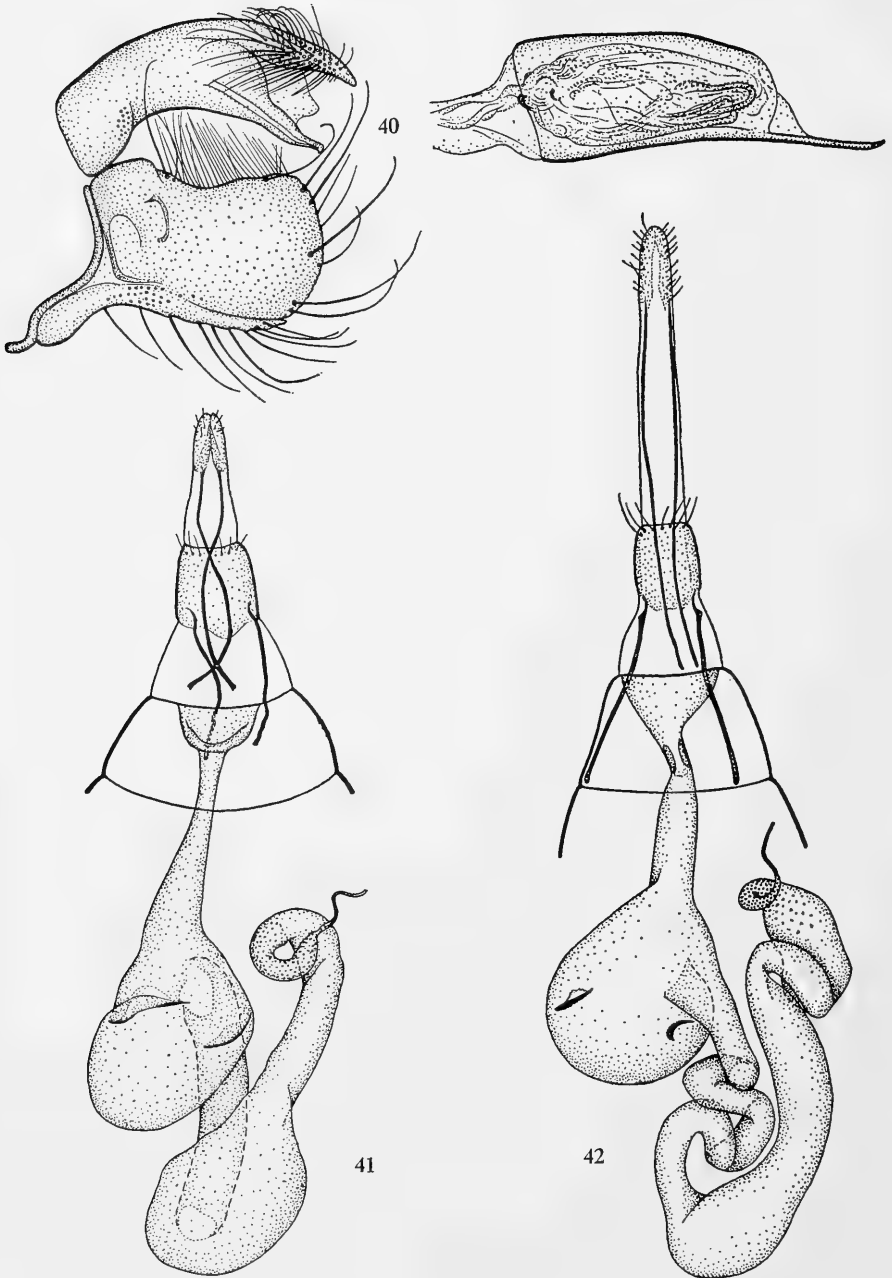


Abb. 40. *Stathmopoda skelloni* (Butler), ♂-Genitalien, GU—15108—BM. Abb. 41. Ditto, ♀-Genitalien, GU—15324—BM. Abb. 42. *S. anticyma* Meyrick, ♀-Genitalien, GU—3794—Mus. Vind.

1917: 61. — Fletcher, 1933: 22. — Issiki, in Esaki et al., 1957: 35, t. 5, f. 142 (Falter, farb.). — Diakonoff, 1967: 217 (dort auch weitere Literatur), f. 323 (♀-Genit., unvollständig).

*Stathmopoda auriferella*: Meyrick, 1911: 286. — Rebel, 1926: 190.

*Stathmopoda tharsalea* Meyrick, 1914a: 199.

*Stathmopoda adulatrix* Meyrick, 1917: 61.

*Stathmopoda cirrhaspis* Meyrick, 1922: 585. — Vietta, 1951: 87 (Lectotypus festgelegt).

*Gelechia? auriferella* Walker: Locus typicus: W-Afrika: Sierra Leone. Lectotypus ♂ (hier festgelegt): "Lectotype" "Type" "38, 11. 8, 546" "Sierra Leone" "*Gelechia? auriferella*" "Lectotype ♂, *Gelechia? auriferella* Walker, teste K. Sattler, 1968" (BM). Das Exemplar besitzt kein Abdomen mehr und ist auch sonst schlecht erhalten, weitere als Syntypen aufzufassende Stücke waren nicht zu finden und aus der Beschreibung ist nicht ersichtlich, ob solche vorhanden sein sollten. Es kann aber kaum ein Zweifel bestehen, daß es sich bei der Art Walkers um die im folgenden als *Stathmopoda auriferella* aufgefaßte handelt.

*Stathmopoda divisa* Walsingham: Locus typicus: W-Afrika: Gambia: Bathurst. Lectotypus ♂ (hier festgelegt): "Lectotype" "Type, H.T." "Bathurst, Gambia, W. Africa, 1885, Carter 1164" "*Stathmopoda* ♂, *divisa* Wlsm., Tr. Ent. Soc. Lond. 1891, 121—2, Pl. 6.61 (1891), Type ♂, descr. figd., 1164" "Walsingham Collection, 1910—427" "Lectotype ♂, *Stathmopoda divisa* Wlsm., teste K. Sattler, 1968". GU—6193—BM (BM). Der Paralectotypus ♀ hat die Daten: "Bathurst, Gambia, W. Africa, 1887, Carter 1100". **Syn. nov.**

*Stathmopoda ischnotis* Meyrick: Locus typicus: W-Australien: Carnarvon. Lectotypus ♂ (hier festgelegt): "Lectotype" "Carnarvon. W. Australia. 21/10/86" "*Stathmopoda ischnotis* Meyr., 1/4. E. Meyrick det., in Meyrick Coll." "Meyrick Coll. B.M. 1938—290" "*ischnotis* Meyr." "Lectotypus ♂, *Stathmopoda ischnotis* Meyrick, 1897. teste F. Kasy, 1969". GU—15074—BM (BM). **Syn. nov.**

*Stathmopoda crocophanes* Meyrick: Locus typicus: Australien: Neu-Süd-Wales: Sydney. Lectotypus ♀ (hier festgelegt): "Lectotype" "Sydney, N.S. Wales, 19/10/76" "*Stathmopoda crocophanes* Meyr., 1/12. E. Meyrick det., in Meyrick Coll." "Meyrick Coll. B.M. 1938—290" "*crocophanes* Meyr." "Lectotypus ♀, *Stathmopoda crocophanes* Meyrick, 1897. teste F. Kasy, 1969". GU—15094—BM (BM). **Syn. nov.**

*Aeoloscelis theoris* Meyrick: Locus typicus: Ceylon: Puttalam. Lectotypus ♀ (hier festgelegt): "Lectotype" "Puttalam, Ceylon, Pole, 9. 04." "*Stathmopoda theoris* Meyr., 5/14. E. Meyrick det., in Meyrick Coll." "Meyrick Coll. B.M. 1938—290" "Lectotype ♀, *Aeoloscelis theoris* Meyrick. teste K. Sattler, 1968" (BM). **Syn. nov.**

*Stathmopoda tharsalea* Meyrick: Locus typicus: Komoren. Lectotypus ♀ (hier festgelegt): "Comoro Isl., Aug. 1911 Leigh, coll. Janse" "*Stathmopoda tharsalea* Meyr., Type no. 239" "Lectotypus ♀, *Stathmopoda tharsalea* Meyrick, 1914. teste L. Vári, 1971". Coll. Transvaal Museum, Pretoria. Der Paralectotypus ♂ befindet sich im (BM) (GU—15159—BM). **Syn. nov.**

*Stathmopoda adulatrix* Meyrick: Locus typicus: N-Indien: Almora. Lectotypus noch nicht festgelegt, weil von den drei in der Publikation genannten Typenexemplaren nur ein als "Syntype" bezeichnetes Stück im (BM) aufzufinden war, das kein Abdomen hat. Es besitzt folgende Etiketten: "Syntype" "Almora, Kumaon, B. bred. 9. 15" "*Stathmopoda adulatrix* Meyr., 1/2. E. Meyrick det., in Meyrick Coll." "Meyrick Coll. B.M. 1938—290" "*adulatrix* Meyr." "Abdomen missing". **Syn. nov.**

*Stathmopoda cirrhaspis* Meyrick: Locus typicus: China: Shanghai. Lectotypus ♂ :

"Type" "Changhai" "*Stathmopoda cirrhaspis* Meyrick type" "Muséum Paris, 1920—1932, coll. L. et J. de Joannis". Coll. Mus. Paris. Der Paralectotypus ♀ befindet sich im (BM) (GU—14399—BM). **Syn. nov.**

Falsche Determinationen: *zernyi*: Amsel, 1935a: 304 (*Apertodiscus*). Der Paratypus von Tabgha erwies sich als *Stathmopoda auriferella* (Walker). Vermutlich auch Amsel, 1935b: 211. Das Exemplar, das ich nicht untersuchen konnte, soll nämlich doppelt so groß sein wie die Exemplare von *Apertodiscus zernyi* Amsel = *Tortilia charadritis* (Meyrick) von Jericho. Siehe auch das bei der letztgenannten Art unter Ökologie gesagt.

Diagnose (untersucht ca. 60 Ex.): Exp. 9,4—13,0 mm. Fühler hell, bräunlich, Scapus meist dunkler, bräunlichgrau. Labialpalpen ca. 2½. Endglied etwas kürzer als das Mittglied; hell, gelblich, die Spitzen oft angedunkelt. Stirn weißlich bis gelblich, glänzend. Patagia gelblich bis bräunlich, manchmal auch dunkler braun. Thorax und Schulterdecken von der gelben Vfl.-Grundfarbe, ersterer hinten manchmal angedunkelt, letztere an der Basis oft mit einem braunen Fleck. Beine hell, bräunlichgrau, erstes Beinpaar aber auf der Oberseite bzw. Außenseite dunkel, graubraun. Abdomen hell, bräunlichgrau. Vfl.: Grundfarbe meist ein leuchtendes helles Gelb, manchmal mehr Schwefel-, manchmal mehr Goldgelb, bei den Exemplaren aus Nubien, Ägypten, Palästina und S-Iran aber ein stumpfes Ockergelb. Vorderrand an der Wurzel braun, ganz an der Basis ein brauner Punkt, etwas von diesem entfernt am Vorderrand ein kleiner brauner Fleck, entlang des Hinterrandes an der Wurzel mehr oder weniger bräunlichgraue Verdunkelung, eventuell auch in der Falte bräunliche Schuppen; distale Hälfte des Vfl. braun mit schwachem violetten Schimmer, oft einen hellen Fleck enthaltend, der in Größe und Form sehr verschieden sein kann, bei manchen Exemplaren nur eine Aufhellung vorhanden, bei anderen ein besonders nach innen schärfer begrenzter Fleck von der gelben Flügelgrundfarbe, wurzelwärts meist spitz vorspringend, bei manchen Exemplaren erreicht dieser Fleck auch breit den Vorderrand, dessen Kante selbst aber braun bleibt. Bei den als *crocophanes* Meyr. beschriebenen Stücken aus Australien ist vielfach auch noch am Innenrand, also unterhalb des Fleckes, eine Aufhellung vorhanden, und der Fleck selbst ist sehr groß, so daß die dunkle Färbung der apikalen Flügelhälfte auf die Flügelspitze und eine schmale braune, am Vorderrand und vor dem Hinterrand nach innen vorspringende Binde reduziert ist. Neben diesen wie eine andere Art aussehenden Stücken gibt es in Australien aber normale von denselben Fundorten und sogar innerhalb einer gezüchteten Serie. Die innere Begrenzung der distalen dunklen Flügelhälfte ist ebenfalls sehr variabel, manchmal schräg, manchmal steil verlaufend, normalerweise springt sie ein Stück unter dem Flügelvorderrand sowie am Innenrand etwas nach innen vor, bei manchen Exemplaren ist die innere Begrenzung des dunklen Feldes aber ziemlich gerade oder konkav. Erwähnt sei noch, daß ein von *Ceratonia*-Schoten gezüchtetes Stück aus Israel bräunlichschwarze Zeichnung und dunkelockergelbe Grundfarbe aufweist. Fransen graubraun. Hfl. bräunlichgrau, an der Wurzel heller, Fransen bräunlichgrau.

Genitalien ♂ (Abb. 43) (untersucht 18 Ex.): Tegumen mit Uncus und Gnathos etwa so lang wie die Valve. Diese mit relativ kräftigem, vom Cucullus stark abgesetzten Costalteil, Ampulla reduziert, Sacculus sehr kräftig, bis etwa ¾ der Valvenlänge reichend, distales Ende als kräftiger Höcker stark vorspringend, Cucullus oval, ventrocaudal etwas eckig. Aedoeagus relativ lang, distal nicht verzüngt, keine auffälligen

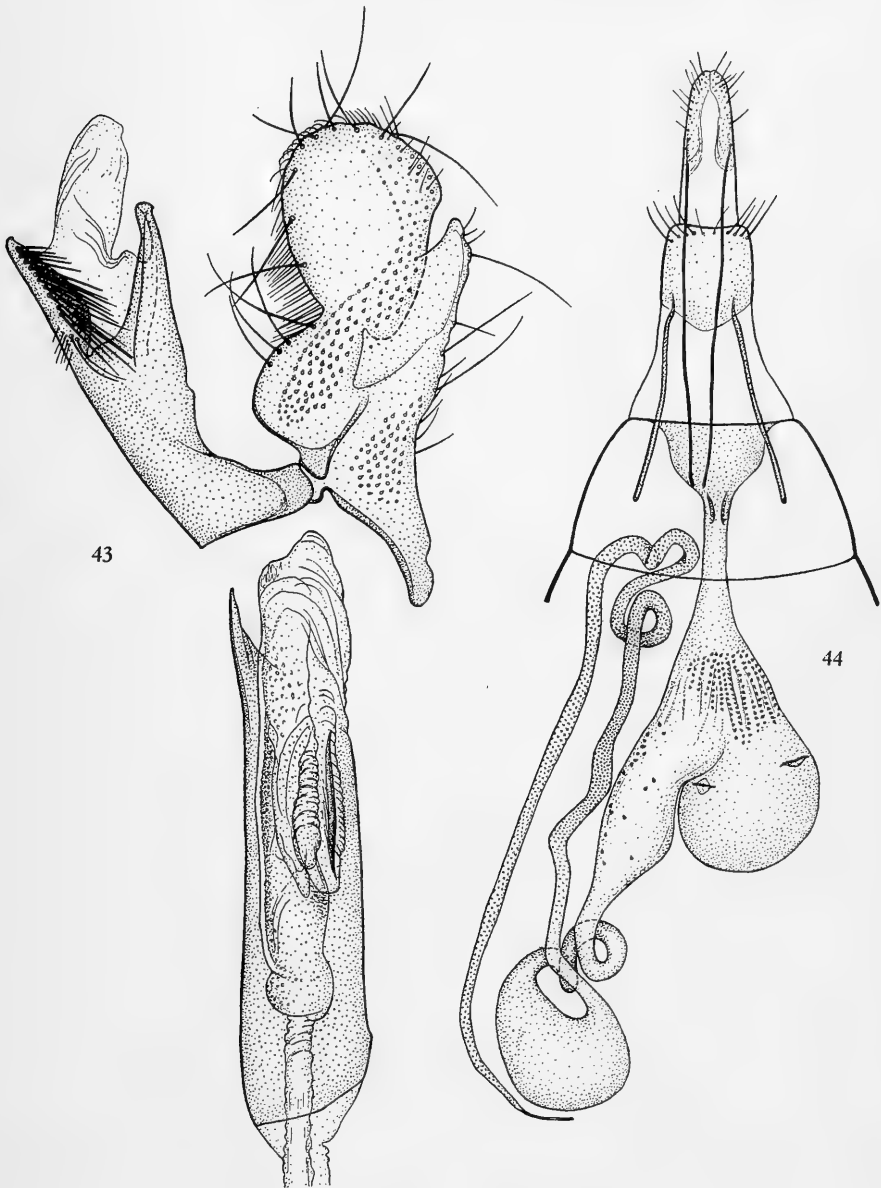


Abb. 43. *Stathmopoda auriferella* (Walker), ♂-Genitalien, GU—3607—Mus. Vind. Abb. 44. Ditto, ♀-Genitalien, GU—3772—Mus. Vind.

Cornuti vorhanden, aber zahlreiche winzige Körnchen bis Stachelchen; distaler Fortsatz kräftig, in eine sklerotisierte Spitze auslaufend.

Genitalien ♀ (Abb. 44) (untersucht 30 Ex.): Antrum etwa so lang wie breit, sich bogig zum Ductus bursae verjüngend, dieser am Anfang mit je einem sklerotisierten Stäbchen auf jeder Seite in der Wand, Corpus bursae mit zwei verhältnismäßig kleinen

Signa in Form sklerotisierter Falten, bei den Exemplaren aus Nubien, Ägypten, Palästina und S-Iran auch noch winzige Dörnchen am Übergang vom Ductus bursae zum Corpus bursae und im zweiten Abschnitt des Corpus bursae, bei den übrigen Exemplaren fehlend oder nur angedeutet. Dieses Merkmal könnte zusammen mit den erwähnten äußeren Unterschieden eventuell zur Aufstellung einer eigenen Subspecies Anlaß geben. Der zweite Abschnitt des Corpus bursae geht nach einigen Windungen in ein blasenförmiges Gebilde über, von dem ein sehr langer Schlauch abgeht; dieser zieht erst nach caudal, wo er etwa in Höhe des Ductus bursae in einen Knäuel von Schlingen übergeht und dann wieder nach cephal, wo er sich zum Ductus seminalis verjüngt. Die Wand des langen Schlauches nach der blasenförmigen Auftreibung enthält feine, quergestellte, mehr oder weniger längliche, bei manchen Exemplaren fast stäbchenförmige Körnchen.

Erste Stände und Ökologie: Die Raupe scheint sich von abgestorbenen Pflanzenteilen, Blüten und Früchten zu ernähren. Von mir wurde aus Nubien eine Serie aus Detritus gezüchtet (von dem die Raupen möglicherweise nur bestimmte Anteile gefressen haben), einige mir vorgelegene Exemplare aus Ägypten tragen den Vermerk "ex 1. aus *Citrus*-Blüten", Rebel (1926: 190) führt ein aus *Zizyphus*-Früchten gezüchtetes Stück an, Exemplare aus Nigeria haben den Vermerk "ex *Sorghum*", aus Australien liegt mir eine Serie vor (als *crocophanes* Meyr.), die aus abgestorbenen Blättern einer *Tristania*-Art gezüchtet worden war, Meyrick (1917: 61) gibt *Helianthus* (= Sonnenblumen)-Köpfe als Aufenthaltsort der Raupen an (für *theoris* Meyr.) und an derselben Stelle für die insbesondere auch auf Grund der Biologie für eine andere Art gehaltene *adulatrix* Kiefernzweige (*Pinus longifolia*), Fletcher (1933: 22) hat die Art aus einem verfaulten Granatapfel gezüchtet, nach mündlicher Mitteilung von Bleszynski sollen in Israel Raupen an *Ceratonia*-Schoten schädlich geworden sein. Nach den bereits vorliegenden Angaben muß damit gerechnet werden, daß *Stathmopoda auriferella* (Walker) als Vorratsschädling auftreten kann. Die Daten der gefangenen bzw. gezüchteten Exemplare liegen alle zwischen Anfang August und Anfang Mai.

Verbreitung: Nach dem untersuchten Material: Nordafrika: Cyrenaika, Ägypten, Nubien; Westafrika: Gambia, Nigeria; Ostafrika: Uganda; Madagaskar; Komoren; Seychellen; Israel (Tabgha, Tel Aviv); S-Iran (Bandar-Abbas); Westpakistan (Karachi); Indien; Ceylon; Java; China (Shanghai, Tien-Mu-Shan); Formosa; Australien. Nach Diakonoff (1967: 218) auch Philippinen: Luzon, nach Issiki, in Esaki et al. (1957: 35) Japan.

Die Art scheint demnach in der äthiopischen und indoaustralischen Region weit verbreitet zu sein und in der Paläarktis nur in gewissen Randgebieten vorzukommen, nämlich dort, wo die Winter milde sind.

Bemerkungen: Die von Meyrick (1911: 286) vertretene Meinung, daß die Variabilität der Zeichnung, nach der er *auriferella*, *divisa* und *theoris* für verschiedene Arten hält, örtlich konstant ist, konnte an dem großen mir vorliegenden Material nicht bestätigt werden, doch scheinen gewisse Populationen zu stärkerer Abweichung zu neigen. Nach Meyrick (1917: 61) unterscheidet sich *adulatrix* von *theoris* (also *auriferella*) nur durch die braune Färbung im hinteren Teil des Kopfes und durch die Biologie. Ersteres Merkmal kommt aber auch bei Exemplaren von *auriferella* aus anderen Gebieten vor. Da deren Raupe offenbar von allen möglichen abgestorbenen Pflanzenteilen leben kann und nicht beobachtet wurde, was die Raupe von *adulatrix*, die an den Zweigen von *Pinus longifolia* gefunden wurde, wirklich gefressen hat, kann auch die Biologie nicht als Hinweis auf einen Artunterschied gewertet werden. Ein zweites von Meyrick nach



dem genannten Merkmal als *adulatrix* determiniertes Exemplar stammt aus Java, es erwies sich bei einer Genitaluntersuchung als *auriferella*.

### *Stathmopoda diakonoffi* nom. nov.

*Stathmopoda divisa* Diakonoff, 1948, Treubia 19: 211, praecoc. durch *Stathmopoda divisa* Walsingham, 1891, Trans. ent. Soc. London 1891: 121.

### *Stathmopoda callichrysa* Lower

Lower, 1893: 184. — Meyrick, 1897: 325.

Locus typicus: Australien: Victoria: Melbourne.

Diagnose: Lower (1893) und Meyrick (1897).

Der Holotypus (Monotypus) konnte von mir nicht untersucht werden, doch gehören die mir vorgelegenen Exemplare mit ziemlicher Sicherheit dieser Art an, da sie mit den Beschreibungen übereinstimmen.

Genitalien ♂ (Abb. 45) (untersucht 1 Ex.): Tegumen mit Uncus und Gnathos etwas über den Distalrand der Valve reichend. Costa vom Cucullus nur wenig abgesetzt, Sacculus relativ kräftig, so lang wie die Valve, distal spitz vorspringend, Cucullus breit

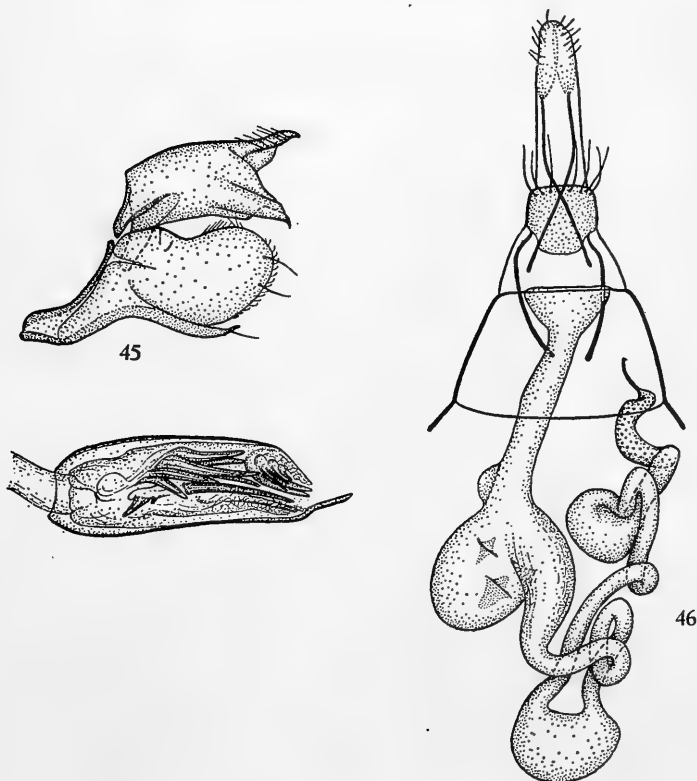


Abb. 45. *Stathmopoda callichrysa* Lower, ♂-Genitalien, GU—15080—BM. Abb. 46. Ditto, ♀ Genitalien, GU—15332—BM

und rund. Aedoeagus im Gegensatz zu dem der meisten anderen *Stathmopoda*-Arten mit einer größeren Anzahl sehr kräftiger und meist auch langer Cornuti.

Genitalien ♀ (Abb. 46) (untersucht 1 Ex.): Am Anfang des Ductus bursae keine Versteifungsstäbchen wie bei *auriferella*. Signa ungleich groß, in Form von sklerotisierten Falten, deren Umgebung ebenfalls sklerotisiert ist, beim größeren Signum weist dieses sklerotisierte Feld eine charakteristische Feinstruktur auf; der zweite Abschnitt des Corpus bursae ähnlich wie bei *auriferella*, aber der Schlauch wesentlich kürzer und mit einer weiteren blasenförmigen Auftreibung, die Wandstruktur des Schlauches erst in seinem Endabschnitt nach der zweiten Blase auftretend.

Erste Stände und Ökologie: Der Monotypus wurde nach Lower (l.c.) von einer *Acacia*-Art gezüchtet; was die Raupe gefressen hat, wird aber nicht angegeben.

Bemerkungen: Die Art wurde wegen ihrer Ähnlichkeit mit *auriferella* mit in die Untersuchungen einbezogen. Nach äußeren Merkmalen unterscheidet sie sich wie folgt: der Thorax ist einschließlich der Schulterdecken braun und an der Flügelwurzel ist ein vom Vorder- bis Hinterrand durchgehender brauner Fleck entwickelt (der nahe dem Vorderrand einen kleinen Fleck von der gelben Flügelgrundfarbe einschließen kann). Die braune apikale Flügelhälfte kann wie bei *auriferella* in der Mitte aufgeheilt sein.

### *Stathmopoda balanarcha* Meyrick

Meyrick, 1921a: 461.

Locus typicus: Indien: Assam: Shillong. Holotypus (Monotypus) ♂: "Holotype" "Shillong, Assam, T.B.F. .9. 19" "*Stathmopoda balanarcha* Meyr., 1/3. E. Meyrick det.,

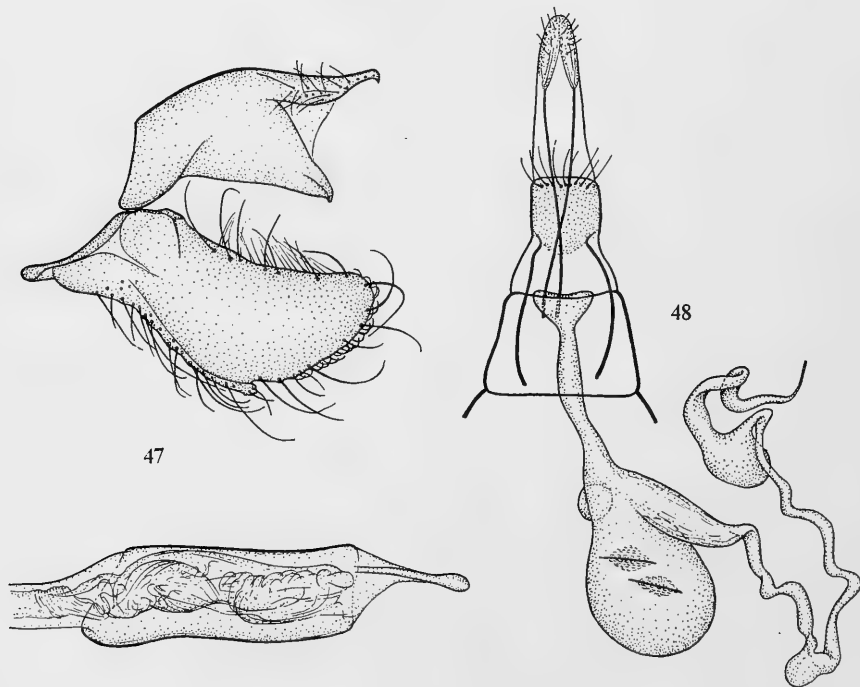


Abb. 47. *Stathmopoda balanarcha* Meyrick, ♂-Genitalien, Holotypus, GU—15326—BM. Abb. 48. Ditto, ♀-Genitalien, GU—15081—BM

in Meyrick Coll." "Meyrick Coll. B.M. 1938—290" "*balanarcha* Meyr.". GU—15326—BM (BM).

Diagnose (untersucht 2 ♂, 3 ♀). Auch diese Art ist *auriferella* ähnlich. Sie unterscheidet sich äußerlich von ihr vor allem dadurch, daß das dunkle apikale Feld des Vfl. weiter wurzelwärts reicht, also das gelbe Wurzelfeld kleiner ist, auch befindet sich in ihm, wenigstens bei den mir vorliegenden Stücken, kein heller Fleck. Während bei *callichrysa* die ganze Thoraxoberseite braun ist, ist sie bei *balanarcha* mit Ausnahme des vorderen Teiles und der basalen Teile der Schulterdecken hell.

Genitalien ♂ (Abb. 47) (untersucht 2 Ex.): Tegumen mit Uncus und Gnathos kürzer als die Valven, Costa nur in Form eines breiten Höckers ausgebildet, nicht stärker vom Cucullus abgesetzt, Ampulla reduziert, Sacculus von etwa 2/3 der Valvenlänge, distal mit einem stumpfen Höcker etwas vortretend, Cucullus nach oben gebogen, distal sich verjüngend. Aedoeagus ohne Cornuti, distaler Fortsatz am Ende verbreitert.

Genitalien ♀ (Abb. 48) (untersucht 2 Ex.): Sehr ähnlich denen von *callichrysa*. Der auffälligste Unterschied besteht im Fehlen einer Struktur im schlauchförmigen Abschnitt des Corpus bursae vor dem Ductus seminalis, ferner sind beide Signa gleich groß.

### Stathmopoda biclavis Meyrick

Meyrick, 1911: 286 (Diagnose!).

Locus typicus: Insel Aldabra. Holotypus (Monotypus) ♀: "Type" "Seychelles: Aldabra. 1908. J.C.F. Freyer." "*Stathmopoda biclavis* Meyr. Type ♀" "Brit. Mus. 1913—170". GU—14398—BM (BM)<sup>1</sup>).

Diagnose: Die Art ist ebenfalls *auriferella* (Walker) ähnlich.

Genitalien ♂: unbekannt.

Genitalien ♀ (Abb. 49) (untersucht 1 Ex.): Antrum länger als breit, mit Längsfalten, dicht mit winzigen Stachelchen besetzt. Signa relativ groß, in Form sklerotisierter Falten, von einem Feld winziger Stachelchen umgeben. Am Anfang des zweiten Teiles des Corpus bursae, der schlauchförmig mit Auftreibungen ist, einige plumpe Dörnchen bzw. Höcker. Wandstruktur nur vor dem Ductus seminalis in einem kurzen, mehr blasenförmigen Abschnitt und dem anschließenden Zipfel.

### Stathmopoda diplaspis (Meyrick)

*Placostola diplaspis* Meyrick, 1887: 280.

*Stathmopoda ovigera* Meyrick, 1913a: 93.

*Stathmopoda diplaspis*: Meyrick, 1914b: 12.

*Placostola diplaspis* Meyrick: Locus typicus: S-Arabien: Aden. Holotypus (Monotypus) ♀: "Holotype" "Aden, Arabia. GHR. 15. 1. 80" "Meyrick Coll. B.M. 1938—290" "Abdomen missing" "*diplaspis* Meyr." "Holotype ♀, *Placostola diplaspis* Meyr. teste K. Sattler, 1971" (BM).

*Stathmopoda ovigera* Meyrick: Locus typicus: Ceylon: Puttalam. Lectotypus ♂ (hier festgelegt): "Lectotype" "Puttalam, Ceylon. Pole. 10. 04." "*Stathmopoda ovigera* Meyr., 5/1; E. Meyrick det., in Meyrick Coll." "Meyrick Coll. B.M. 1938—290", "*ovigera*

<sup>1</sup>) Die Angabe "Seychelles: Aldabra" ist fehlerhaft, weil Aldabra nicht zu den Seychellen, sondern zu einer eigenen Inselgruppe gehört.

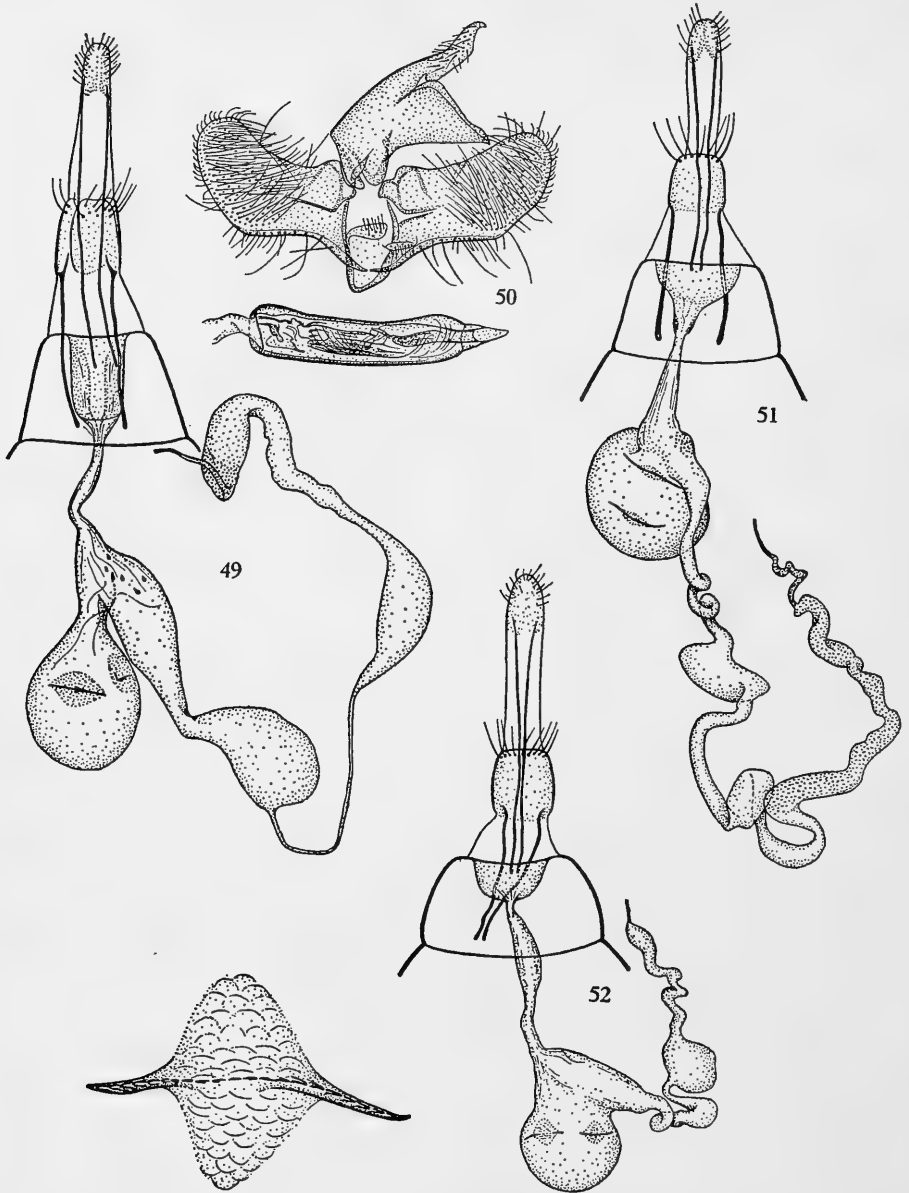


Abb. 49. *Stathmopoda biclavis* Meyrick, ♀-Genitalien, Holotypus, GU—14398—BM. Abb. 50. *S. diaspis* (Meyrick), Lectotypus von *Stathmopoda ovigera* Meyrick, ♂-Genitalien, GU—15071—BM. Abb. 51. Ditto, ♀-Genitalien, GU—15106—BM. Abb. 52. *S. placida* Meyrick, Lectotypus von *Stathmopoda isoleuca* Meyrick, ♀-Genitalien, GU—15162—BM (Daneben das linke Signum stärker vergrößert)

Meyr." "Lectotypus ♂, *Stathmopoda ovigera* Meyr., 1913. teste F. Kasy, 1968". GU—15071—BM (BM). Syn. nov.

Bemerkung: Da der Monotypus von *Placostola diplaspis* Meyrick kein Abdomen mehr besitzt, kann die Synonymie von *Stathmopoda ovigera* Meyrick zu jener Art nur indirekt bewiesen werden. Material, das mir aus dem Iran zur Verfügung steht, zeigt in den äußeren Merkmalen gegenüber der Type von *Placostola diplaspis* Meyrick keinen Unterschied, weshalb ich es als zu dieser Art gehörend betrachte. Die Genitalien dieser Stücke stimmen völlig mit denen der *Stathmopoda ovigera*-Typen aus Ceylon überein.

Diagnose (untersucht 6 ♂, 5 ♀): Exp. 9,3—10,5 mm. Fühler ockerfarben, Scapus an der Unterseite weißlich. Labialpalpen ca. 3, Endglied etwas kürzer als das Mittelglied; gelblichweiß, Spitzenglied mehr ockerfarben. Stirn weißlich, glänzend. Patagia ockerbräunlich, Thorax und Schulterdecken gelblichweiß. Beine gelblichweiß, distale Teile mehr ockerfarben, an den Enden auch dunkelbraun. Vfl. glänzend, ockerbraun, an den Rändern der zwei großen glänzenden weißen Flecke dunkler; der eine dieser Flecke bei ca. 1/3, etwa trapezförmig, am Flügelhinterrand sehr breit, am Vorderrand schmal, der zweite bei ca. 2/3, bei den Exemplaren aus S-Indien und Ceylon (*ovigera* Meyrick) in Form eines liegenden Eies, am Vorder- und Hinterrand noch einen schmalen Streifen der dunklen Grundfarbe freilassend, bei den Exemplaren von den anderen Fundorten den Vorderrand breit erreichend und nur am Hinterrand einen schmalen Streifen freilassend. Fransen bräunlichgrau, am Apex etwas dunkler. Hfl. einschließlich der Fransen gelblichgrau, diese am Apex etwas bräunlich.

Genitalien ♂ (Abb. 50) (untersucht 4 Ex.): Tegumen mit Uncus und Gnathos etwas kürzer als die Valve, Gnathos an der Basis sehr breit, Uncus ziemlich grazil. Valven distal nach oben gebogen, Costa höckerförmig, Ampulla völlig reduziert, Sacculus bis etwa 2/3 der Valvenlänge reichend, distal nicht vortretend, Distalrand des Cucullus stark gerundet, ventrocaudal etwas abgeschrägt. Aedoeagus ohne Cornuti, in der Mitte etwas verjüngt, ziemlich schlank, distaler Fortsatz kräftig, in eine ziemlich plumpe Spitze auslaufend, Anelluslappen distal verbreitert, relativ groß.

Genitalien ♀ (Abb. 51) (untersucht 4 Ex.): Antrum breit, sich bogig zum Ductus bursae verjüngend, dessen Anfangsteil an beiden Seiten etwas sklerotisiert. Die zwei Signa etwas in der Größe verschieden, in Form von langen sklerotisierten Falten ausgebildet, der in den Schlauch übergehende Abschnitt des Corpus bursae an der Basis auf einer Seite mit zahlreichen winzigen Dörnchen in der Wand, der schlauchförmige Abschnitt sehr lang und vielfach gewunden, stellenweise auch blasenförmig erweitert, der Abschnitt mit Wandstruktur vor dem Ductus seminalis lang, die genannte Struktur bei dieser Art ziemlich auffällig, weil relativ grob, dörnchenartig.

Erse Stände und Ökologie: Zwei der untersuchten Ex. aus S-Indien tragen einen Vermerk, nach dem die Raupe an *Ficus glomerata* gefunden wurde und an dieser Pflanze möglicherweise räuberisch von Schildläusen der Gattung *Pulvinaria* gelebt hat. Erscheinungszeiten der Imagines nach dem untersuchten Material: Jänner (S-Arabien), Mai bis Anfang Juni (NW-Pakistan), Juni (Elbursgebirge bei Teheran), August (Keredj bei Teheran, Shiraz), Oktober (Ceylon), November und Dezember (S-Indien).

Verbreitung: Bisher bekannt aus S-Arabien, Iran, NW-Pakistan, S-Indien, Ceylon.

### Stathmopoda placida Meyrick

*Stathmopoda placida* Meyrick, 1908: 396. — Diakonoff, 1967: 217, f. 319, 320 (♂-Genit.), f. 724 (Falter, phot.).

*Stathmopoda isoleuca* Meyrick, 1913a: 93.

*Stathmopoda placida* Meyrick: Locus typicus: Burma: Rangun. Der Holotypus, der sich im Indian Museum befinden müßte, konnte nicht untersucht werden. Der Paratypus im British Museum besitzt kein Abdomen mehr. Untersucht wurde ein als *placida* bestimmtes ♀ von Karwar bei Bombay, das wie der Paratypus aussieht, und ein von Meyrick determiniertes ♀ von Thailand, das sowohl in äußeren Merkmalen wie im Genital mit dem Exemplar von Karwar übereinstimmt.

*Stathmopoda isoleuca* Meyrick: Locus typicus: Indien: Konkan bei Bombay. Lectotypus ♀ (hier festgelegt): "Lectotype" "Konkan, Bombay. L C Y. .05" "*Stathmopoda isoleuca* Meyr., 2/2. E. Meyrick det., in Meyrick Coll." "Meyrick Coll. B.M. 1938—290" "*isoleuca* Meyr." "Lectotypus ♀, *Stathmopoda isoleuca* Meyrick, 1913, teste F. Kasy, 1968". GU—15162—BM (BM). Syn. nov.

Diagnose: Meyrick (1908, 1913). Die Art ist *diplaspis* sehr ähnlich, die Grundfarbe ist aber dunkler, mehr schokoladebraun, Thorax und Tegulae sind dunkelbraun mit heller Bestäubung, die Stirn ist weißlich, der übrige Kopf hellbraun, die Patagia dunkelbraun. Die beiden weißen Querbinden sind besonders breit, die innere geht am Flügelhinterrand bis zur Wurzel, es bleibt also im Gegensatz zu *diplaspis* nur am Vorderrand ein kleiner Fleck der dunklen Grundfarbe übrig. Die Art wirkt schmalflügeliger als *diplaspis*.

Genitalien ♂: Diakonoff (1967). Aus Mangel an Material kann derzeit allerdings nicht entschieden werden, ob die von Diakonoff für die Philippinen angegebene Art mit der *placida* sensu Meyrick identisch ist, dazu wären vor allem ♀ von den Philippinen erforderlich.

Genitalien ♀ (Abb. 52) (untersucht 2 Ex.): Sehr ähnlich denen von *diplaspis*, die Signa sind etwas zarter und anders gebaut, das eine enthält in einer Reihe angeordnete Stacheln, an der Basis des in den Schlauch übergehenden Abschnittes des Corpus bursae fehlen die Dörnchen, auch fehlt die bei *diplaspis* ziemlich auffällige Wandstruktur im schlauchförmigen Abschnitt des Corpus bursae vor dem Ductus seminalis. Ein weiterer Unterschied besteht darin, daß bei *placida* das Antrum zahlreiche sehr feine, aber verhältnismäßig lange Stachelchen enthält.

### Stathmopoda plinthiota Meyrick

*Stathmopoda plinthiota* Meyrick, 1910: 454 (Diagnose!).

Locus typicus: Borneo: Kuching. Holotypus (Monotypus) ♂: "Holotype" "Kuching, Borneo. JH. .4. 06" "*Stathmopoda plinthiota* Meyr., 1/1. E. Meyrick det., in Meyrick Coll." "Meyrick Coll. B.M. 1938—290" "*plinthiota* Meyr." "Abdomen missing" (BM).

Diagnose: Die Art ist sehr ähnlich *Stathmopoda placida*, aber die äußere Querbinde ist gelblich gefärbt.

### Stathmopoda optiscaspis Meyrick

*Stathmopoda optiscaspis* Meyrick, 1931a: 175. — Issiki, in Esaki et al., 1957: 35, t. 5, f. 141 (Falter, farb.). — Kuroko, 1959: 3.

Locus typicus: Japan: Honshu: Provinz Kii: Hasimoto. Holotypus (Monotypus) ♂:

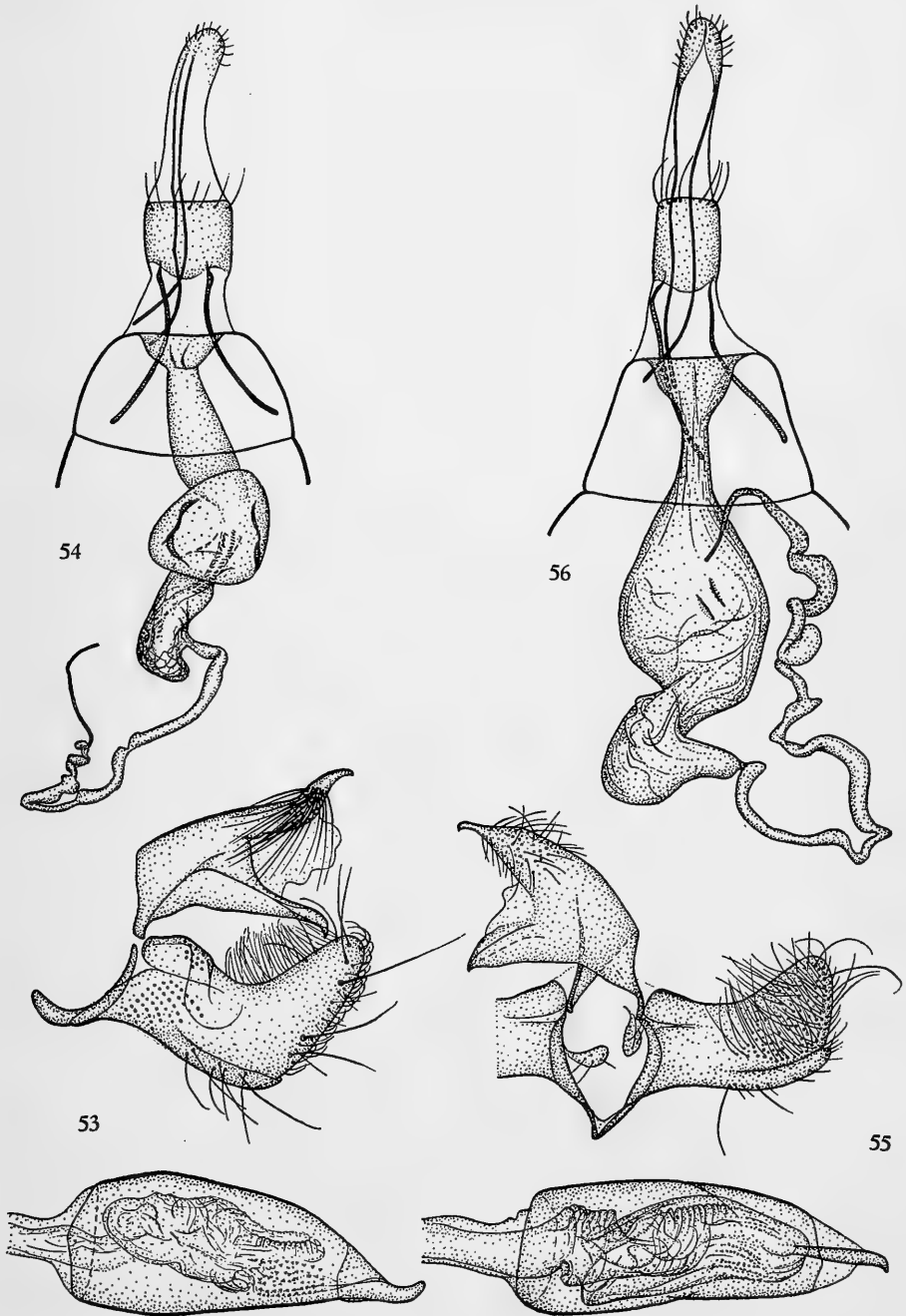


Abb. 53. *Stathmopoda opticaspis* Meyrick, Holotypus, ♂-Genitalien, GU—15169—BM. Abb. 54. Ditto, ♀-Genitalien, GU—UOP—SM—505. Abb. 55. *S. moriutiella* sp. n., Holotypus, ♂-Genitalien, GU—UOP—SM—507. Abb. 56. Ditto, Paratypus, ♀-Genitalien, GU—UOP—SM—509

"Holotype" "Hasimoto, Japan. SI. 5. 9. 20" "*Stathmopoda opticaspis* Meyr., 1/1. E. Meyrick det., in Meyrick Coll." "Meyrick Coll. B.M. 1938—290" "*opticaspis* Meyr.". GU—15169—BM (BM).

Diagnose (untersucht 3 ♂, 1 ♀): Exp. 10,0 — 11,0 mm. Fühler hell, Oberseite gelblich, Unterseite weißlich. Labialpalpen ca. 3, Endglied etwas länger als das Mittelglied; Innenseite weißlich, Außenseite gelblich, an der Basis braun. Stirn weißlich, glänzend, Vertex und Patagia hellgelb. Thorax auf der Dorsalseite hellgelb, in der Mitte braunschwarz mit einem Paar silbrig glänzender weißlicher Punkte, ein solcher Punkt auch hinter dem Kopf, Schulterdecken hellgelb. Beine an den Innenseiten und Spitzen weißlich, an den Außenseiten gelb. Abdomen hell, gelblichgrau. Vfl.: an der Wurzel am Vorderrand ein silbrigglänzender Punkt, anschließend ein schwarzbraunes Feld, dessen äußere Begrenzung zum Hinterrand schräg nach innen verläuft, in diesem dunklen Feld entlang des Vorderrandes und in der Falte je eine gelbe Strieme, die beiden an der Wurzel miteinander verschmolzen, nach außen an das dunkle Basalfeld ein trapezförmiges Feld von silbrigweißer Farbe anschließend, der an dieses angrenzende distale Teil des Flügels braun, aber wesentlich heller als das Basalfeld, in ihm bei ca. 2/3 der Flügelänge ein hellgelber Fleck, der am Vorderrand breit ist und sich zum Hinterrand, den er nicht ganz erreicht, stark verschmälert, wobei seine äußere Begrenzung sehr schräg zum Hinterrand verläuft, während die innere steiler ist und eventuell in der Mitte distalwärts einspringt. Fransen bräunlichgrau, an der Flügelspitze mehr braun. Die Art ist ähnlich *plinthiota*, bei der auch die innere Binde weißlich, die äußere gelblich ist. Die Zeichnung des Thorax ist aber anders.

Genitalien ♂ (Abb. 53) (untersucht 3 Ex.): Tegumen mit Uncus und Gnathos etwas kürzer als die Valve, Costa vom Cucullus kaum abgesetzt, Sacculus kräftig, distal spitz vortretend, bis ca. 3/4 der Valvenlänge reichend, Cucullus fast rechtwinkelig nach oben gebogen, distal sich verjüngend, dorsocaudal gerundet. Aedoeagus verhältnismäßig groß und plump, distal verjüngt, distaler Fortsatz am Ende stumpf und gekrümmt, keine größeren Cornuti vorhanden, aber ein Feld zahlreicher kleiner, sehr kurzer und an der Basis breiter Stachelchen.

Genitalien ♀ (Abb. 54) (untersucht 1 Ex.): Ductus bursae breit, sackförmig. Die zwei relativ großen Signa von gleicher Größe, ihr Rand gesägt. Der zweite Abschnitt des Corpus bursae langgestreckt, zunächst sackförmig, dann in einen langen schlauchförmigen Abschnitt, der einige Auftreibungen enthält, übergehend. Der sackförmige Anfangsteil enthält Stacheln, besonders an seiner Basis.

Erste Stände und Ökologie: Ein Exemplar von Honshu: Izumi trägt den Vermerk: "Bred from? Sphagnum palustre L.". Von Moriuti erhielt ich dazu die Auskunft, daß die Raupen an einem Moos gefressen hatten, das noch nicht bestimmt werden konnte. Die Falter stammen vom Juli bis September.

Verbreitung: Japan: Insel Honshu: Izumi und Provinz Kii: Hasimoto; Insel Shikoku: Iyo. China: Shanghai (fälschlich als *basiplectra* Meyrick in Coll. Meyrick. Diese Art ist überhaupt keine *Stathmopoda*, sondern gehört zu den Walshiidae, wie noch in einer anderen Publikation ausgeführt werden soll). Nach Kuroko (1959) auch Insel Kyushu: Hikosan.

#### *Stathmopoda moriutiella* spec. nov.

Locus typicus: Japan: Insel Honshu: Narita bei Chiba. Holotypus ♂: "Narita, Chiba,



Japan; 8. VI. 1968. K. Kotayashi et Yamazaki". GU—UOP—SM—507 ♂. Coll. Entomological Laboratory, University of Osaka Prefecture, Sakai.

Diagnose (untersucht 1 ♂, 3 ♀): Exp. 10,5—12,0 mm. Fühler gelblichgrau, glänzend, Labialpalpen ca.  $2\frac{1}{2}$ , Endglied etwas kürzer als das Mittelglied; hell, gelblichgrau, glänzend. Kopf gelblichgrau, glänzend, Patagia ockergelb, Thorax am Rücken ockergelb, in der Mitte ein dunkelbrauner Fleck, davor ein hellgrauer glänzender; Schulterdecken dunkelbraun, am Innenrand, besonders distal, ockergelb. Beine hell, gelblichgrau, glänzend, Hintertibien auf der Oberseite dicht mit langen borstenartigen Haaren besetzt. Abdomen hell, glänzend gelblichgrau. Vfl. hell, glänzend gelblichgrau, an der Wurzel am Vorderrand ein dunkelbrauner Fleck, an den ein Feld mit ockergelber Beschuppung anschließt, diese in der Falte und am Hinterrand des Flügels weiter distalwärts reichend, zwischen der Falte und dem Vorderrand ist das gelbe Feld außen bräunlich begrenzt, auch der Flügelvorderrand an der Wurzel bräunlich; am dunkelbraunen Fleck distalwärts angrenzend, innerhalb des gelben Feldes gelegen, ein Fleck von der hellgrauen glänzenden Vfl-Grundfarbe. Fransen hell, gelblichgrau. Hfl. einschließlich der Fransen hell, gelblichgrau.

Genitalien ♂ (Abb. 55) (untersucht 1 Ex.): Tegumen mit Uncus und Gnathos etwas kürzer als die Valve. Diese etwa parallelrandig, in der Mitte eingebuchtet, Costa nur schwach entwickelt, Ampulla reduziert, Sacculus aber sehr kräftig, bis zum Distalrand der Valve reichend und mit einem stumpfen Höcker distal vortretend, Cucullus sich distal gleichmäßig verjüngend, Ende gerundet, der Außenrand fast senkrecht zum Sacculus. Aedoeagus verhältnismäßig groß, distal sich etwas verjüngend, distaler Fortsatz kräftig, am Ende umgebogen, keine größeren Cornuti vorhanden, aber ein Feld winziger, kurzer, an der Basis breiter Stachelchen. Anelluslappen länglich, distal verbreitert. Das Genital ist ähnlich dem von *opticaspis* Meyrick, aber durch die Form der Valve gut zu unterscheiden.

Genitalien ♀ (Abb. 56) (untersucht 3 Ex.): Antrum etwa so lang wie breit, allmählich sich zum Ductus bursae verengend, dieser kurz. Die zwei Signa gleich groß, verhältnismäßig klein, in Form sklerotisierter Falten mit gesägtem Rand. Bei einem der drei untersuchten ♀ außerdem einige winzige Dörnchen in der Wand des Corpus bursae vorhanden. An dieses eine zweite, kleinere blasenförmige Bildung ansetzend, die in einen langen schlauchförmigen Abschnitt übergeht, der sich zum Ductus seminalis verjüngt, am Übergang zu diesem ein längerer Abschnitt mit feiner Wandstruktur.

Erste Stände und Ökologie: Ein Exemplar wurde aus einer Puppe erhalten, die an *Picea excelsa* gefunden worden war, ob die Raupe an diesem Baum gelebt und was sie gefressen hat, ist jedoch unbekannt. Die Imagines wurden im Juni gefangen, das gezüchtete Stück schlüpfte im Juli.

Verbreitung: Japan: Insel Honshu (Izumi: Sakai, Gihu: Nyugawa; Narita: Chiba) und Insel Hokkaido: Paratypen: Sapporo, 3 ♀: "Japan, Honsyu, Izumi: Sakai. 13. VI. 1959. T. Saito", GU—UOP—SM—506 ♀. "Japan, Honsyu, Gihu: Nyugawa. 25. VI. 1954. S. Issiki", GU—UOP—SM—509 ♀. "Japan-Hokkaido, Sapporo, emerged 11. VII. 1958, reared from pupa on *Picea excelsa* Link.", GU—UOP—SM—508 ♀. Alle in derselben coll. wie der Holotypus.

Bemerkungen: Die neue Art, die ich meinem Kollegen S. Moriuti, Sakai, Japan, widme, ist offenbar mit *opticaspis* Meyrick näher verwandt.

**Stathmopoda dicitra** Meyrick

Meyrick, 1935: 85 (Diagnose!).

Locus typicus: China: Tien-Mu-Shan. Holotypus (Monotypus) ♀: "Holotype" "Tien-Mu-Shan, China. C. 5000 .9. 32" "*Stathmopoda dicitra* Meyr., 1/1. E. Meyrick det., in Meyrick Coll." "Meyrick Coll. B.M. 1938—290" "*dicitra* Meyr." "Abdomen missing" (BM).

Bemerkungen: Das Stück ist auch abgesehen vom Verlust des Abdomens sehr schlecht erhalten. Die Art könnte identisch mit *opticaspis* oder auch *plinthiota* sein.

**Stathmopoda nitida** Meyrick

Meyrick, 1913a: 93 (Diagnose!).

Locus typicus: N-Australien: Port Darwin. Holotypus, ♀: "Holotype" "Port Darwin, N. Australia. FPD. .10" "*Stathmopoda nitida* Meyr., 1/1. E. Meyrick det., in Meyrick Coll." "Meyrick Coll. B.M. 1938—290" "*nitida* Meyr.". GU—15156—BM (BM).

Diagnose: Die Art ist ähnlich *diplaspis* und *placida*, sie unterscheidet sich außer durch die größere Expansion vor allem durch die dunklen Hfl. von diesen zwei Arten.

Genitalien ♂: unbekannt.

Genitalien ♀ (Abb. 57) (untersucht 1 Ex.): Ähnlich dem von *diplaspis* und *placida*, die zwei Signa sind ähnlich wie bei letzterer Art, also eines mit einer Reihe spitzer Höckerchen, sie unterscheidet sich von dieser aber durch das Vorhandensein einer Struktur im letzten Abschnitt des schlauchförmigen Teiles des Corpus bursae, von *diplaspis* durch die viel kleineren Signa und die viel geringere Länge des schlauchförmigen Abschnittes des Corpus bursae.

**Stathmopoda dactylas** Meyrick

Meyrick, 1921b: 175 (Diagnose!).

Locus typicus: Java: Buitenzorg. Holotypus ♀: "M 262" "W. Java, Buitenz[org] 1893" "Holotype: *Stathmopoda dactylas* Meyr." "Type... [unleserlich]" "Museum Leiden. *Stathmopoda dactylas* Type. Det. E. Meyrick". GU—3803 ♀ — Mus. Vind. Coll. Rijksmuseum van Natuurlijke Historie, Leiden. Der Paratypus, der sich im (BM) befindet, stammt von Celebes: Makassar.

Genitalien ♂: unbekannt.

Genitalien ♀ (Abb. 58) (untersucht 2 Ex.): Die zwei Signa von sehr unterschiedlicher Größe. Das eine sehr lang, in Form eines Viertelmondes mit unregelmäßig gezacktem Rand, das zweite nicht einmal halb so lang, als sklerotisierte Falte mit einigen kleinen Zähnen. Im zweiten Abschnitt des Corpus bursae zahlreiche unregelmäßig gezackte Höckerchen. Der anschließende schlauchförmige Abschnitt sehr lang, auf einen strukturlosen Abschnitt folgt ein etwa ebenso langer mit feinen Körnchen in der Wand. Beim Holotypus, der erst später untersucht wurde, erscheint der schlauchförmige Abschnitt des Corpus bursae im Gegensatz zur Abbildung in seiner ganzen Länge etwa gleich breit, die besonders dünnen Stellen im anderen Präparat sind also offenbar durch stärkere Schrumpfung bedingt. Beim Holotypus sind im Antrum keine Längsfalten wie in der Abbildung zu sehen. Das Genital ist ähnlich dem von *opticaspis*, der Hauptunterschied besteht darin, daß letztere ziemlich kräftige Stacheln im zweiten Abschnitt des Corpus bursae besitzt und bei ihr die zwei Signa etwa gleich groß sind.

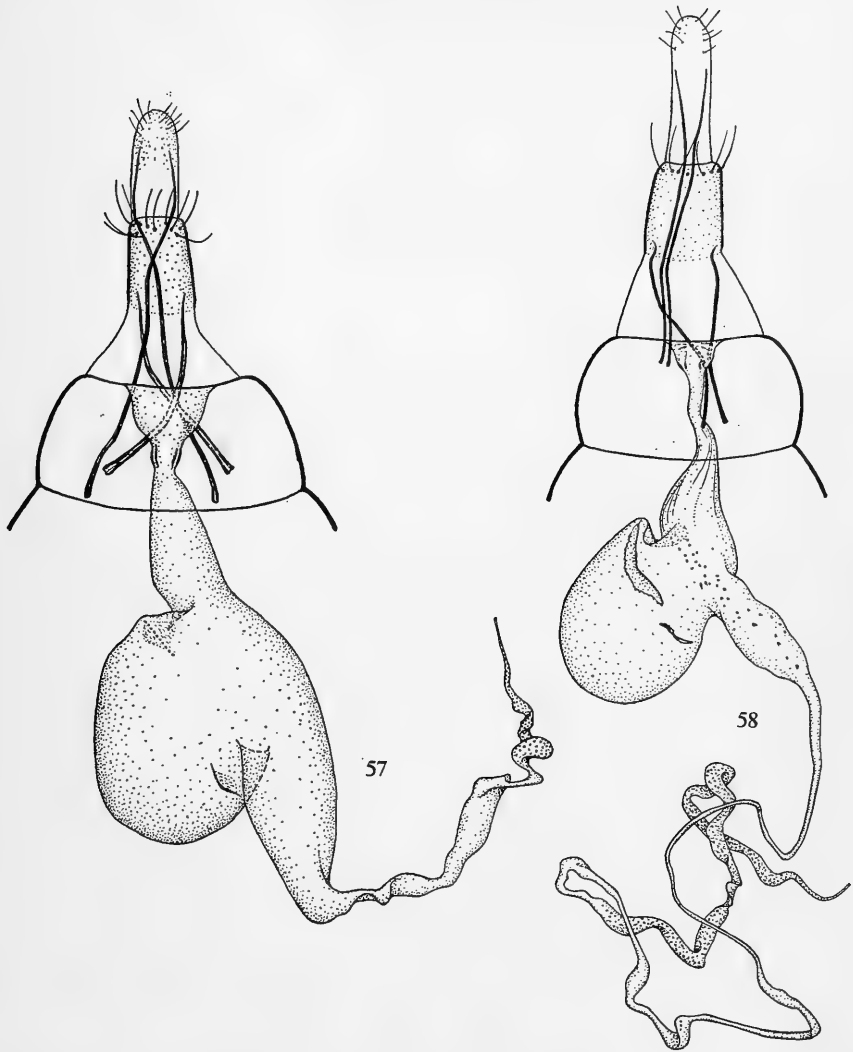


Abb. 57. *Stathmopoda nitida* Meyrick, Holotypus, ♀-Genitalien, GU—15156—BM. Abb. 58. *S. dactylis* Meyrick, Paratypus, ♀-Genitalien, GU—15173—BM

### *Stathmopoda cissota* Meyrick

Meyrick, 1913a: 84 (Diagnose!).

Locus typicus: Ceylon: Hakgala. Lectotypus ♀ (hier festgelegt): "Lectotype" "Hakgala, Ceylon. EEG. .3. 07" "*Stathmopoda cissota* Meyr., 1/2. E. Meyrick det., in Meyrick Coll." "Meyrick Coll. B.M. 1938—290" "*cissota* Meyr." "Lectotypus ♀, *Stathmopoda cissota* Meyrick, 1913. teste F. Kasy, 1968". GU—15200—BM (BM).

Genitalien ♂ (Abb. 59) (untersucht 1 Ex.): Tegumen mit Uncus und Gnathos etwa so lang wie die Valve. Letztere mit stufenförmig abgesetztem Costalteil, Ampulla in Form eines fingerartig gekrümmten Fortsatzes, Sacculus kräftig, etwa von 2/3 der Valvenlänge,

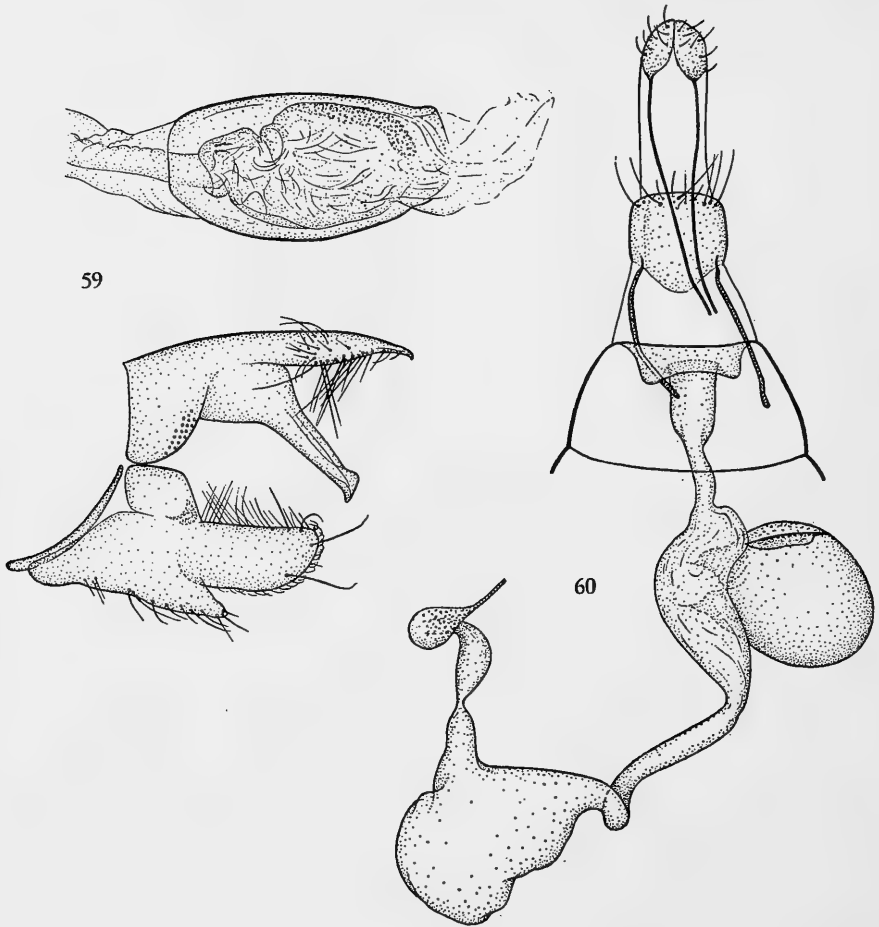


Abb. 59. *Stathmopoda cissota* Meyrick, ♂-Genitalien, GU—15197—BM (Aedoeagusspitze beschädigt). Abb. 60. Ditto, Lectotypus, ♀-Genitalien, GU—15200—BM

distal stark vorspringend, Ende stumpf, Cucullus etwa parallelrandig, ventrocaudal und distal gleichmäßig gerundet, dorsocaudal mehr eckig. Aedoeagus verhältnismäßig groß, in der Mitte etwas bauchig, ohne größere Cornuti, aber mit einem länglichen Feld winziger gedrungener Dörnchen. Der distale Fortsatz im Präparat anscheinend beschädigt.

Genitalien ♀ (Abb. 60) (untersucht 1 Ex.): Antrum breit, vom Ductus bursae stärker abgesetzt, der blind endende Abschnitt des Corpus bursae mit nur einem, aber großen Signum. Dieses ist länglich, quergestellt, in seiner Umgebung befinden sich winzige kurze Stachelchen. Der zweite Abschnitt des Corpus bursae geht in einen Schlauch über, der sich zu einer zarthäutigen Blase erweitert, an die ein wieder schlauchförmiger Abschnitt anschließt, der sich nach einer Krümmung zum Ductus seminalis verjüngt, im Bereich dieser Krümmung und im anschließenden Zipfel körnelige Wandstruktur.

*Stathmopoda callopis* Meyrick

Meyrick, 1913a: 91 (Diagnose!).

Locus typicus: Indien: Assam: Khasi Hills. Holotypus ♀: "Holotype" "Khasi Hills, Assam. .5. 1907" "*Stathmopoda callopis* Meyr., 1/2. E. Meyrick det., in Meyrick Coll." "Meyrick Coll. B.M. 1938—290" "*callopis* Meyr.". GU—15189—BM (BM). Das zweite Exemplar der Coll. Meyrick gehört einer ganz anderen Art an.

Genitalien ♂ (Abb. 61) (untersucht 2 Ex.): Tegumen mit Uncus und Gnathos bis zum Valvenende reichend. Costa schwach entwickelt, vom Cucullus nicht abgesetzt, Ampulla zapfenförmig, Sacculus bis etwa zur Valvenmitte reichend, distal nicht vortretend, Cucullus distal sich mäßig verjüngend, Distalrand breit gerundet. Aedeoagus ohne Cornuti, aber mit schütter verteilten winzigen Stachelchen; distaler Fortsatz spatelförmig, in der Mitte mit einer Rinne, Anelluslappen länglich, in der Mitte am breitesten.

Genitalien ♀ (Abb. 62) (untersucht 3 Ex.): Blind endender Abschnitt des Corpus bursae mit nur einem, aber großen Signum, das in der Mitte verbreitert ist. Der zweite Abschnitt des Corpus bursae, der einige plumpe Dörnchen enthält, geht in einen

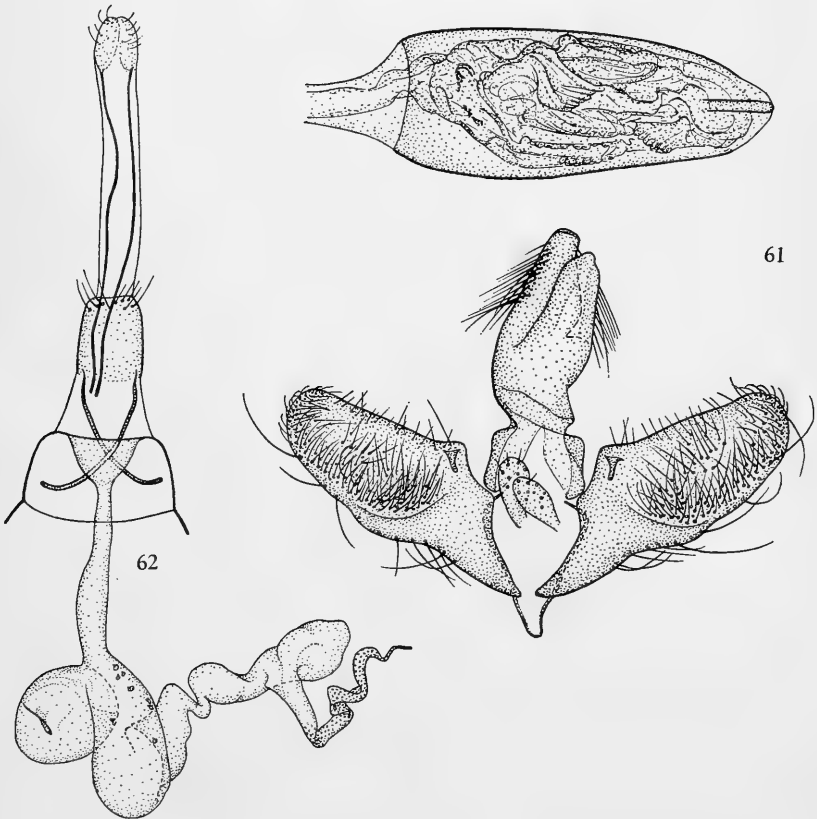


Abb. 61. *Stathmopoda callopis* Meyrick, ♂-Genitalien, GU—3925—Mus. Vind. Abb. 62. Ditto, ♀-Genitalien, Holotypus, GU—15189—BM

längeren schlauchförmigen Abschnitt über, der mehrfach gewunden ist und blasige Aufreibungen enthält, die Zone mit der körneligen Wandstruktur am Übergang zum Ductus seminalis ziemlich lang.

Verbreitung: Die Art liegt mir außer vom Typenfundort auch aus Nepal: East Jubing, 1600 m und Katmandu-Tal: Godavari, 1600—1800 m, vor.

### *Stathmopoda iners* Meyrick

Meyrick, 1913a: 87 (Diagnose!).

Locus typicus: Ceylon: Maskeliya. Holotypus (Monotypus) ♀: "Holotype" "Maskeliya, Ceylon. Pole .3. 04" "*Stathmopoda iners* Meyr., 1/1. E. Meyrick det., in Meyrick Coll." "Meyrick Coll. B.M. 1938—290" "*iners* Meyr.". GU—15196—BM (BM).

Genitalien ♂: unbekannt.

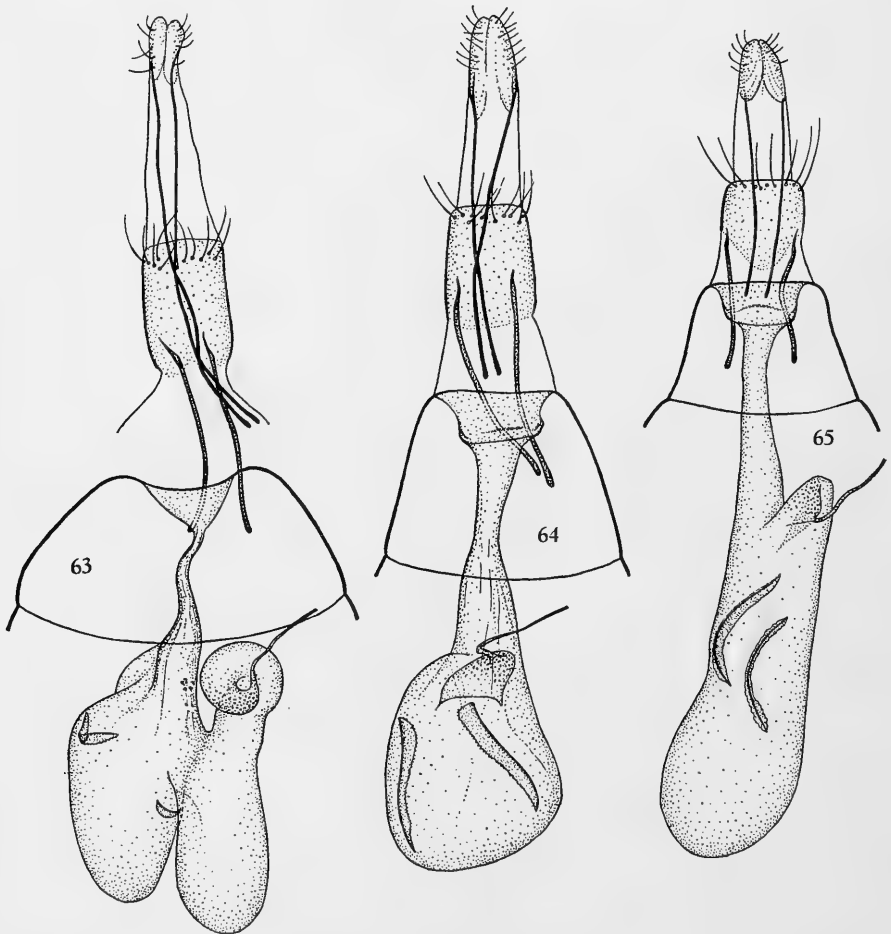


Abb. 63. *Stathmopoda iners* Meyrick, Holotypus, ♀-Genitalien, GU—15196—BM. Abb. 64. *S. tetramma* Meyrick, Holotypus, ♀-Genitalien, GU—15201—BM. Abb. 65. *S. triloba* Meyrick, Lectotypus, ♀-Genitalien, GU—15203—BM

Genitalien ♀ (Abb. 63) (untersucht 1 Ex.): Zwei etwa halbmondförmige Signa vorhanden, das eine etwa doppelt so groß wie das andere, Rand des größeren gezackt, des kleineren ziemlich glatt. Am Übergang vom Ductus bursae zum Corpus bursae einige sklerotisierte Höckerchen. Die beiden Abschnitte des Corpus bursae etwa gleich groß, der ohne Signa setzt sich caudal in einen kurzen breiten Schlauch fort, der nach einer Krümmung in den Ductus seminalis übergeht, vor diesem, schon im sich verzweigenden Schlauch, körnelige Wandstruktur.

### *Stathmopoda tetrarma* Meyrick

Meyrick, 1913a: 86 (Diagnose!).

Locus typicus: Südindien: Nilgiri Hills. Lectotypus ♀ (hier festgelegt): "Lectotype" "Nilgiri Hills, S. India. HLA. 6000' .5. 07" "*Stathmopoda tetrarma* Meyr., 3/3. E. Meyrick det., in Meyrick Coll." "Meyrick Coll. B.M. 1938—290" "*tetrarma* Meyr." "Lectotypus ♀, *Stathmopoda tetrarma* Meyrick, 1913. teste F. Kasy, 1968". GU—15201—BM (BM).

Genitalien ♂: unbekannt.

Genitalien ♀ (Abb. 64) (untersucht 2 Ex.): Antrum vom Ductus bursae stärker abgesetzt. Die zwei Signa etwa gleich groß, in Form von in der Längsrichtung angeordneten Leisten mit gesägtem Rand, die in ihrem caudalen Teil am breitesten sind. Zweiter Abschnitt des Corpus bursae zu einem Zipfel reduziert, der am Übergang des Ductus bursae in das Corpus bursae ansetzt, am Übergang zum Ductus seminalis körnelige Wandstruktur.

### *Stathmopoda triloba* Meyrick

Meyrick, 1913a: 87 (Diagnose!).

Locus typicus: Ceylon: Maskeliya. Lectotypus ♀ (hier festgelegt): "Lectotype" "Maskeliya, Ceylon. De Mowbray. .6. 06" "*Stathmopoda triloba* Meyr., 1/2. E. Meyrick det., in Meyrick Coll." "Meyrick Coll. B.M. 1938—290" "*triloba* Meyr." "Lectotypus ♀, *Stathmopoda triloba* Meyrick, 1913, teste F. Kasy, 1968". GU—15203—BM (BM).

Genitalien ♂: unbekannt.

Genitalien ♀ (Abb. 65) (untersucht 5 Ex.): ähnlich *tetrarma*, die Signa aber etwa in der Mitte am breitesten, das Corpus bursae länger, daher die Signa nicht so weit nach unten reichend.

Verbreitung: mir außer vom Typenfundort auch aus Indien (Bombay, Kanara) und Nepal (Hetaura) vorgelegen.

### *Stathmopoda commoda* Meyrick

Meyrick, 1913a: 85 (Diagnose!).

Locus typicus: Indien: Assam: Khasi Hills. Lectotypus ♀ (hier festgelegt): "Lectotype" "Khasi Hills, Assam. .7. 1906" "*Stathmopoda commoda* Meyr., 8/20. E. Meyrick det., in Meyrick Coll." "Meyrick Coll. B.M. 1938—290" "*commoda* Meyr." "Lectotypus ♀, *Stathmopoda commoda* Meyrick, 1913. teste F. Kasy, 1968". GU—15198—BM (BM).

Genitalien ♂ (Abb. 66) (untersucht 4 Ex.): Tegumen mit Uncus und Gnathos etwa

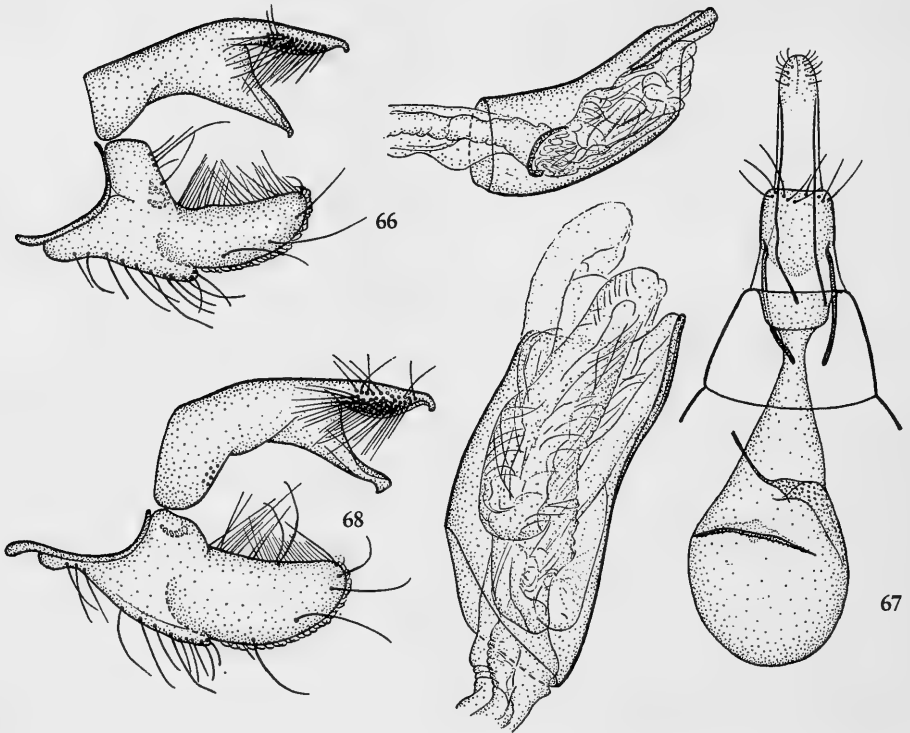


Abb. 66. *Stathmopoda commoda* Meyrick, ♂-Genitalien, GU—15199—BM. Abb. 67. Ditto, Lectotypus, ♀-Genitalien, GU—15198—BM. Abb. 68. *S. leptoclista* Meyrick, Holotypus, ♂-Genitalien, GU—15204—BM (Aedoeagus gequetscht)

so lang wie die Valven. Diese an der Basis breit, der kurze Costalteil stufenförmig vom schmalen Cucullus abgesetzt, Ampulla stark gekrümmt und relativ kräftig, Sacculus etwa bis zur halben Valvenlänge reichend, distal mit einem runden Höcker vorspringend, Cucullus mit fast geradem Dorsalrand und schwach gekrümmtem Ventralrand, dorso-caudal daher ziemlich eckig; Aedoeagus schwach gekrümmt, ohne Cornuti, distaler Fortsatz am Ende etwas verbreitert. Das Genitale ist sehr ähnlich dem von *cissota*, doch besitzt bei dieser der Aedoeagus, der verhältnismäßig größer ist, eine große Zahl winziger Cornuti.

Genitalien ♀ (Abb. 67) (untersucht 4 Ex.): Antrum gut vom Ductus bursae abgesetzt, letzterer kurz, sich allmählich zum Corpus bursae erweiternd, nur ein, aber sehr langes Signum vorhanden, dieses quergestellt, schmal, am Rand gesägt; zweiter Abschnitt des Corpus bursae zu einem Zipfel mit körneliger Wandstruktur reduziert, der in den Ductus seminalis übergeht.

#### *Stathmopoda leptoclista* Meyrick

Meyrick, 1929: 541 (Diagnose!).

Locus typicus: Indien: Assam: Shillong. Holotypus (Monotypus) ♂: "Holotype" "Shillong, Assam, TBF. 5000' .9. 27" "*Stathmopoda leptoclista* Meyr., 2/2. E. Meyrick det., in Meyrick Coll." "Meyrick Coll. B.M. 1938—290" "*leptoclista* Meyr.". GU—15204—BM (BM).

Genitalien ♂ (Abb. 68) (untersucht 2 Ex.): Ähnlich denen von *commoda*, aber der



Cucullus breiter und der Costalteil deshalb nicht so stark stufenförmig abgesetzt, Ampulla schwach gekrümmt. Aedoeagus ohne Cornuti.

Genitalien ♀ : unbekannt.

Verbreitung: Außer dem Holotypus lag mir noch ein zweites ♂ und zwar aus China. Prov. Szetschwan: Mt. Omei vor.

### *Stathmopoda sycastis* Meyrick

Meyrick, 1917: 62.

Locus typicus: Westpakistan: Peshawar-Distrikt: Tarnab. Holotypus (Monotypus) ♀ : "Holotype" "Peshawar, Punjab[?], TBF. bred .7. 16" "*Stathmopoda sycastis* Meyr., 2/2. E. Meyrick det., in Meyrick Coll." "Meyrick Coll. B.M. 1938—290" "*sycastis* Meyr." "Abdomen missing" (BM).

Diagnose (untersucht 5 ♂, 2 ♀) : Exp. 12,5 - 14,5 mm. Fühler hell, gelblich. Labialpalpen ca. 2½, Endglied etwas länger als das Mittelglied; hell, gelblich. Kopf hell, ockergelblich, Patagia dunkel, graubraun. Thorax ockergelblich, caudal aber graubraun, Schulterdecken ockergelblich. Beine hell, gelblich, Vorderbeine distal stellenweise ange-dunkelt. Hintertibien auf der Oberseite der Länge nach mit langen stachelartigen Borsten besetzt, solche auch in der Umgebung der Sporen, auch am Ende des ersten Tarsen-gliedes stachelartige, aber kleinere Borsten. Vfl. sehr schmal (Form und Geäder siehe Abb. 33, untersucht 2 Ex., halbseitig), Grundfarbe hell ockergelblich; an der Wurzel ein Fleck von dieser Farbe, davor, insbesondere am Hinterrand der Flügel, graubraun angedunkelt, in der Flügelmitte eine schwächere, querbindenartige, nach beiden Seiten allmählich in die helle Grundfarbe übergehende Verdunkelung, auch die Flügelspitze angedunkelt. Fransen gelblichgrau. Hfl. einschließlich der Fransen gelblichgrau, die Spitze heller, gelblich.

Genitalien ♂ (Abb. 71 und 72) (untersucht 5 Ex.): Tegumen mit Uncus und Gnathos bis auf die Höhe der Valvenspitzen reichend, an der Basis der Gnathos ein eckiger Vorsprung am Tegumen. Valven relativ kurz und an der Basis sehr breit, Costalteil etwa 1/3 der Valvenlänge einnehmend, vom Cucullus stufenförmig abgesetzt, Ampulla lang und grazil, gebogen, Sacculus bis etwa zur Valvenhälfte reichend, distal nicht vortretend, Cucullus sich distal stark verjüngend, Spitze gerundet, nach oben gebogen. Aedoeagus gekrümmt, sich distal verjüngend, ohne Cornuti, distaler Fortsatz plump, vom übrigen Aedoeagus nicht abgesetzt, Spitze stärker sklerotisiert, Anelluslappen schmal, Diaphragma mit stachelartigen Borsten. Die Art besitzt am 8. Abdominal-segment ein Paar Coremata in Form langer, in tiefen Taschen steckender Bündel von Haaren mit stumpfen Enden, gleichartige Haare finden sich, wie auch bei anderen *Stathmopodidae*, noch in Form eines lockeren Kranzes sowie zweier Büschel an der Basis der Valven (Abb. 69).

Genitalien ♀ (Abb. 70) (untersucht 2 Ex.): Antrum etwa so lang wie breit, vom Ductus bursae abgesetzt, bei einem der zwei untersuchten Exemplare mit winzigen Körnchen. Blind endender Abschnitt des Corpus bursae mit zwei etwa gleich großen Signa in Form sklerotisierter Falten, eines mit einer schräg abstehenden Spitze, die Umgebung der Signa mit winzigen Stachelchen. Zweiter Abschnitt des Corpus bursae mit in Streifen angeordneten plumpen Dornen auf breiten Platten, die größtenteils miteinander verwachsen sind, der anschließende schlauchförmige Abschnitt lang, stellenweise mit Windungen, vor dem Ductus seminalis ein langer Abschnitt mit körneliger Wandstruktur

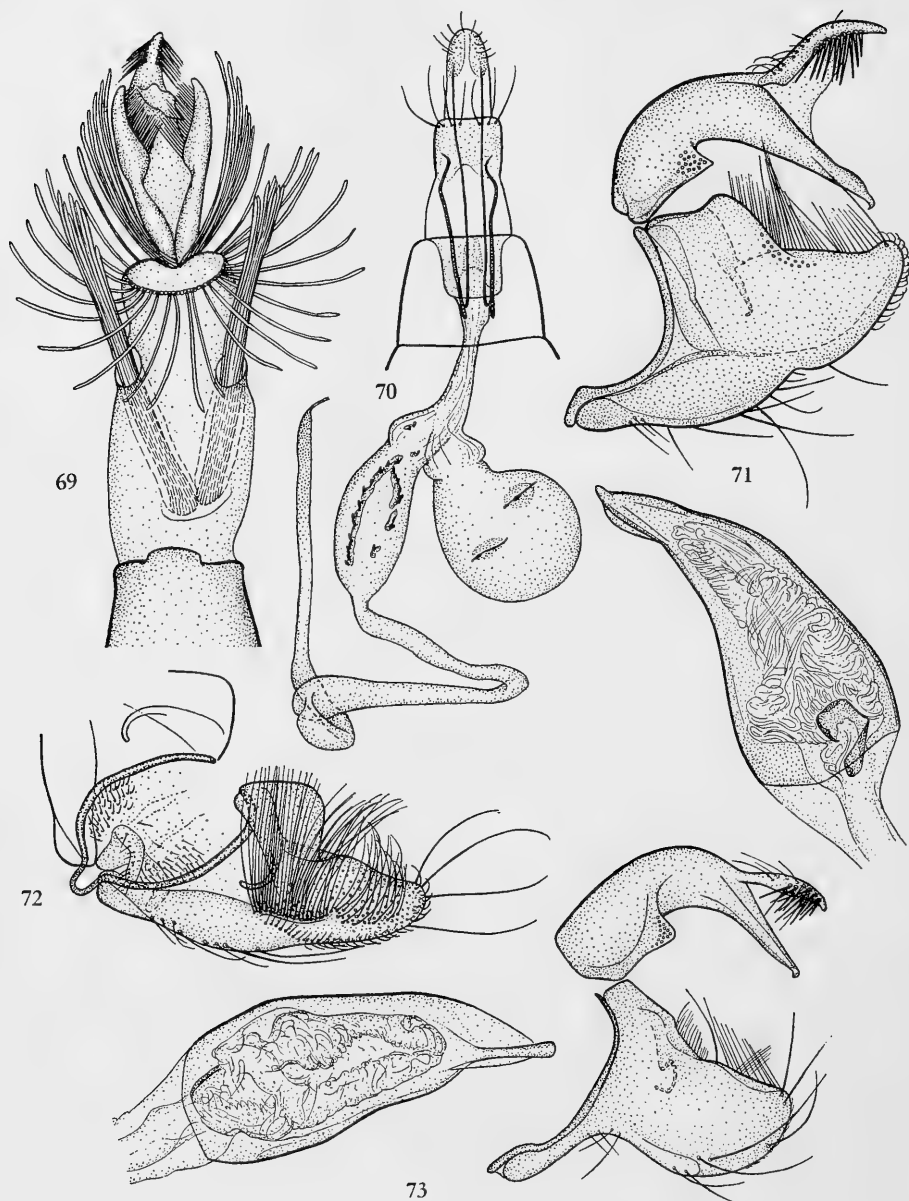


Abb. 69. *Stahmopoda sycastis* Meyrick, Abdomenspitze des ♂ von ventral. Abb. 70. Ditto, ♀-Genitalien, GU—3615—Mus. Vind. Abb. 71. Ditto, ♂-Genitalien, lateral, GU—3614—Mus. Vind. Abb. 72. Ditto, ♂-Genitalien, Valve von innen, GU-16129—BM. Abb. 73. *S. astricta* Meyrick, Holotypus, ♂-Genitalien, GU—15202—BM

Erste Stände und Ökologie: Einige der mir vorgelegenen Exemplare waren aus Raupen gezüchtet worden, die in Feigenfrüchten gelebt hatten. Für die in Nuristan gefangenen Stücke kommt *Ficus nuristanica* in Frage.

Verbreitung: Afghanistan: Nuristan: nordwestl. Barikot; Westpakistan: Tarnab, Lyallpur; Indien: Uttar Pradesh: Dehra Dun; Bombay.

**Stathmopoda astricta** Meyrick

Meyrick, 1913a: 86 (Diagnose!).

Locus typicus: Südindien: Nilgiri Hills. Holotypus (Monotypus) ♂: "Holotype" "Nilgiri Hills, S. India. HLA. 3500' .7. 07" "*Stathmopoda astricta* Meyr., 2/2. E. Meyrick det., in Meyrick Coll." "Meyrick Coll. B.M. 1938—290" "*astricta* Meyr.". GU—15202—BM (BM).

Genitalien ♂ (Abb. 73) (untersucht 1 Ex.): Ähnlich denen von *sycastis*, der Costalteil der Valve aber nicht so stark abgesetzt, daher die Valve an der Basis nicht so breit, Cucullus breiter, Sacculus schmaler, der Höcker an der Basis der Gnathos nicht so eckig, sondern gerundet. Coremata ähnlich wie bei *sycastis*.

Genitalien ♀: unbekannt.

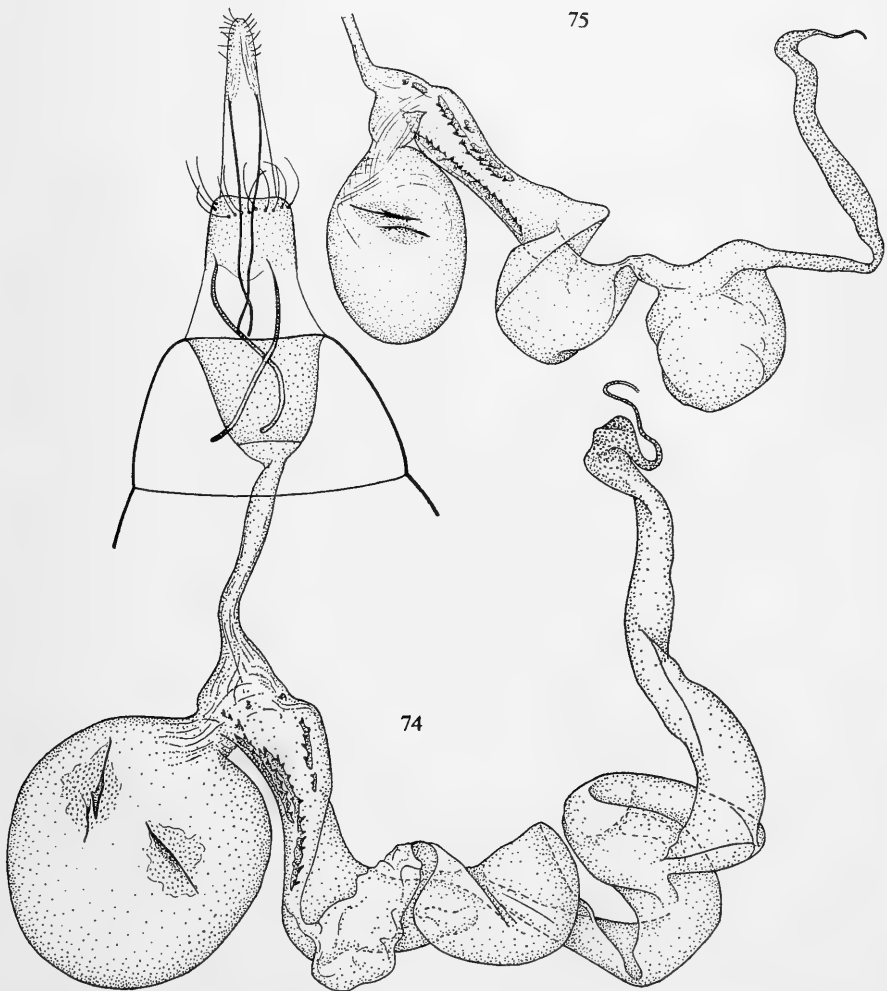


Abb. 74. *Stathmopoda sycophaga* Meyrick, Lectotypus, ♀-Genitalien, GU—15157—BM. Abb. 75. *S. ignominiosa* Meyrick, Holotypus, ♀-Genitalien, unvollständig, GU—15194—BM

**Stathmopoda aprica** Meyrick

Meyrick, 1913a: 86 (Diagnose!).

Locus typicus: Ceylon: Martala. Holotypus (Monotypus) ♂: "Holotype" "Martala Ceylon, JP. 10. 04" "*Stathmopoda aprica* Meyr., 1/1. E. Meyrick det., in Meyrick Coll." "Meyrick Coll. B.M. 1938—290" "*aprica* Meyr." "Abdomen missing" (BM).

Die Art könnte mit der vorigen identisch sein. Da das einzige Exemplar kein Abdomen mehr besitzt, läßt sich diese Frage derzeit nicht klären.

**Stathmopoda sycophaga** Meyrick

Meyrick, 1913a: 87 (Diagnose!).

Locus typicus: Indien: Bengal: Pusa. Lectotypus ♀ (hier festgelegt): "Lectotype" "Pusa, Bengal. HML bred 5. 07" "*Stathmopoda sycophaga* Meyr., 2/2. E. Meyrick det., in Meyrick Coll." "Meyrick Coll. B.M. 1938—290" "*sycophaga* Meyr." "Lectotypus ♀, *Stathmopoda sycophaga* Meyrick, 1913. teste F. Kasy, 1968". GU—15157—BM (BM).

Die Beschreibung erfolgte nach 1 ♂. Dem Paralectotypus, ♀, der die gleichen Funddaten hat, fehlt das Abdomen.

Genitalien ♂: unbekannt.

Genitalien ♀ (Abb. 74) (untersucht 2 Ex.): Antrum etwas länger als breit. Signa ungleich ausgebildet, eines mit einem schräg abstehenden Dorn, in der Umgebung der Signa winzige Dörnchen. Der zweite Abschnitt des Corpus bursae in Form eines breiten Schlauches mit mehreren Krümmungen, im Anfangsteil mit zahlreichen plumpen Dörnchen auf langgestreckten Sockeln, die zum Teil miteinander verschmolzen sind, am Übergang zum Ductus seminalis eine kurze Zone mit winzigen Dörnchen in der Wand.

Erste Stände und Ökologie: Die Raupe wurde in Früchten von *Ficus glomerata* gefunden.

**Stathmopoda ignominiosa** Meyrick

Meyrick, 1913a: 86 (Diagnose!).

Locus typicus: Indien: Coorg: Dibidi. Holotypus (Monotypus) ♀: "Holotype" "Dibidi, N. Coorg. Newcome. 4. 3. 07" "*Stathmopoda ignominiosa* Meyr., 1/1. E. Meyrick det., in Meyrick Coll." "Meyrick Coll. B.M. 1938—290" "*ignominiosa* Meyr." GU—15194—BM (BM).

Genitalien ♂: unbekannt.

Genitalien ♀ (Abb. 75) (untersucht 1 Ex., Abdomen beschädigt): Sehr ähnlich denen von *sycophaga*, aber die Zone mit den winzigen Dörnchen in der Wand an Übergang zum Ductus seminalis ist wesentlich länger und die Dörnchen im Anfangsteil des schlauchförmigen Abschnittes des Corpus bursae sind deutlich in zwei Reihen angeordnet.

Bemerkungen: Vielleicht wird sich, wenn einmal mehr Material zur Verfügung steht, *S. ignominiosa* als identisch mit *S. sycophaga* erweisen oder zu einer Subspecies dieser Art reduziert werden müssen.

**Stathmopoda ficivora** spec. nov.

Locus typicus: UdSSR: Turkmenien: Kara-Kala. Holotypus ♀: "Kara-Kala, Turkm., Gebi-Seut 3. 8. Krassilnikova 1967" "*Apertodiscus ficivora* sp. n. Krassilnikova in litt."

GU—3843—Mus. Vind. Coll. Zoologicheski Institut Akademii Nauk SSSR, Leningrad. 85 Paratypen, ♂ und ♀, vom selben Fundort, z.Tl. gezüchtet, aus den Jahren 1963 und 1967, in derselben Coll. wie der Holotypus, in Coll. Naturhistorisches Museum, Wien und in Coll. W. Glaser, Wien.

Falsche Determination: *zernyi* Amsel: Krassilnikova, 1966: 245 (*Apertodiscus*).

Diagnose (untersucht 21 ♂ und ♀): Exp. 11,8 - 13,0 mm. Fühler hell, gelblich. Labialpalpen ca. 2, 7, Endglied etwa so lang wie das Mittelglied; gelblich. Kopf hell, ockergelblich, glänzend, hinten bräunlich. Thorax mit Schulterdecken ockergelblich, in

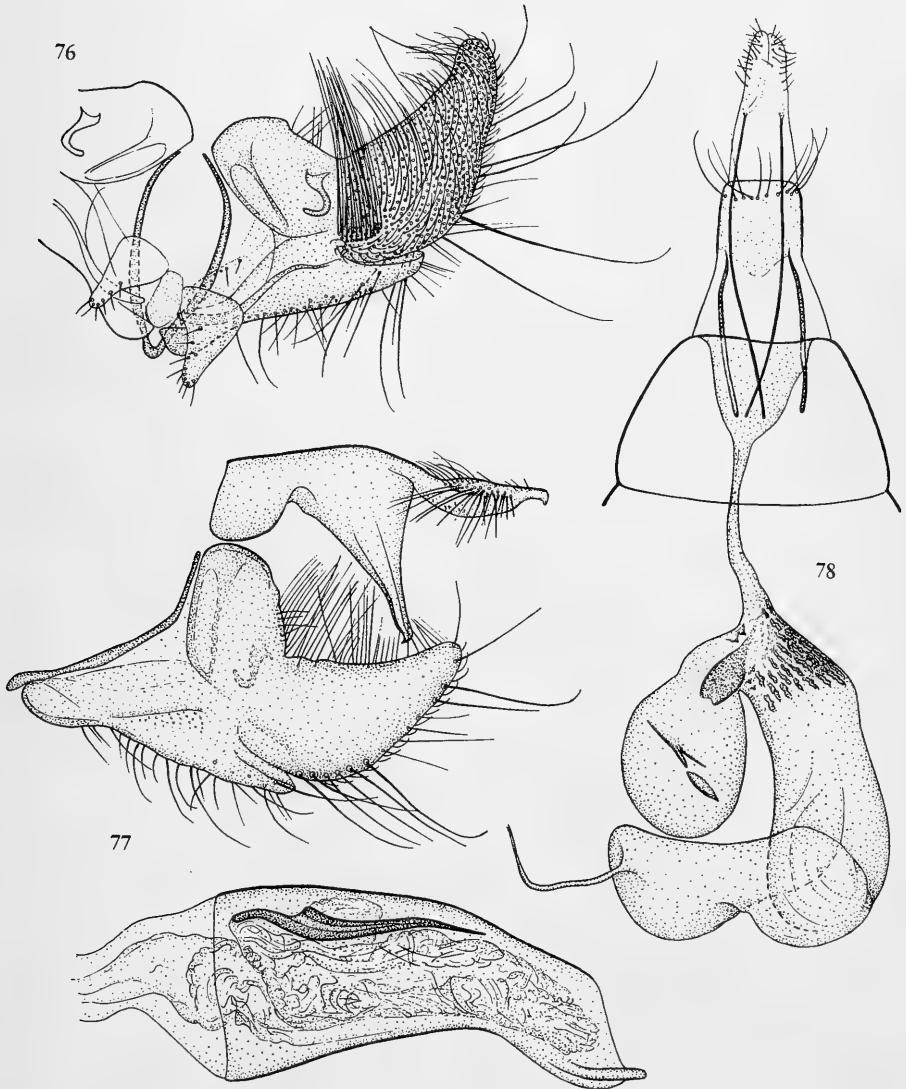


Abb. 76. *Statmopoda ficivora* sp. n. ♂-Genitalien, Valve von innen, GU—3844—Mus. Vind. Abb. 77. Ditto, ♂-Genitalien, GU—3809—Mus. Vind. Abb. 78. Ditto, ♀-Genitalien, GU—3845—Mus Vind.

der Mitte bräunlich, letztere an ihrer Basis außen mit einem bräunlichgrauen Fleck. Beine hell, gelblich, Hintertibien auf der Oberseite dicht mit langen, stachelartigen schräg abstehenden Haaren besetzt, Glieder der Hintertarsen distal angedunkelt. Abdomen hell, gelblichgrau. Vfl. sehr schmal, hell ockergelblich mit bräunlichgrauen unscharf begrenzten Binden bzw. Flecken in folgender Anordnung: ein Fleck an der Wurzel über die ganze Flügelbreite reichend, bei ca.  $\frac{1}{4}$  am Vorderrand ein länglicher Fleck, am Hinterrand, aber mehr distal, ein ebensolcher Gegenfleck, zwischen beiden die gelbliche Grundfarbe nur als sehr schmaler Streifen erhalten, oft die beiden Flecke überhaupt zu einer sehr schrägen Binde verschmolzen, bei ca.  $\frac{3}{4}$  eine Querbinde, die sehr schräg wurzelwärts zum Innenrand zieht, ferner mit Ausnahme des Apex auch der ganze Flügelvorderrand bräunlichgrau. Fransen hell, gelblichgrau. Hfl. einschließlich der Fransen hell, bräunlichgrau, aber die Spitze (ohne Fransen) von der gelblichen Vorderflügelgrundfarbe, offenbar im Zusammenhang mit der Ruhestellung des Falters, in der diese Flügelspitzen über den Rand der Vfl. vorstehen.

Genitalien ♂ (Abb. 76 und 77) (untersucht 2 Ex.): Tegumen mit Uncus und Gnathos etwa bis zur Valvenspitze reichend. Valven an der Basis breit, Costalteil bis zu etwa  $\frac{1}{3}$  der Valvenlänge reichend, vom Cucullus stufenförmig abgesetzt, Ampulla als kräftiger Haken mit breiter Basis ausgebildet, Sacculus bis zu ca.  $\frac{2}{3}$  der Valvenlänge reichend, kräftig, distal mit einem Höcker vorspringend. Cucullus stark nach oben gebogen, sich stark verjüngend, Dorsalrand schwach, Ventralrand stark gebogen, distales Ende gerundet. Aedoeagus distal gekrümmt und sich verjüngend, mit einem sehr großen, stachelförmigen, schwach s-förmig gekrümmten Cornutus; Anelluslappen an der Basis breit, distal stark verjüngt, Ende gerundet.

Genitalien ♀ (Abb. 78) (untersucht 3 Ex.): Ähnlich denen von *sycophaga* Meyrick, der Größenunterschied zwischen den zwei Signa stärker, die winzigen Stachelchen in der Umgebung der Signa fehlen, das kleinere Signum breiter, mit gesägtem Rand. Die auf länglichen Sockeln sitzenden Dornen im basalen Teil des schlauchförmigen Abschnittes des Corpus bursae nicht in deutlichen Reihen angeordnet, außer diesen eine auffällige, längliche, sklerotisierte Platte vorhanden, der schlauchförmige Abschnitt kürzer als bei *sycophaga* und mehr blasenförmig, Ductus seminalis fast ohne Übergang entspringend, körnelige Wandstruktur nur an der Basis des Ductus seminalis oder überhaupt fehlend.

Erste Stände und Ökologie: Nach Krassilnikova (l.c.) lebt die Raupe im Mai bis Juni in Feigenfrüchten (*Ficus carica*), wodurch sie schädlich wird. Die Falter schlüpfen zwischen dem 22. VII. und 21. VIII.

Verbreitung: Bisher anscheinend nur aus Turkmenien: Kara-Kala bekannt.

### Stathmopoda pedella (Linnaeus)

*Phalaena (Tinea) pedella* Linnaeus, 1761: 367.

*Tinea alucitella* [Denis & Schiffermüller], 1775: 144.

*Tinea cylindrella* Fabricius, 1777: 295.

*Tinea angustipennella* Hübner, [1796]: t. 29, f. 197 (Falter, farb.).

*Ypsolophus cylindricus* Fabricius, 1798: 507.

*Oecophora fastuosella* Costa, [1836]: 279, t. 2, f. 7 (Falter, farb.).

*Cosmopteryx pedella*: Zeller, 1839: 210 (*alucitella* Denis & Schiffermüller, *angustipennella* Hübner, Synonyme).

*Stathmopoda pedella*: Herrich-Schäffer, 1853: 283. — Stainton, 1854: 228 (*cylindrella* Fabricius, *cylindricus* Fabricius, Synonyme). — Heinemann & Wocke, 1877: 427. — Meess, in Hofmann &

Spuler, 1907—1910: 389. t. 89, f. 73a, b (Falter, farb.). — Hartig, 1939: 19 (*fastuosella* Costa, Synonym). — Riedl, 1969: 715 (dort auch weitere Literatur), f. 40 (Falter, phot.), f. 119 (Kopf, lateral), f. 146 (Geäder), f. 196 (Abdomenbasis: Verstärkungsleisten), f. 284 ( $\delta$ -Genit.), f. 371 ( $\varphi$ -Genit., unvollständig).

*Phalaena (Tinea) pedella* Linnaeus: Locus typicus: Schweden. Lectotypus  $\delta$  (hier festgelegt): "Lectotype" "*pedella*" "*pedella* 894" "Lectotype  $\delta$ , *Phalaena (Tinea) pedella* Linnaeus, teste K. Sattler, 1971". Coll. Linnean Society, London. Der Lectotypus wurde aus zwei Exemplaren ausgewählt, das zweite, 1  $\varphi$ , wurde zum Paralectotypus designiert.

*Tinea alucitella* [Denis & Schiffermüller]: Locus typicus: Umgebung von Wien. Typus: verloren.

*Tinea cylindrella* Fabricius: Locus typicus: Hamburg.

*Tinea angustipennella* Hübner: Locus typicus: Europa, wahrscheinlich Umgebung von Augsburg. Typus: verloren.

*Ypsolophus cylindricus* Fabricius: Locus typicus: Hamburg. Ungerechtfertigte Emen-dation von *Tinea cylindrella* Fabricius, 1777.

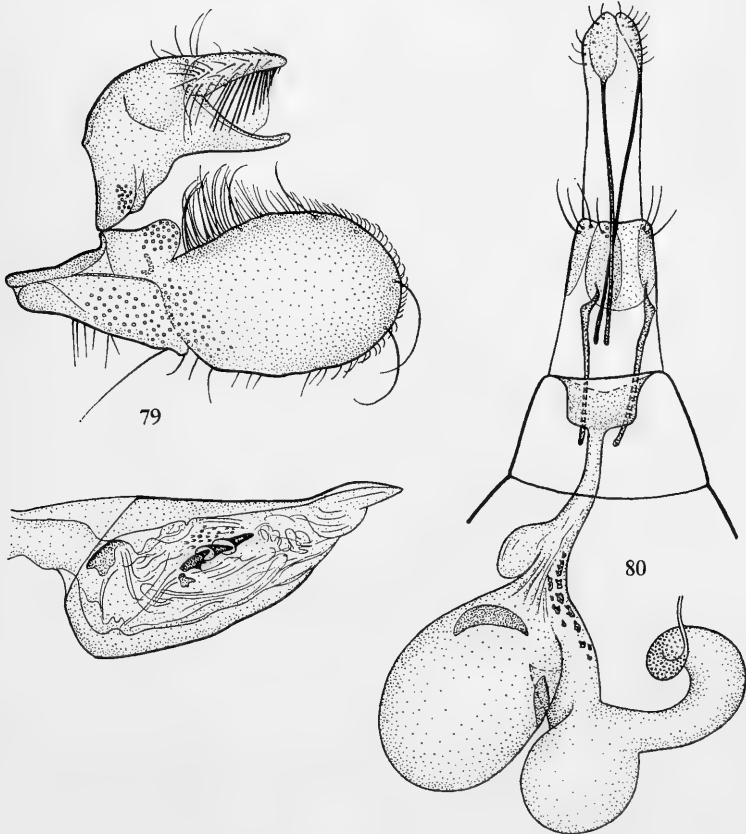


Abb. 79. *Stathmopoda pedella* (Linnaeus).  $\delta$ -Genitalien, GU—3724—Mus. Vind. Abb. 80. Ditto,  $\varphi$ -Genitalien, GU—3741—Mus. Vind.

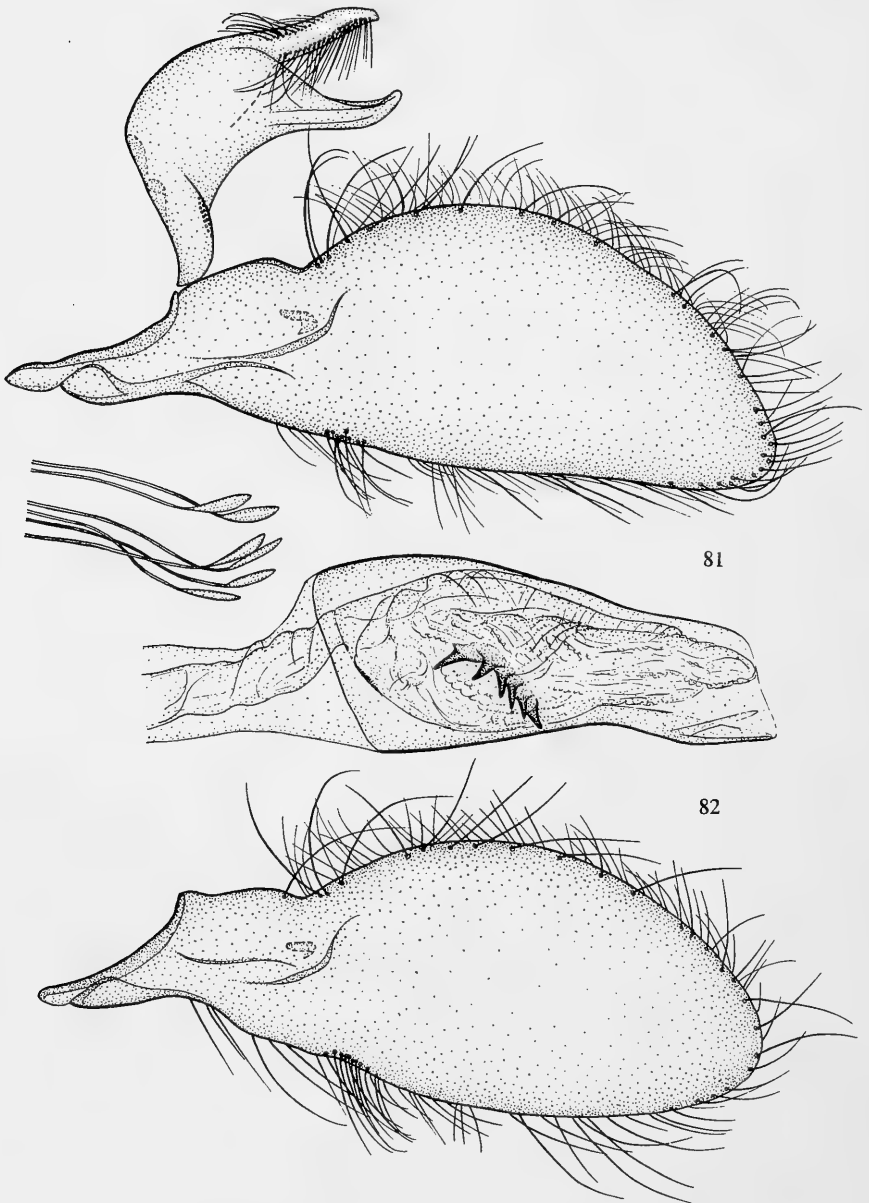


Abb. 81. *Stelmopoda hexatyla* Meyrick, Lectotypus, ♂-Genitalien (daneben Duft(?) Schuppen, stärker vergrößert), GU—15301—BM. Abb. 82. *S. hexatyla* ssp. *informis* (Meyrick), Lectotypus. ♂-Genitalien, Valve, GU—15195—BM

*Oecophora fastuosella* Costa: Locus typicus: S-Italien: Neapel: Camaldoli. Typus: verloren.

Diagnose: Heinemann & Wocke (1877: 427), Meess, in Hofmann & Spuler (1907—10: 389), Riedl (1969: 715).



Genitalien ♂ (Abb. 79) (untersucht 3 Ex.): Tegumen mit Uncus und Gnathos etwa halb so lang wie die Valve. Costa kurz, vom Cucullus stark abgesetzt, vor diesem höckerförmig vortretend; Sacculus kräftig, von mehr als  $1/3$  der Valvenlänge, distal nur wenig vortretend, Cucullus oval, ziemlich gleichmäßig gerundet. Aedoeagus distal sich verjüngend, distaler Fortsatz spitz, mehrere hintereinander liegende plumpe Cornuti vorhanden, manchmal überdies ein Feld sehr kleiner Cornuti.

Genitalien ♀ (Abb. 80) (untersucht 3 Ex.): Antrum etwa so lang wie breit, Signa viertelmondförmig, mit gesägtem Rand, eines etwas kleiner; am Übergang zum zweiten Abschnitt des Corpus bursae unregelmäßig geformte Dörnchen mit breiten Grundplatten, z. Tl. untereinander verwachsen. Der zweite Abschnitt des Corpus bursae besteht zunächst aus einem kurzen breiten Schlauch, der sich zu einer Blase erweitert, an die wieder ein kurzer breiter Schlauch anschließt, der sich nach einer Krümmung zum Ductus seminalis verjüngt; nur in dem sich schon verjüngenden Abschnitt Wandstruktur.

Erste Stände und Ökologie: Nach verschiedenen Literaturangaben lebt die Raupe im Spätsommer in den noch grünen weiblichen Kätzchen von *Alnus glutinosa* und *A. incana*, angeblich aber auch in Gallen.

Verbreitung: In Europa anscheinend weit verbreitet, im Norden aus Schweden, im Osten aus Kasan und dem Gouv. Perm bekannt.

### *Stathmopoda hexatyla* Meyrick

Meyrick, 1907a: 744 (Diagnose!).

Locus typicus: Ceylon: Madulsima. Lectotypus ♂ (hier festgelegt): "Lectotype" "Madulsima, Ceylon. Vaughan .10. 05" "*Stathmopoda hexatyla* Meyr., 4/7. E. Meyrick det., in Meyrick Coll." "Meyrick Coll. B.M. 1938—290" "*hexatyla* Meyr." "Lectotypus ♂, *Stathmopoda hexatyla* Meyrick, 1907. teste F. Kasy, 1968". GU—15301—BM (BM).

Genitalien ♂ (Abb. 81) (untersucht 2 Ex.): Tegumen mit Uncus und Gnathos nur bis etwa  $1/3$  der Valvenlänge reichend, Uncus und Gnathos nicht divergierend, sondern etwa parallel zueinander. Vor dem Tegumen ein dichtes Büschel Duft(?)—Schuppen. Valve sehr lang, Costa nur von ca.  $1/5$  der Valvenlänge, nicht stärker vom Cucullus abgesetzt, Ampulla hakenförmig gekrümmt, Sacculus von ca.  $1/4$  der Valvenlänge, nicht stärker abgesetzt oder distal vortretend, Ventralrand des Cucullus fast gerade, Dorsalrand stark gekrümmt, Ventrocaudaleck gerundet. Aedoeagus distal verjüngt, etwas gekrümmt, mit mehreren in einer Reihe angeordneten Cornuti in Form gedrungener Stacheln auf breiten Sockeln. Distaler Fortsatz bandförmig, vom übrigen Aedoeagus nicht stärker abgesetzt. Anelluslappen zipfelförmig, also distal sich verschmälernd.

Genitalien ♀ (Abb. 83) (untersucht 4 Ex.): Antrum etwas sklerotisiert, vom Ductus bursae stärker abgesetzt. Am Übergang vom Ductus zum Corpus bursae mehr oder weniger deutlich in Reihen angeordnete, plumpe, unregelmäßig geformte Dörnchen. Die zwei etwa gleich großen Signa relativ klein, mit gezackten Rändern. Zweiter Abschnitt des Corpus bursae in Form eines breiten, nach caudal sich umbiegenden Schlauches, der sich nach einer Seite zu einer blasenförmigen Ausbauchung erweitert, an dieser sitzt ein Zipfel, der in den Ductus seminalis übergeht, nur dieser kurze Zipfel mit körneliger Wandstruktur.

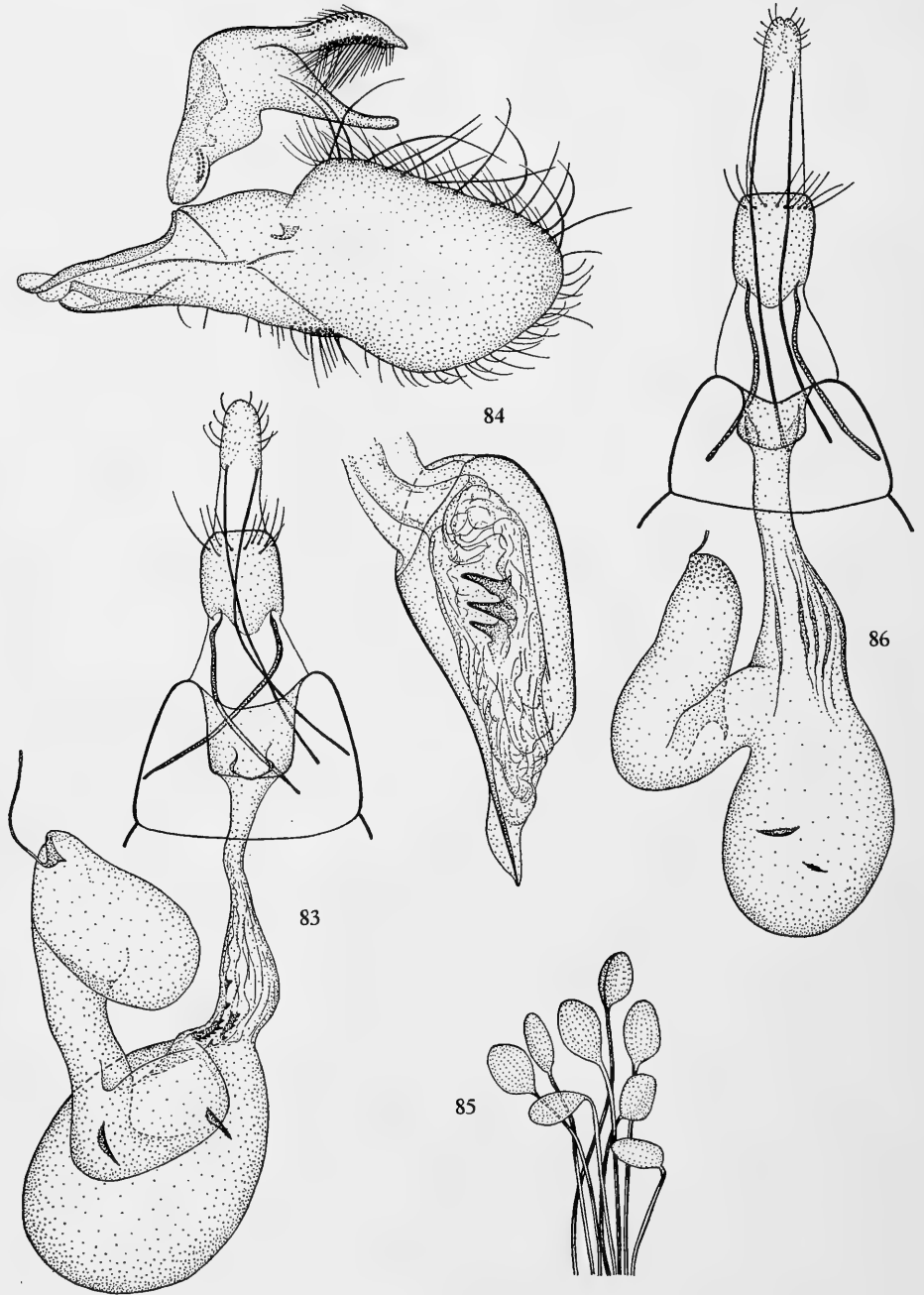


Abb. 83. *Stathmopoda hexatyla* Meyrick, ♀-Genitalien, GU—15302—BM. Abb. 84. *S. stimulata* Meyrick, ♂-Genitalien, GU—16136—BM. Abb. 85. Ditto, Duft(?)—Schuppen (stärker vergrößert). Abb. 86. Ditto, ♀-Genitalien, GU—16136—BM

*Stathmopoda hexatyla informis* (Meyrick) stat. nov.

*Stathmopoda informis* Meyrick, 1913a: 87 (Diagnose!).

Locus typicus: Indien: Assam: Khasi Hills. Lectotypus ♂ (hier festgelegt): "Lectotype" "Khasi Hills, Assam. .6. 1906" "*Stathmopoda informis* Meyr., 2/3. E. Meyrick det., in Meyrick Coll." "Meyrick Coll. B.M. 1938—290" "*informis* Meyr." "Lectotypus ♂, *Stathmopoda informis* Meyrick, 1913. teste F. Kasy, 1968". GU—15195—BM (BM).

Im ♂-Genital (untersucht Lecto- und Paralectotypus) sind keine auffälligeren Unterschiede gegenüber den zwei von Ceylon vorliegenden Männchen von *hexatyla* festzustellen, außer daß bei *informis* die Valven breiter sind (Abb. 82). Beide Exemplare haben nur drei Cornuti, die zwei *hexatyla* von Ceylon weisen 5 bzw. 6 auf. Bei der nahestehenden *stimulata* Meyrick wurde eine nicht geographisch bedingte Variabilität zwischen 3 und 5 Cornuti festgestellt, weshalb dem genannten Unterschied keine besondere Bedeutung beigemessen werden kann. Ein offenbar zu *informis* gehörendes ♀ vom Typenfundort (das in der Coll. Meyrick fälschlich als *stimulata* bestimmt war) unterscheidet sich im Genital (GU—16352—BM) von den typischen *hexatyla* aus Ceylon nur dadurch auffälliger, daß die beiden Signa größer sind. Äußerlich unterscheiden sich die *informis*-Stücke von den Khasi Hills durch die helle Färbung von den dunkelgelben *hexatyla*-Exemplaren aus Ceylon. In diesem Zusammenhang sind auch drei Exemplare aus Nepal: Junbesi, 2750 m (Coll. Zoologische Sammlungen des Bayerischen Staates, München) interessant. Sie gehören nach dem Bau der Genitalien ebenfalls zu *hexatyla*. Die zwei Männchen haben noch breitere Valven als die Stücke aus Assam, die Cornutzahlen sind 7 und 8 (wobei je zwei Cornuti sehr klein sind) und beim ♀ sind die Signa noch größer als bei der ssp. *informis* aus Assam. Die Tiere sind wie die aus dem letztgenannten Gebiet gefärbt, also bleich. Schließlich ist auch noch ein ♀ zu erwähnen, das sich in der Coll. Walsingham im (BM) fand. Es hat die Fundortetikette "Perak [Malaysia] Doherty 18. No." und stimmt im Bau des Genitals ebenfalls sehr gut mit *hexatyla* überein, doch sind die beiden Signa auffällig in der Größe verschieden, das eine ist nämlich  $5 \times$  so lang wie das andere. Äußerlich stimmt es durch die helle Färbung mit *hexatyla informis* überein. Ob hier mehrere nahestehende Arten vorliegen oder *hexatyla* zur Rassenbildung neigt, muß derzeit aus Materialmangel offen bleiben. Es dürfte jedenfalls vorderhand besser sein, *informis* nur als ssp. von *hexatyla* aufzufassen.

*Stathmopoda stimulata* Meyrick

Meyrick 1913a: 84 (Diagnose!).

Locus typicus: Indien: Assam: Khasi Hills. Lectotypus ♂ (hier festgelegt): "Lectotype" "Khasi Hills, Assam. .6. 1906" "*Stathmopoda stimulata* Meyr., 6/9. E. Meyrick det., in Meyrick Coll." "Meyrick Coll. B.M. 1938—290" "*stimulata* Meyr." "Lectotypus ♂, *Stathmopoda stimulata* Meyrick, 1913. teste F. Kasy, 1968". GU—16351—BM (BM).

Genitalien ♂ (Abb. 84) (untersucht 4 Ex.): Tegumen mit Uncus und Gnathos von ca. 1/3 der Valvenlänge, seitlich am Tegumen je ein runder Höcker. Vor dem Tegumen ein Büschel Duft(?)-Schuppen, deren Enden stark verbreitert sind (Abb. 85). Valve mit

etwa parallel zueinander verlaufendem Dorsal- und Ventralrand, Costa von etwa  $\frac{1}{4}$  der Valvenlänge, vom Cucullus deutlich abgesetzt, Ampulla gekrümmt, an der Basis ziemlich breit, Sacculus kräftig, bis etwa zur Valvenmitte reichend, spitz endend, aber kaum vorspringend, Cucullus distal sich etwas verbreiternd, Dorsalrand ziemlich gerade, ventrocaudal und dorsocaudal stark gerundet, Distalrand nur schwach gekrümmt. Aedoeagus distal sich verjüngend, mit mehreren in einer Reihe angeordneten kräftigen Cornuti in Form stumpfer Dornen auf breiten Grundplatten, distaler Fortsatz bandartig, in der Mitte geteilt, Anelluslappen schmal, an der Basis kaum breiter.

Genitalien ♀ (Abb. 86) (untersucht 5 Ex.): Antrum schwach sklerotisiert, vom Ductus bursae stärker abgesetzt. Am Übergang vom Ductus bursae zum Corpus bursae im Gegensatz zu *hexatyla*, der das Genitale sonst ähnlich ist, keine Dornen oder ähnliche Gebilde, sondern stärker sklerotisierte Längsfalten. Signa relativ klein, das eine etwa doppelt so lang wie das andere, das größere mit gesägtem Rand. Bei zwei mir aus China vorliegenden Exemplaren ist der Größenunterschied zwischen den Signa geringer als bei den anderen. Der zweite Abschnitt des Corpus bursae ähnlich wie bei *hexatyla*, aber nicht nach einer Seite ausgebaucht. Körnelige Wandstruktur wie bei dieser nur im zipfelförmigen Abschnitt vor dem Ductus seminalis.

Verbreitung: Nach dem untersuchten Material Indien: Assam: Khasi Hills; Indien: Coorg; Ceylon: Maskeliya und Colombo; West China: Szetschwan: Mt. Omei; Kwanhsien.

### *Stathmopoda monobathra* Meyrick

Meyrick, 1937: 150 (Diagnose!).

Locus typicus: Indien: Poona bei Bombay. Holotypus (Monotypus) ♀: "Holotype" "Poona, Bombay, RM. 30.4.22" "*Stathmopoda monobathra* Meyr., 1/1. E. Meyrick det., in Meyrick Coll." "Meyrick Coll. B.M. 1938—290" "*monobathra* Meyr.". GU—15327—BM (BM).

Genitalien ♂: unbekannt.

Genitalien ♀ (Abb. 87) (untersucht 1 Ex.): Antrum kelchförmig, schwach sklerotisiert, am Grunde einige stärker sklerotisierte Falten und Vorsprünge. Ductus bursae sich sackförmig erweiternd. Zwei große, ungleich ausgebildete Signa vorhanden, das eine mit einem im Querschnitt flachen, schräg nach innen stehenden Stachel, das andere nur mit einem Grat, der an einem Ende in einen kleinen Stachel übergeht. Der zweite Abschnitt des Corpus bursae schlauchförmig, lang, am Übergang in den eigentlichen Ductus seminalis mit Wandstruktur, im Anfangsteil, bzw. noch im Ductus bursae, Dörnchen.

### *Stathmopoda balanistis* Meyrick

Meyrick, 1913a: 89 (Diagnose!).

Locus typicus: Indien: Assam: Khasi Hills. Holotypus (Monotypus) ♂: "Holotype" "Khasi Hills, Assam. .10. 1906" "*Stathmopoda balanistis* Meyr., 2/2. E. Meyrick det., in Meyrick Coll." "Meyrick Coll. B.M. 1938—290" "*balanistis* Meyr.". GU—15328—BM (BM).

Genitalien ♂ (Abb. 88) (untersucht 1 Ex.): Tegumen mit Uncus und Gnathos bis zu etwa  $\frac{2}{3}$  der Valvenlänge reichend. Valven verhältnismäßig schmal, Costalteil von ca.  $\frac{1}{3}$  der Valvenlänge, vom Sacculus schwach stufenförmig abgesetzt, Ampulla grazil,

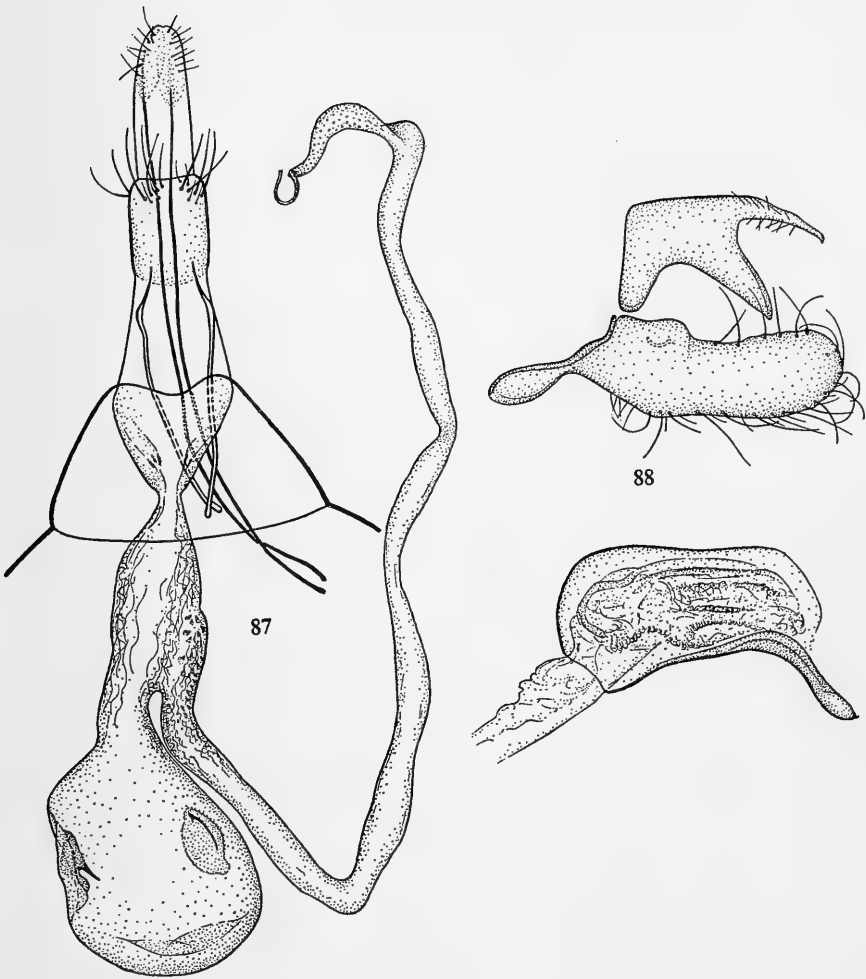


Abb. 87. *Stathmopoda monobathra* Meyrick, Holotypus, ♀-Genitalien, GU—15327—BM. Abb. 88. *S. balanistis* Meyrick, Holotypus, ♂-Genitalien, GU—15328—BM

Sacculus von ca. 1/3 der Valvenlänge, nicht hervortretend, Cucullus ziemlich gerade, Dorsal- und Ventralrand parallel zueinander, distal gleichmäßig gerundet. Am Saccus ein Büschel Haarschuppen. Aedoeagus gedrunken, ohne Cornuti, distaler Fortsatz stark sklerotisiert und sehr kräftig, nach außen gekrümmt, distal etwas verbreitert.

Genitalien ♀ : unbekannt.

### *Stathmopoda horrida* Meyrick

Meyrick, 1936a: 618 (Diagnose!).

Locus typicus: Java: Mt. Gedé. Holotypus (Monotypus) ♀ : "Holotype" "Mt Gedé. 2650'. Java. LGK. bred .34" "*Stathmopoda horrida* Meyr., 1/1. E. Meyrick det., in Meyrick Coll." "Meyrick Coll. 1938—290" "*horrida* Meyr.". GU—15348—BM" (BM).

Genitalien ♂: unbekannt.

Genitalien ♀ (Abb. 89) (untersucht 1 Ex.): Ostium sehr breit, Antrum am Grunde mit winzigen Stacheln. Ductus bursae am Anfang mit einer kropfförmigen Auftreibung, die zahlreiche Falten und streifenförmige Verdickungen in der Wand enthält. Nur ein, aber sehr großes, quergestelltes Signum in Form einer sklerotisierten Falte vorhanden. Zweiter Abschnitt des Corpus bursae zunächst schlauchförmig, dann zu einer länglichen Blase erweitert, die wieder, aber seitlich, in ein kurzes schlauchförmiges Stück übergeht, an das der Ductus seminalis ansetzt, vor diesem eine kurze Zone mit Wandstruktur.

Erste Stände und Ökologie: Die Raupe wurde in einem Zweig eines unbekanntes Baumes gefunden.

Bemerkungen: Die Art weicht von den meisten anderen *Stathmopoda*-Arten dadurch ab, daß die Stacheln an den hinteren Tergiträndern nicht nur in wenigen Reihen angeordnet sind, sondern in Form breiter Streifen.

### *Stathmopoda haematosema* Meyrick

Meyrick, 1933: 431. — Issiki, in Esaki et al., 1957: 35; t. 5, f. 140 (Falter, farb.). — Kuroko, 1959: 4.

Locus typicus: Japan: Honshu: Tokio. Holotypus (Monotypus) ♀: "Holotype" "Tokyo, Japan. SI. 18. 7. 32" "*Stathmopoda haematosema* Meyr., 1/1. E. Meyrick det., in Meyrick Coll." "Meyrick Coll. B.M. 1938—290" "*haematosema* Meyr." "Abdomen missing" (BM).

Die Art wurde von Meyrick nach einem einzigen ♀ beschrieben. Es besitzt kein Abdomen mehr, doch existiert in der Coll. Entomological Laboratory, University of Osaka Prefecture ein ♂, das die gleichen Funddaten wie der Holotypus hat und damit den Aussagewert einer Type besitzt. Dieses erwies sich artgleich mit einem ♂ von einem anderen Fundort, zu dem ein ♀ mit den gleichen Funddaten existiert. Aufgrund dieses und weiteren Materials konnte daher die Art geklärt werden.

Diagnose (untersucht 2 ♂, 3 ♀): Exp. 8,5 - 10,9 mm. Fühler hell, gelblichgrau, glänzend. Labialpalpen ca. 3, Endglied etwa so lang wie das Mittelglied; hell gelblichgrau, glänzend. Stirn hell, gelblichgrau, Vertex hellgelb beschuppt, Thorax mit Schulterdecken hellgelb, vorne am Thorax jederseits ein dunkelgelber Fleck. Beine hell, gelblichgrau. Abdomen hell, gelblichgrau. An den Hinterrändern der Tergite nicht wie sonst bei *Stathmopoda*-Arten deutliche Stachelreihen, sondern feine, leicht ausfallende Stacheln über die ganze Breite der Tergite ungleichmäßig verteilt, allerdings an den Hinterrändern gehäuft.

Genitalien ♂ (Abb. 90) (untersucht 2 Ex.): Tegumen mit Uncus und Gnathos etwas kürzer als die Valven, Gnathos distal breit gerundet. Valven relativ kurz und breit, Costa von ca. 1/3 der Valvenlänge, vom Cucullus nicht abgesetzt, Ampulla reduziert, Sacculus breit und kräftig, bis zum Valvenende reichend, distal mit einem stumpfen, nach dorsal gerichteten Zahn endend, Cucullus breit, gerundet. Aedoeagus distal etwas verjüngt, mit mehreren sehr kräftigen, in der Längsrichtung angeordneten Cornuti, in Form langer, etwas gekrümmter Stacheln, die sich an der Basis keulenförmig verbreitern, distaler Fortsatz nur wenig über die Aedoeagusspitze vorstehend, mehr als leistenartige Versteifung in der Wand ausgebildet. Anelluslappen verhältnismäßig groß, streifenförmig, an den breiten Enden schräg abgestutzt.

Genitalien ♀ (Abb. 91) (untersucht 2 Ex.): Der an das Antrum anschließende Ab-

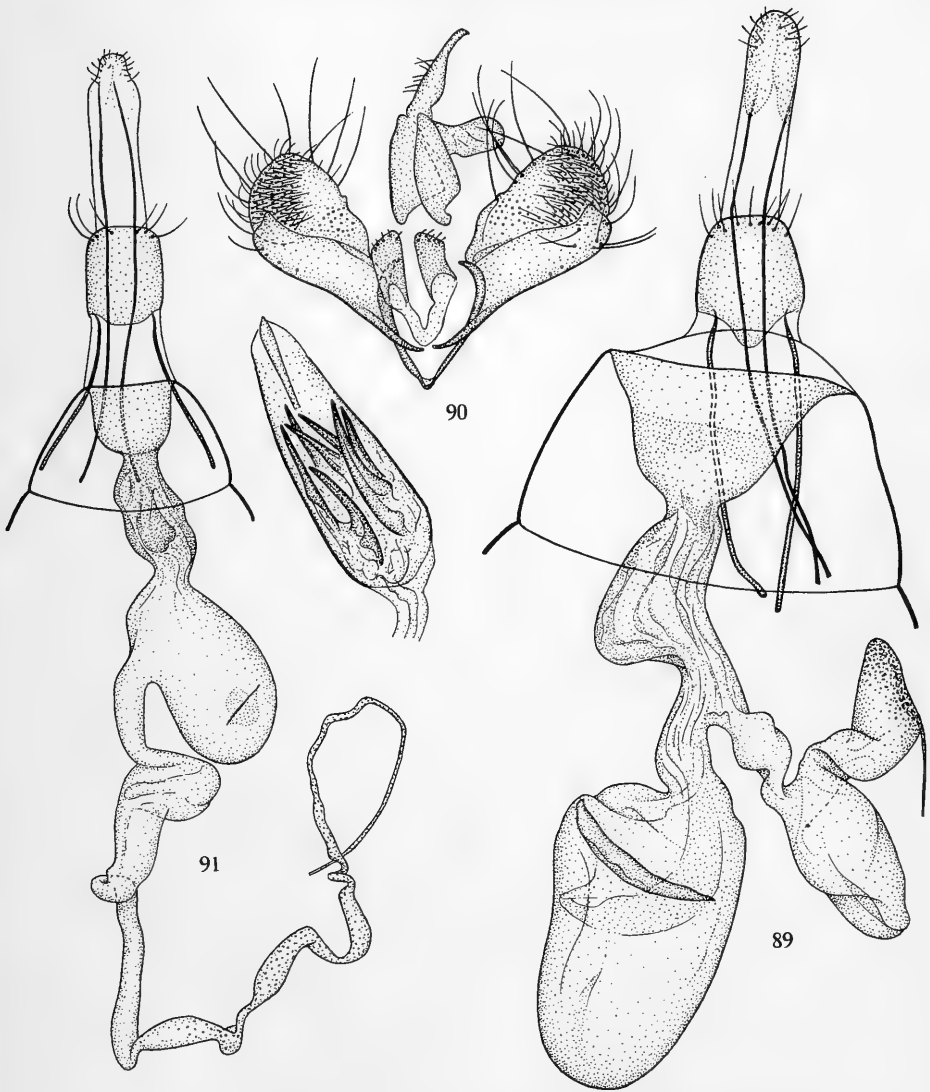


Abb. 89. *Stahmopoda horrida* Meyrick, Holotypus, ♀-Genitalien, GU—15348—BM. Abb. 90. *S. haematosema* Meyrick. ♂-Genitalien, GU—UOP—SM—501. Abb. 91. Ditto, ♀-Genitalien, GU—UOP—SM—503

schnitt des Ductus bursae kropfännlich verbreitert und stark gefältelt. Nur ein Signum vorhanden, in Form einer sklerotisierten Falte, deren Rand mit Zähnen versehen ist, diese Falte von einem Feld winziger Stachelchen umgeben. Zweiter Abschnitt des Corpus bursae sehr lang, schlauchförmig, mit blasigen Auftreibungen, der Abschnitt mit Wandstruktur lang.

Erste Stände und Ökologie: unbekannt, Falter Ende VI. und VII.

Verbreitung: Japan: Insel Honshu: Tokio und Harima: Totihara bei Tajima-Ikuno. Nach Kuroko (1959) auch Insel Kyushu: Hikosan.

### Stathmopoda masinissa Meyrick

*Stathmopoda masinissa* Meyrick, 1906: 410. — 1914b: 11, t. 2, f. 37a (Kopf, lateral), f. 37b (Hinterbein).

*Kakivoria flavofasciata* Nagano, 1916: 136, t. 4, f. 1—18 (alle Stadien, Teile der Imago und Totalansicht). — Issiki, in Esaki et al., 1957: 35, t. 5, f. 139 (Falter, farb.). — Moriuti, in Issiki et al., 1969: 120; Textf. 60 (Raupe: Chaetotaxie), t. 57, f. 228 (Falter, Raupe. farb.).

*Stathmopoda albidorsis* Meyrick, 1931b: 75.

*Stathmopoda masinissa* Meyrick: Locus typicus: Ceylon: Matale. Holotypus (Monotypus) ♂: "Holotype" "Matale, Ceylon. I P. .10. 04" "*Stathmopoda masinissa* Meyr., 1/1. E. Meyrick det., in Meyrick Coll." "Meyrick Coll. B.M. 1938—290" "*masinissa* Meyr.". GU—15346—BM (BM).

*Kakivoria flavofasciata* Nagano: Locus typicus: In der Beschreibung nicht genannt, nach schriftlicher Mitteilung von Moriuti aber zweifellos Japan: Honshu: Gifu. Typenmaterial nach Auskunft des Genannten verlorengegangen. **Syn. nov.**

*Stathmopoda albidorsis* Meyrick: Locus typicus: China: Kwanhsien. Holotypus (Monotypus) ♀: "Holotype" "Kwanhsien, China. F. .7. 30" "*Stathmopoda albidorsis* Meyr., 1/1. E. Meyrick det., in Meyrick Coll." "Meyrick Coll. B.M. 1938—290" "*albidorsis* Meyr.". GU—15329—BM (BM). **Syn. nov.**

Diagnose (untersucht 3 ♂, 4 ♀): Exp. 16 - 17 mm (nach Nagano (l.c.) 13 - 17 mm). Fühler hell, gelblich. Labialpalpen ca.  $3\frac{1}{2}$ , Endglied ca.  $1\frac{1}{3}$  des Mittelgliedes, also deutlich länger; hell, gelblich, an der Außenseite, besonders am Grunde, angedunkelt. Kopf hell, gelblich, glänzend. Thoraxoberseite dunkel, bräunlichgrau, glänzend, in der Mitte ein gelblicher Fleck, Schulterdecken ebenfalls dunkel, bräunlichgrau. Beine hell, gelblich, Mittelschienen auf der Oberseite bräunlichgrau behaart, Hinterschienen auf der

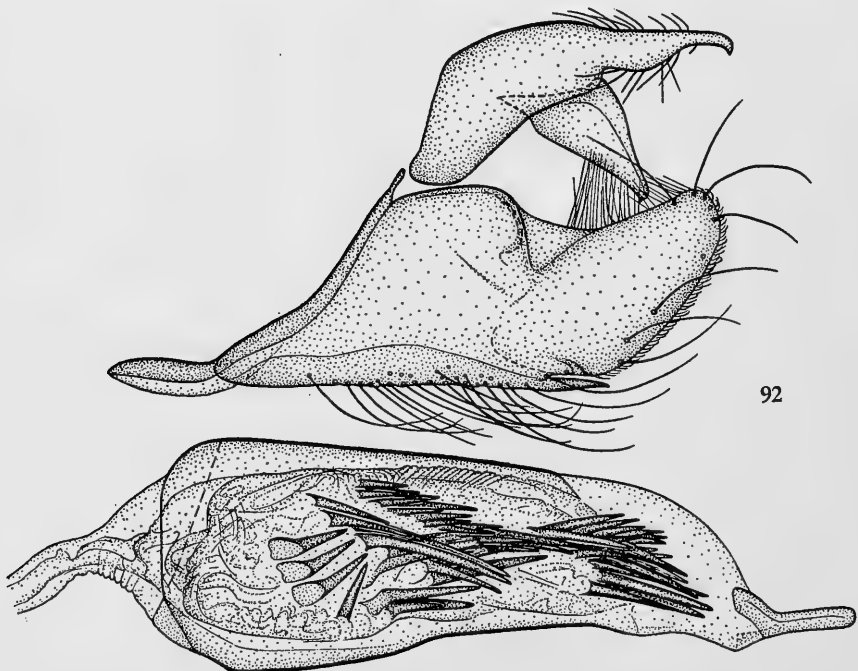


Abb. 92. *Stathmopoda masinissa* Meyrick, Holotypus, ♂-Genitalien, GU—15346—BM



Oberseite mit sehr kräftigem Büschel ebenso gefärbter Haare. Abdomen auf der Oberseite bräunlichgrau, an der Spitze gelblich, die kräftigen Stacheln an den Tergiträndern braun hervortretend, Unterseite hell, gelblich. Vfl. einschließlich der Fransen dunkel, bräunlichgrau, glänzend, bei ca. 4/5 eine gelbliche, unscharfe Querbinde, die den Hinterrand nicht ganz erreicht. Hfl. einschließlich der Fransen dunkel, bräunlichgrau, an der Wurzel zwischen dem pcu und dem Rand der Zelle ein unbeschuppter und daher glasig durchscheinender Streifen, der nicht ganz bis zum Flügelrand reicht.

Genitalien ♂ (Abb. 92) (untersucht 2 Ex.): Tegumen mit Uncus und Gnathos bis zum Valvenende reichend. Costa kräftig, höckerartig, Ampulla als unregelmäßiger, kräftiger Höcker ausgebildet, Sacculus bis etwa  $\frac{3}{4}$  der Valvenlänge reichend, sein distales Ende spitz, stachelartig vorspringend, Cucullus nach oben gebogen, ziemlich kurz, distal sich verjüngend, Dorsalrand konkav, dorsocaudal ziemlich gerundet. Aedoeagus relativ groß, mit zahlreichen kräftigen, stachelartigen Cornuti, die in mehreren Gruppen angeordnet sind, die basale Gruppe aus kürzeren, plumperen Stacheln bestehend, distaler Fortsatz stark sklerotisiert, gerade, relativ kurz, am Ende gerundet.

Genitalien ♀ (Abb. 93) (untersucht 2 Ex.): Antrum länger als breit, der anschließende Ductus bursae kropfförmig verbreitert, mit zahlreichen Falten und Ver-

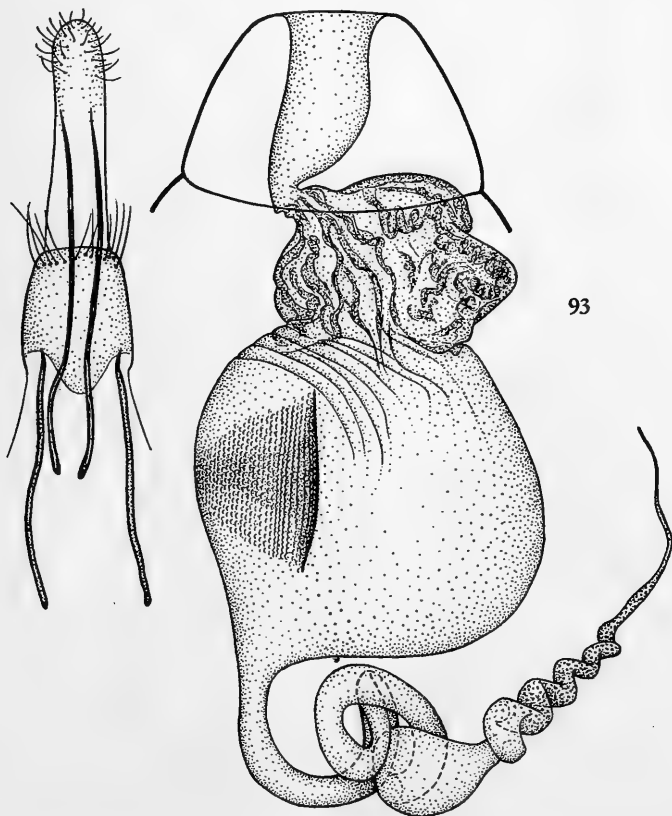


Abb. 93. *Stabmopoda masinissa* Meyrick, Holotypus von *S. albidorsis* Meyrick, ♀-Genitalien, GU—15329—BM

dickungen in der Wand. Der erste Abschnitt des Corpus bursae kugelig, mit nur einem, aber sehr großen Signum in Form einer weit hineinreichenden sklerotisierten Falte, deren Umgebung ebenfalls sklerotisiert ist und eine schuppenartige Feinstruktur aufweist. Zweiter Abschnitt des Corpus bursae schlauchförmig, strukturierte Zone vor dem Ductus seminalis lang, korkzieherartig gewunden.

Erste Stände und Bionomie: Siehe Nagano (l.c.) und Moriuti (l.c.). Die Art hat (in Japan) zwei Generationen im Jahr. Die Raupe frisst an den Früchten von *Diospyros kaki* (Fam. Ebenaceae) im Juni, Juli und wieder von August bis Oktober. Imagines vom Mai bis August, das Exemplar von Ceylon vom Oktober. Die Art tritt in Kakifrukt-Kulturen als Schädling auf.

Verbreitung: Ceylon: Matale; China: Kwanhsien; Japan: Honshu.

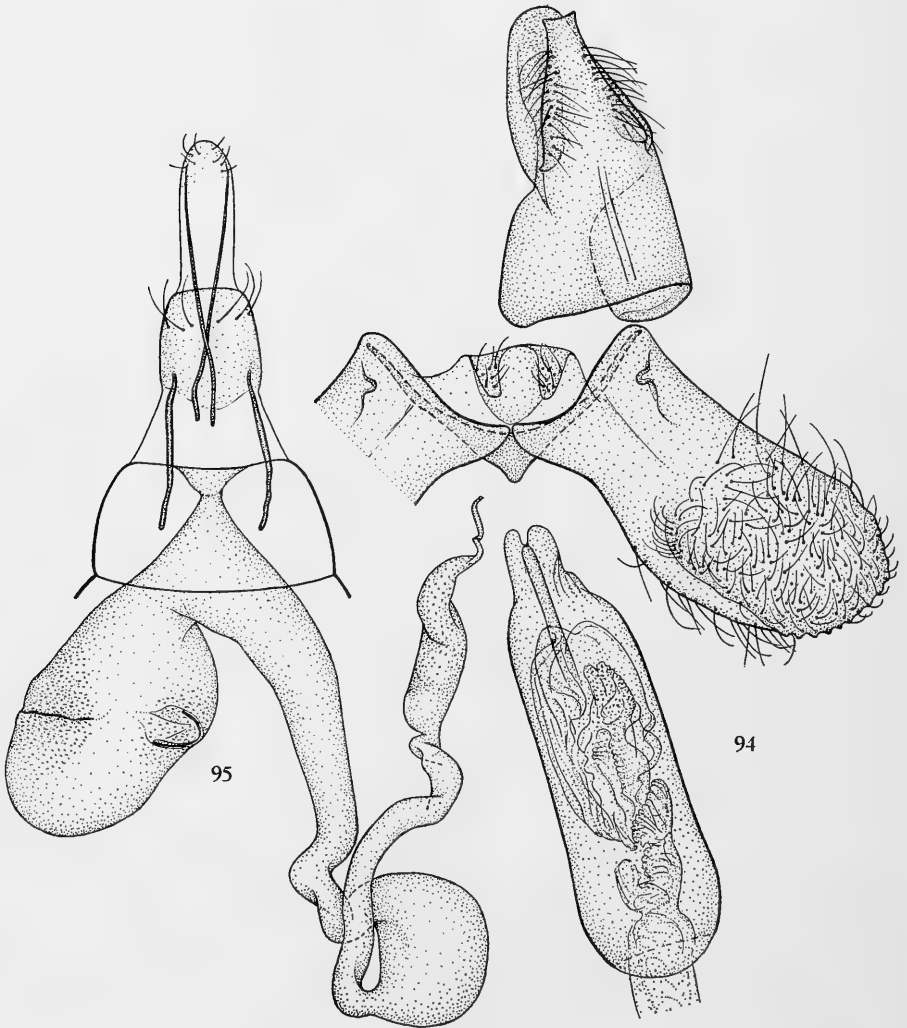


Abb. 94. *Stathmopoda tacita* (Meyrick), ♂-Genitalien, GU—16142—BM. Abb. 95. Ditto, ♀-Genitalien, GU—16143—BM

*Stathmopoda tacita* (Meyrick) comb. nov.

*Agrioscelis tacita* Meyrick, 1913a: 96 (Diagnose!).

Locus typicus: Indien: Assam: Khasi Hills. Lectotypus ♀ (hier festgelegt): "Lectotype" "Khasi Hills, Assam. .4. 1907" "*Agrioscelis tacita* Meyr., 1/8. E. Meyrick det., in Meyrick Coll." "Meyrick Coll. B.M. 1938—290" "*tacita* Meyr." "Lectotypus ♀, *Agrioscelis tacita* Meyrick, 1913. teste F. Kasy, 1968" (BM).

Genitalien ♂ (Abb. 94) (untersucht 2 Ex.): Tegumen breit, mit Uncus und Gnathos nicht ganz bis zu den Valvenenden reichend, Costa kurz, nicht vom Cucullus abgesetzt, Ampulla nur als runder Höcker ausgebildet, Sacculus bis fast zum Valvenende reichend, distal nicht vortretend, an der Valvenbasis konkav, Cucullus distal breit und gleichmäßig gerundet, Dorsalrand etwas konkav. Aedoeagus ohne Cornuti, distal sich kaum verjüngend, distaler Fortsatz breit und kurz, Anelluslappen zipfelförmig, also distal sich verjüngend.

Genitalien ♀ (Abb. 95) (untersucht 2 Ex.): Zwei große Signa in Form sklerotisierter Falten vorhanden, deren Umgebung mit feinen Stachelchen bedeckt ist. Zweiter Abschnitt des Corpus bursae schon kurz nach dem Antrum abzweigend, in Form eines breiten Schlauches, der sich allmählich verengt und dann nach einigen Windungen in ein blasenförmiges Gebilde übergeht, das sich wieder zu einem längeren, mehrfach gekrümmten Schlauch verjüngt, Endteil dieses Schlauches vor dem Ductus seminalis mit Wandstruktur.

*Hieromantis* Meyrick

Meyrick, 1897: 315. — 1914b: 9.

Typus: *Hieromantis ephodophora* Meyrick (festgelegt in der Urbeschreibung, monotypisch).

Diagnose: Meyrick (1897 und 1914). Die Angabe, daß Ocellen vorhanden sind, konnte bei einer Überprüfung nicht bestätigt werden.

Ergänzungen: Geäder des Gattungstypus (Abb. 96): Im Vfl. r aus 5 Ästen bestehend, im Bereich  $m_1$  bis  $cu_2$  eine Ader fehlend.



Abb. 96. *Hieromantis ephodophora* Meyrick, Geäder, Flügelpräp.—15115—BM

Genitalien ♂ (Abb. 97): Ohne gattungstypische Merkmale. Der Aedoeagus des Gattungstypus mit einem kräftigen Cornutus. *Hieromantis resplendens* Bradley besitzt am 8. Tergit zwei lange spitze Fortsätze, die Haarbüschel tragen, *Hieromantis munerata* Meyrick hat nur ganz kurze Fortsätze, beim Gattungstypus *ephodophora* sind überhaupt keine zu finden.

Genitalien ♀ (Abb. 98): Nur ein Signum vorhanden, an das ein langgestrecktes Feld

kleiner Papillen anschließt, ferner gibt es noch ein zweites kleineres solches Feld, wahrscheinlich als Rest eines Signums.

Bemerkungen: Die Gattung unterscheidet sich von *Stahmopoda*, mit der sie unt. and. die langgewimperten Fühler gemeinsam hat, durch breite Augendeckel, als Gattungsunterschied kann auch der auffällige Spiegel am Hinterrand des Vfl. gewertet werden.

### Hieromantis ephodophora Meyrick

Meyrick, 1897: 315 (Diagnose!).

Locus typicus: Australien: Queensland: Brisbane. Lectotypus ♀ (hier festgelegt): "Lectotype" "Brisbane, Queensland, 28/9/79" "*Hieromantis ephodophora* Meyr., 2/8. E. Meyrick det., in Meyrick Coll." "Meyrick Coll. B.M. 1938—290" "*ephodophora* Meyr." "Lectotype ♀, *Hieromantis ephodophora* Meyr., teste K. Sattler, 1971" (BM).

Genitalien ♂ (Abb. 97) (untersucht 2 Ex.): Tegumen mit Uncus und Gnathos bis zum Valvenende reichend. Costa nicht abgesetzt, Sacculus bis zum Distalrand der Valve reichend, aber distal nicht vortretend, Cucullus distal sich etwas verbreiternd und nach oben gebogen, Ventrocaudalrand stark gerundet, Distalrand schwach gerundet, Ventral- und Dorsalrand der Valve ziemlich gerade. Aedoeagus mit einem kräftigen Cornutus und sklerotisiertem spitzen Fortsatz.

Genitalien ♀ (Abb. 98) (untersucht 2 Ex.): Antrum etwa so lang wie breit, im caudalen Abschnitt mit winzigen Körnchen in der Wand. Nur ein Signum vorhanden,

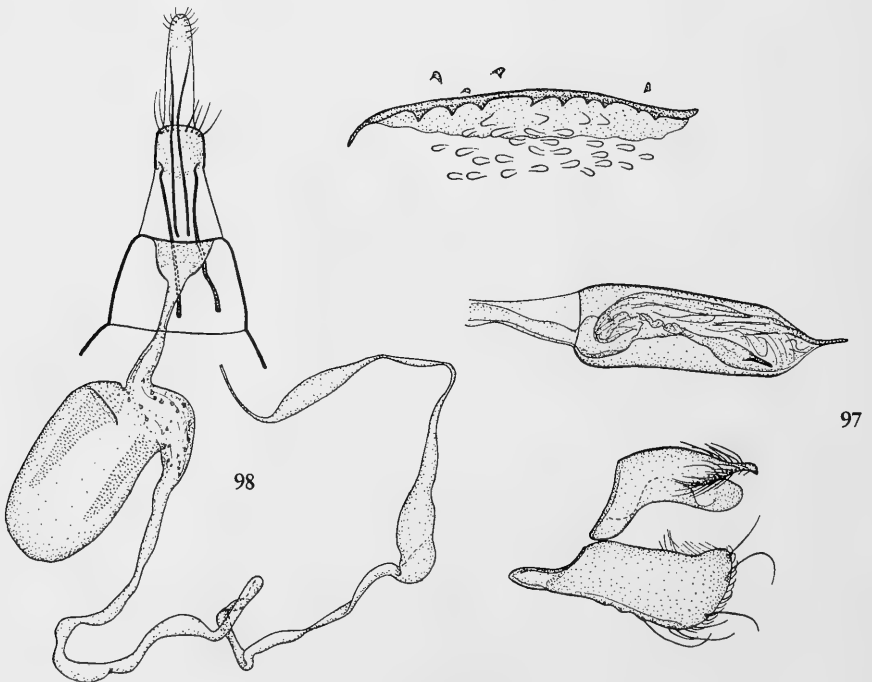


Abb. 97. *Hieromantis ephodophora* Meyrick, ♂-Genitalien, GU—16128—BM. Abb. 98. Ditto, ♀-Genitalien, GU—15115—BM (oben Signum, stärker vergrößert)

in Form eines Viertelmondes, dessen innerer Rand unregelmäßig gezackt ist, in der Umgebung des Signums schütter verteilt kleine Höcker und nach unten anschließend ein langgestrecktes Feld kleiner Papillen. Ein solches Feld findet sich auch an einer zweiten Stelle im Corpus bursae. Am Übergang zum zweiten Abschnitt des Corpus bursae auf breiten Grundplatten sitzende Dörnchen. Der schlauchförmige Abschnitt lang, im Endteil an zwei Stellen etwas blasig aufgetrieben, ohne deutliche Wandstruktur vor dem Ductus seminalis.

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# TIJDSCHRIFT VOOR ENTOMOLOGIE

UITGEGEVEN DOOR

DE NEDERLANDSE ENTOMOLOGISCHE VERENIGING

Deel 116

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Afl. 18

## REGISTER VAN DEEL 116

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- \* An asterisk denotes a name new to science

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## CORRIGENDA VOOR DEEL 116

Pag. 191, regel 2 van boven: schrappen!

„ 191, line 2 from top: delete!

„ 211, regel 10 van boven: staat "uperside", lees "upperside"

„ 211, line 10 from top, "uperside", should read "upperside"

„ 225, regel 1 van boven vervangen door:

„ 225, line 1 from top substitute by:

"Discussion. The difference between Le Cerf's description and mine is considerable".











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