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PARASITID MITES ASSOCIATED WITH BUMBLEBEES IN ALBERTA, CANADA (ACARINA: PARASITIDAE; HYMENOPTERA: APIDAE). II. BIOLOGY

By

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Parasitid Mites Associated with Bumblebees in Alberta, Canada (Acarina: Parasitidae; Hymenoptera: Apidae). II. Biology[1]

LYNN A. RICHARDS AND K. W. RICHARDS

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ABSTRACT

Mites of five species of *Parasitus,* associated with *Bombus* in Alberta, Canada, were studied. Life cycle is typically egg, larva, protonymph, deutonymph, and adult, with a duration of about 20-26 days. Cultures of these mites indicate the most effective food to be pollen and wax mixtures. However, protonymphs and deutonymphs failed to molt in culture on any food. Populations of *P. favus, P. perthecatus* and *P. fimetorum* have increasing deutonymphal populations with a lower more constant adult mite population. Deutonymph increase is synchronous with queen production. Deutonymphs are phoretic on queens, except *P. fimetorum* which is not phoretic on bumblebees.

Parasitus is not restricted to one species of *Bombus,* but is more commonly found with *B. bifarius, B. occidentalis* and *B. frigidus.*

The percentage of queens with only one species of *Parasitus* was 59.8% while the percent of nests with two or more species was 78%. Mechanisms of dispersion other than establishing queens includes superseding queens, *Psithyrus,* foragers, and males.

Attached to some *Parasitus* deutonymphs were *Scutacarus acarorum.*

INTRODUCTION

The purpose of this study was to investigate the relationships between mites of the Genus *Parasitus* and the bumblebees. Field work was conducted in southwestern Alberta, Canada, from May 26 through August 25, 1970, and April 25

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[1] Contribution number 1530, Department of Entomology, University of Kansas, Lawrence, Kansas.

through August 25, 1971, on the east side of Prairie Bluff Mountain, 49° 20′N, 114° 06′ W, at about 5200 feet elevation. Taxonomy of these *Parasitus* is reported by Richards (in press).

The biological data associating *Parasitus* mites with *Bombus* have been reported by Frison (1926), Plath (1934), Sellnick (1938), Kühnelt (1950), Hughes (1959), Free and Butler (1959), Skou, Holm and Haas (1963), Husband (1968), and Chemielewski (1971).

Bumblebees of the following species of *Bombus* and *Psithyrus* were encountered in the study area: *B. appositus* Cresson; *B. bifarius nearcticus* Handlirsch; *B. californicus* F. Smith; *B. centralis* Cresson; *B. flavifrons* Cresson; *B. frigidus* F. Smith; *B. huntii* Greene; *B. melanopygus* Nylander; *B. mixtus* Cresson; *B. nevadensis* Cockerell; *B. occidentalis* Greene; *B. rufocinctus* Cresson; *B. ternarius* Say; *B. terricola* Kirby; *B. vagans* F. Smith; *P. insularis* (F. Smith); *P. suckleyi* (Greene); and *P. fernaldae* Franklin.

The following is an abbreviated account of the life cycle of *Bombus* (for more detail the works of Hobbs (1964-1968) and Hasselrot (1960) should be consulted). The bumblebee queens appear in the spring after hibernating all winter. When they emerge in early May they start feeding on nectar and pollen and begin looking for nesting sites. If a suitable site is found, the nest material is arranged by the queen and she begins to build an egg cup out of wax and pollen. A honey pot is built either before, after, or at the same time as the first brood eggs are laid. When the queen is incubating the brood she keeps her brood temperature about 37-38 C (98 F) (Hasselrot 1960). The temperature drops when she leaves the nest to forage and rises rapidly when she returns.

When the first workers emerge they assist the queen in expanding the nest, caring for additional brood (feeding and food foraging), and maintaining a constant nest-temperature. More workers are usually produced as the season progresses until queen and male eggs are laid. At the end of July or beginning of August, the colonies produce males and queens and begin to break up. After mating, the queens hibernate in chambers in the soil, and the following spring they initiate new colonies. The males and all the workers have died by the time winter arrives. Queens differ from workers most conspicuously in their larger sizes and greater ovarian development; intermediates between the castes are known in some species.

ACKNOWLEDGEMENTS

To Dr. G. A. Hobbs, John Virostek and Evan Gushel and to the Canadian Department of Agriculture Lethbridge, Alberta, Canada, we extend special thanks for permission to use equipment and for help in setting up a field laboratory. Thanks go, too, to Dr. R. W. Husband, Adrian College, Adrian Michigan, who sent us refrence materials, ideas and advice, and for his helpful review of the manuscript. We wish also to thank Drs. R. E. Beer, J. H. Camin and C. D. Michener, University of Kansas, for assistance and advice in this project. Our thanks go also to Mr. and Mrs. William Richards and Deborah Richards for their help.

METHODS AND MATERIALS

To obtain a suitable number of *Bombus* nests for study, 1048 artificial domiciles were placed in natural settings in 1970, and 1080 in 1971. These domiciles were wooden boxes with upholsterer's cotton used as nesting material (Hobbs, Virostek, Nummi 1960; Hobbs, Nummi, Virostek 1962; Hobbs 1967a). They were placed in groups of four: one above ground, one on the surface, one false underground (i.e., on the surface but with an entrance tube covered by a piece of sod), and one underground. Natural nests found in the area were also collected.

Field collected bumblebees were checked for number, genera, and where possible species of mites. In late summer, new queens, workers and males were collected from nests and checked for mites. Nest materials were sorted for mites. The upholsterer's cotton was pulled apart and mites collected into 70% alcohol with a small brush. Similarly, the bee broods were carefully cleaned of mites. When natural nests were collected, the nesting materials were put into plastic bags, and dirt surrounding the nests was also gathered. The broods were carefully picked over for mites, while the nesting material and dirt were placed on white paper and sorted in a manner similar to that for the artificial domiciles.

The deutonymphs from field collected bumblebees and from bee nests, as well as adults, protonymphs and larvae from nests were collected and observed alive in small culture dishes. Culture dishes were constructed from plastic containers used to store zippers, 25 mm deep and 30 mm in diameter. A plaster of Paris and charcoal mixture (Huber, 1958) was poured into the bottom, 5-7 mm deep. Small culture dishes were made from plastic vials 14 mm high filled with the plaster and charcoal mixture to within about 7 mm of the top and covered with a 15 mm cover slip. The small culture dishes were used to observe eggs, larvae and protonymphs. To retain adequate humidity a few drops of water were added to the plaster charcoal mixture when needed.

Mating pairs of *Parasitus* initiated cultures used for the life history studies of *P. favus* and *P. perthecatus*. Three pairs of *P. perthecatus*, four pairs of *P. favus* and two pairs of *P. hobbsi* were collected in a mating attitude. All of these pairs, except one of *P. hobbsi* and one of *P. favus*, were cultured. The eggs laid by the females were removed from the culture dishes containing the parents and placed in the smaller dishes. The information gathered gave an indication of lengths of certain life stages, but low numbers and lack of temperature control in the field laboratory were variables that could not be controlled. Temperatures of the cultures followed the outside air temperatures except on cold days when the field laboratory was heated. Mating pairs were collected on June 22, 24, 29, July 9, August 7, 10, 11, 15, and 20, 1971. All pairs collected in June and July were placed in individual cultures.

REARING STUDIES

The life histories of the *Parasitus* species associated with bumblebees are typical of most Parasitidae. The mites pass through the stages of egg, larva, protonymph, deutonymph, and adult.

Mating: In each case observed the female was on top and the male underneath, their ventral sides together. The male used the apophyses on his second pair of legs to grasp the female's fourth pair of legs. The male's third pair of legs wrapped around the female's opisthosoma, and the fourth pair curled up around the posterior end of the female's body but were not clasped tightly. The female carried the male around in this position seemingly unhindered by his presence. If disturbed, the pair quickly separated.

Five days after a pair was placed in the culture, a male of *P. favus* was seen trying to copulate with the female, indicating that mating may occur more than once. Costa (1964) noted for *P. copridis* Costa that males mate several times with the same female. On one occasion a male was seen trying to mate with a deutonymph. Possibly this was a female deutonymph near the time of final molting. The males of *P. coleoptratorum* molt first and pursue the female deutonymphs, which upon molting are immediately mated (Rapp

1959). Newman (1943) states that males of *Poecilochirus necrophori* Vitzthum, a closely related genus, copulate successfully only with newly molted females.

Eggs: In this study 0-8 eggs were laid per day by females of *P. perthecatus,* and 0-1 egg were laid per day by *P. favus.* The eggs were laid under the pieces of pollen and wax, in the cotton nesting material from bumblebee nests, on the plaster of Paris surface, and rarely on the side of the plaster container. Rapp (1959) reports *P. coleoptratorum* females to lay one egg every one to two hours, with each female laying between 100 to 130 eggs. Eggs of *P. favus* and *P. perthecatus* were oval in shape, 0.39-0.44 mm long, and no difference was noted between the eggs of these species. In three cultures of *P. perthecatus,* 26 eggs were seen; 10 hatched into larvae an average of 3.9 days (range 3-6) after being laid. In one *P. favus* culture, four eggs were laid; one hatched after five days. Mating pairs collected in August did not lay eggs, and lived an average of only eight days after being collected. At this time in mite phenology, few deutonymphs are molting since they quickly become phoretic in the nests.

Larvae and protonymphs: Two *P. perthecatus* larvae, one three days and the other six days old, molted into protonymphs and each lived an additional six days. The single *P. favus* larva molted after six days into a protonymph, which lived an additional two days.

Deutonymphs: Deutonymphs overwinter on bumblebee queens and molt, becoming adults after the queen establishes a nest. Thirty attempts were made to induce deutonymphs collected from the spring queens to molt, without success. The deutonymphs lived in culture up to 61 days. Possibly these deutonymphs did not molt because of the type of food offered, the temperature fluctuations, the humidity, the lack of some stimulus provided by the bees themselves, or combinations of these factors.

Adults: Since no deutonymphs molted, the only information on adult longevity was obtained from adults collected from nests (Table 2). They survived from 3 to 12 days. This gives an indication of minimum longevity, if the mites' survivorship was the same in the cultures and in the nests, and if the mites collected were on the average the same age. No difference was found between the longevities of males and females for *P. hobbsi, favus,* and *perthecatus.* For comparison of known life history see Table 1.

Longevity on Different Foods: Larvae and protonymphs in culture dishes were offered the pollen-wax mixture used for construction by bumblebees. One larva and five protonymphs were collected from bumblebee nests, eleven larvae were reared from eggs laid by females of mating pairs, and 13 larvae from single females. Larvae and protonymphs were never observed feeding. Larvae lived an average of 3.8 (range 1-8) days. Six of twenty-five larvae molted into protonymphs. Protonymphs lived an average of 4.3 (range 1-10) days before dying.

TABLE 1. Durations of life stages in days for *Parasitus* species found on the beetle *Copridis hispanus* (L.), on other beetles, and on bumblebees.

Parasitus species	references	egg	larvae	protonymph	deutonymph
P. copridis	Costa, 1964		1-2	1-2	79+
P. coleoptratorum	Rapp, 1959	2	3	5	10+
P. perthecatus		3-6	3-6	?	
P. favus		5	6	?	

Table 2. Longevity in culture of males and females of *P. hobbsi*, *P. perthecatus*, and *P. favus* taken from *Bombus* nests.

Parasitus species	no. cultured		avg. no. days survived in culture		range in days	
	♀	♂	♀	♂	♀	♂
P. hobbsi	1	1	10	10		
P. favus	4	7	6.75	6.75	3-11	2-12
P. perthecatus	6	3	8	7.7	4-10	3-10

Deutonymphs were offered a number of possible foods with the results indicated below:

Pollen and wax—lived 5-61 days ($\bar{x}=18.5$, n=20).

Pollen of *Erythronium grandiflorum* Pursh—lived 6-17 days ($\bar{x}=13.3$, n=9).

Yeast—lived 6-25 days ($\bar{x}=13.0$, n=13). Once a deutonymph was seen feeding on yeast.

Acarid mites and yeast—lived 7-24 days ($\bar{x}=14.3$, n=6); four *P. favus* and two *P. perthecatus*. No response towards acarids. Dr. R. Husband observed a *Parasitus* deutonymph with an acarid mite in its chelicerae (personal communication, 1972).

Adult bumblebee pieces—lived 1-46 days ($\bar{x}=22.0$, n=8). The mites congregated around the fresh muscle.

Bumblebee larvae—no response.

Honey—no response.

In two cases, deutonymphs were seen eating another deutonymph, and once eating eggs laid by a female *Parasitus*.

Adults were also supplied with several possible foods with the following results:

Pollen and wax—lived 2-36 days ($\bar{x}=9.0$, n=36). Several times, mites were seen with pieces of pollen and wax in their chelicerae. The pieces of pollen-wax became pock-marked after being in the cultures for a few days. The mites did not feed on moldy pollen-wax. Costa (1964) noted that *P. copridis* would stay in mold-free areas in a culture, and that the copris beetles inhibited growth of mold. If mold grew in his cultures uninhibited, the mites died.

Acarid mites and yeast—lived 9-12 days ($\bar{x}=10.0$, n=3).

Bumblebee larvae—no response.

Females were twice seen eating their own eggs. Females of *P. coleoptratorum* were reported by Rapp (1959) to frequently eat their own unfertilized eggs. In my study one male was seen eating another male; one female was seen eating another female, and one female was seen eating a *Parasitus* larva. Rapp (1959) states that younger stages of *P. coleoptratorum* are easy prey for older stages.

A female was observed feeding on a chironomid larva as she was being collected from a nest. However, chironomid larvae were not common in nests, and are not important as a food source.

When these mites approach the possible food, the first pair of legs are waved in front and contact the food first. Experiments conducted by Rapp (1959) with *P. coleoptratorum* on the Haller's organ of tarsus I and on sense organs of the last segment of the palps show both to have a positive response to odors.

Parasitus use a variety of food in the bumblebee nests, as indicated from the above observations. Although mites fed on bumblebee muscle in culture, it is not known if the mites actually feed on the adult bees in the nest. Frequently mites crowd on a bee, especially the queen, early in the season after she has returned from a foraging trip. The mites might be feeding on nectar (Stebbing 1965) or on pollen. However, none congregated anywhere in the nest, not even around honey or pollen stores and there was no response to honey placed in the cultures. Therefore, it seems unlikely that they would be attracted to a bumblebee because of honey stuck to her pile. A number of other stimuli might attract the mites to the bee, such as increased body temperature, pollen, CO_2, and movements. Plath (1934), Skou, Holm, and Haas (1963), and Chemlewski (1971) suggest that *Parasitus* species feed on excrement from bumblebees and their larvae. *P. coleoptratorum*, a strict carnivore, feeds on other mites and small invertebrates found in dung (Rapp 1959). *Parasitus copridis* is reported (Costa 1964) to feed on nematodes and possibly collembolans and other small arthropods. Kühnelt (1950) reports the *Parasitus* species in soil will feed on nematodes and small insect larvae. Since a variety of small arthropods are found in bumblebee nests, the associated *Parasitus* might use many of them for food, although only two direct observations verifying this have been made. All life stages of parasitiform mites usually use the same type of food (Hirschman 1959), so it is possible these species of *Parasitus* also use the same food in all life stages.

Longevity varies among mites fed the same foods. The averages indicate that deutonymphs may do better on muscle, or on pollen and wax, but none did well enough to molt. Some mites may not have fed, but survived on food reserves left over from winter or built up before being collected. Perhaps some stimulus from the

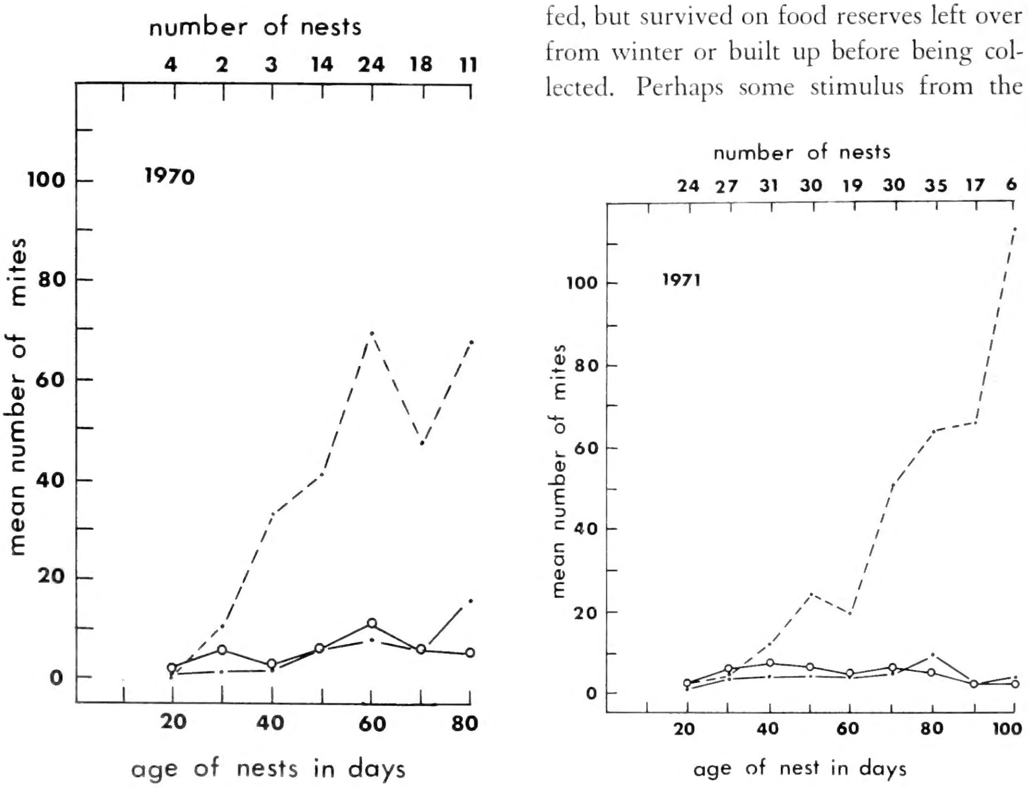


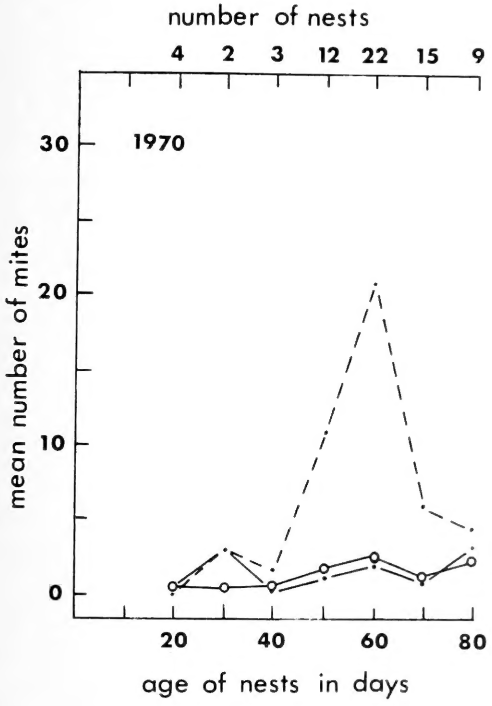
Fig. 1. Population fluctuations of *P. favus* from all *Bombus* nests. deutonymph – – –, male ·—·, female o—o.

bumblebee causes the deutonymphs to start feeding and to molt. The deutonymphs were able to survive longer in culture than any other stage of *Parasitus*. Since the deutonymph is the phoretic stage, it must be able to survive on the bees, presumably with no food, from the time the new queens leave the nest, through hibernation, until the following spring when the queens have established colonies. No significant difference in life spans between adults given wax and pollen and adults given yeast and acarids was found. Since adults were collected from nests, food reserves obtained in the nest may have been adequate to produce the eggs laid in culture. An inadequate food source may have been the reason these mites laid eggs irregularly and in such low numbers as compared to *P. coleoptratorum*. No life cycle was ever completed on any of the foods tried in rearing tests in this study.

NEST STUDIES

Noting the ages of the *Bombus* nests and the condition of the deutonymphs in them (assuming a fully engorged deutonymph is near the time of final molting), studies of populations of *Parasitus* suggest that *P. favus* and *P. perthecatus* have more than one generation per year. A deutonymph collected 22 July 1970, had the adult structures of a male *P. perthecatus* visible through the deutonymph cuticle. The collection site, a *B. occidentalis* nest, contained 103 workers, 19 cell eggs, 677 larvae, and 190 pupae. From a second nest inspected on 17 July 1970, fully engorged deutonymphs and a female of *P. favus* with the deutonymph's dorsal shield still on her were collected. In another nest which had already produced bumblebee sexuals, a deutonymph of *P. perthecatus* was collected while molting to become a female. Thus new adults are produced during the summer as well as spring when the overwintered deutonymphs mature.

Studying the age composition of the *Parasitus* populations from nests of differ-



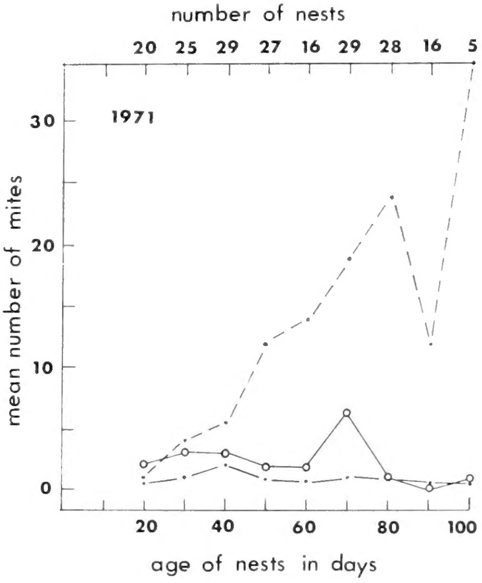
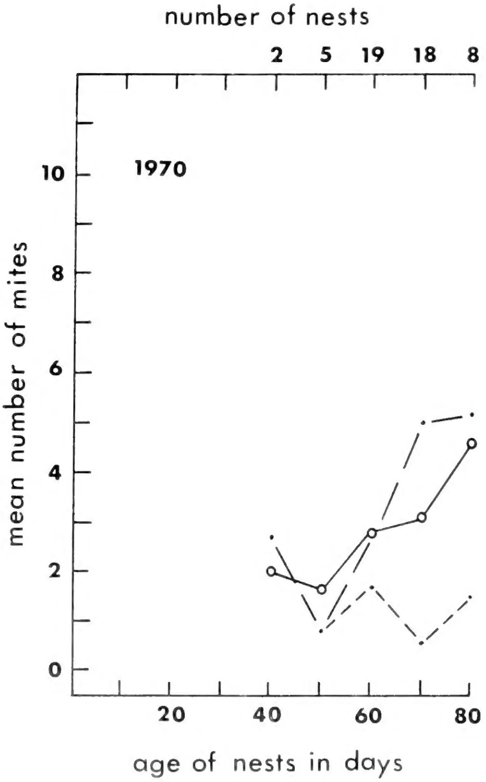


Fig. 2. Population fluctuations of *P. perthecatus* from all *Bombus* nests. deutonymph – – –, male ·—·, female o—o.

ent ages gives some additional information on the duration of the different life history stages. The youngest bumblebee nest collected was 11 days old (from establishment by the queen to date of collection). Adults of both sexes of *P. perthecatus* were present at this time. A 12 day old nest contained adults of *P. favus*. Larvae of *Parasitus* were encountered in a 14 day nest but not in the two younger ones; however, lack of larvae observed from younger nests may be due to the small sample size. Protonymphs were found in 16 day nests, and occurred in 62.5% of the nests (24) 16 to 22 days old. Thus *Parasitus* deutonymphs must molt, become adults, mate, and lay eggs within at least 14 days. Since a minimum of six days is required (Table 1) in culture from egg deposition to protonymphs of *P. favus* and *P. perthecatus* and as much as twelve days may be needed, it is likely that the overwintered deutonymphs molt before the *Bombus* nests are 11 days old. Such would be necessary in order to have protonymphs in the nests as early as 16 days after their establishment. One might speculate that deutonymphs molt into adults within 7 days after nest-establishment. By this time the bumblebee queen has rearranged the nest material, constructed the first brood cells, laid a full complement of eggs, and constructed and partly filled a honey pot. The length of time from nest establishment to deutonymphs' molting may be similar to the duration of the summer deutonymph stage. Thus we can estimate the total length of the summer life cycle from egg to adult to be 20-26 days for these two species of *Parasitus*.

Population-curve analyses are difficult because the exact life cycle data are not available, the movement of deutonymphs in and out of the nest on workers and



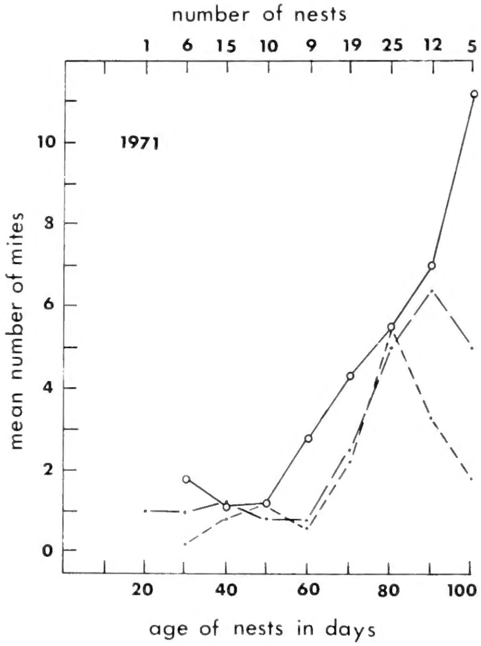


Fig. 3. Population fluctuations of *P. hobbsi* from all *Bombus* nests, deutonymph – – –, and ·—·, female o—o.

queens was not measured, and the number of mites initiating the populations is not known. The low numbers of *P. hobbsi* and *P. inquilinobombus* make the interpretations of their curves less meaningful, since the sample size is smaller. The data are based on nests up to 80 days old in 1970 but were continued to 100 days in 1971.

The population curves for *P. favus* (Fig. 1) show an increase in deutonymphs at least up to 80 days after nest establishment in 1970 and 100 days after nest establishment in 1971. This species may be limited by the length of the season. Some colonies of *B. californicus, B. appositus,* and *B. rufocinctus,* the last three bee species to emerge and establish nests in 1970, were producing queens as early as 43 to 49 days after nest establishment. Since the increase in deutonymphs occurs at the same time as the early queen production, most of the deutonymphs must become phoretic at this time. Therefore, the deutonymph population increases while the adult population remains more or less constant. The population curves for *P. perthecatus* (Fig. 2) are similar to those of *P. favus.*

The population fluctuation curves for the relatively rare *P. hobbsi* (Fig. 3) and *P. inquilinobombus* (Fig. 4) in 1971 both show a decline in males and deutonymphs near the end of the summer (late populations were not sampled in 1970). This decline seems strange since overwintering is in the deutonymphal stage.

P. fimetorum was not found in nests less than 40 days old in 1970, but was collected after 20 days in 1971 (Fig. 5). The lack of observation of this species earlier in the season in 1970 may have been sam-

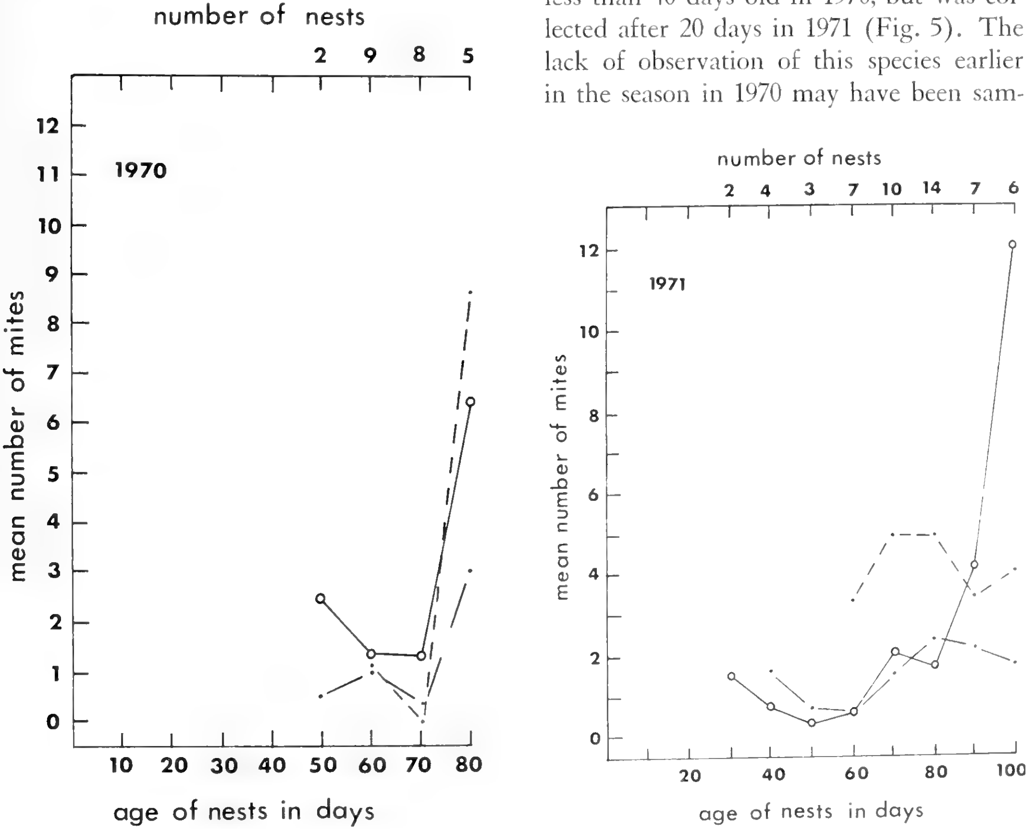


Fig. 4. Population fluctuations of *P. inquilinobombus* from all *Bombus* nests. deutonymph ‒ ‒ ‒, male ·—·, female o—o.

pling error. However, *P. fimetorum* is not phoretic on bumblebees. Production of deutonymphs increased at the same time as that of *P. favus* and *P. perthecatus*. Perhaps high deutonymph production is a function of time rather than of bumblebee life cycle; or the phoretic host if any of *P. fimetorum* may be available at the same time as bumblebee queens. *P. fimetorum* was more common than *P. hobbsi* and *P. inquilinobombus* (Table 3).

Nests occupied by bumblebees the previous season had no *Parasitus* even though old cells and food pots still contained potential food and protection.

SPECIFICITY

All five species of *Parasitus* occurred in nests of all the species of *Bombus* in the study area, except for those species of *Bombus* for which only one nest was available for inspection (Table 3). *Parasitus favus* and *P. perthecatus* were identified from all bumblebee species collected in the field, except for those *Bombus* species of which five or fewer individuals were collected with *Parasitus* on them. Thus, *P. favus* and *P. perthecatus* show no precise restrictions as to *Bombus* species. Because *P. hobbsi* and *P. inquilinobombus* are not as common but do occur in nests of all *Bombus* species, and have been identified from more than one species of field-collected queens, I assume that they also are not restricted by *Bombus* species (Table 4).

Randomness of distribution using the Poisson formula was calculated for the genus *Parasitus*, using only field-collected

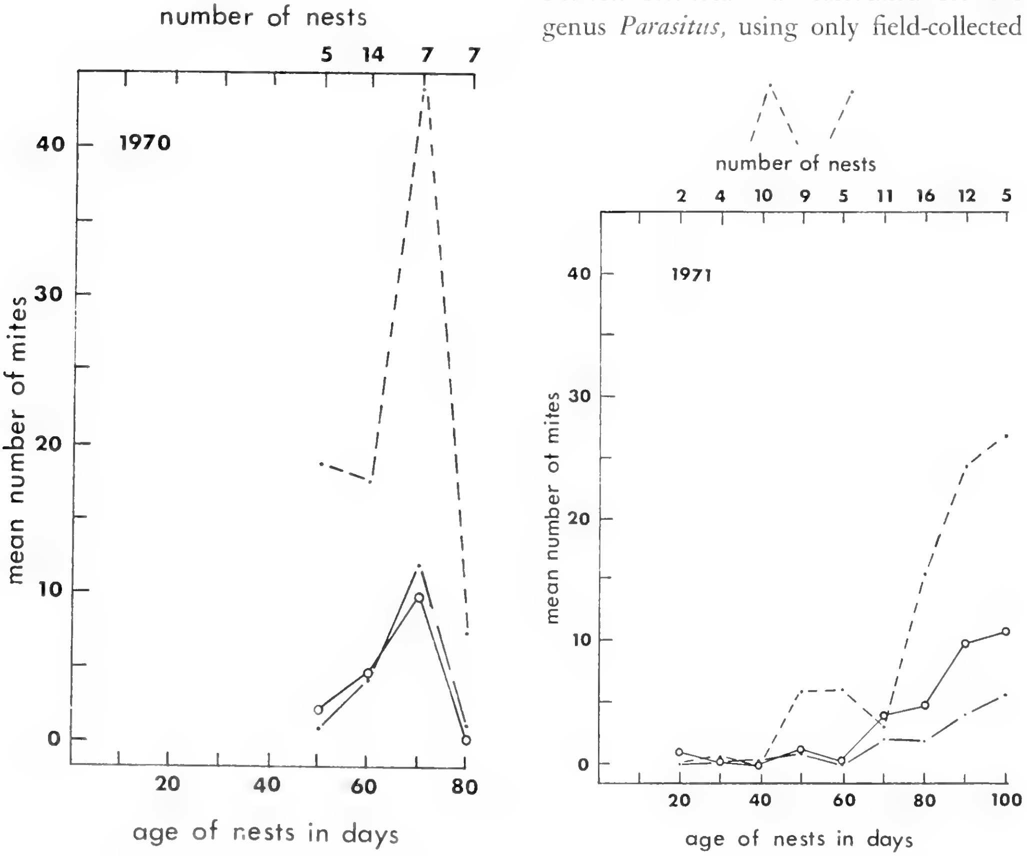


Fig. 5. Population fluctuations of *P. fimetorum* from all *Bombus* nests. deutonymph – – –, male ·—·, female o—o.

TABLE 3. Mean number of *Parasitus* species per *Bombus* nest.

	nests			mean number of *Parasitus* per nest				
Bombus species	total sorted	% with *Parasitus*	total	*P. hobbsi*	*P. favus*	*P. perthecatus*	*P. inquilinobombus*	*P. fimetorum*
B. appositus	74	86.5	48.32	1.63	31.80	9.45	0.52	4.95
B. bifarius	73	94.5	69.22	5.04	42.36	14.88	2.90	4.04
B. californicus	29	96.5	42.21	2.00	22.64	11.46	0.20	5.88
B. centralis	1	100	1.00	0	0	1.00	0	0
B. flavifrons	23	100	59.43	2.34	39.90	14.73	0.20	1.83
B. frigidus	45	95.5	107.04	7.27	57.50	8.72	4.44	18.40
B. huntii	2	100	61.00	6.50	43.00	2.50	8.00	1.00
B. melanopygus	1	100	6.00	0	3.00	3.00	0	0
B. mixtus	50	92	52.36	1.97	28.79	6.13	0.80	14.55
B. nevadensis	1	100	64.00	7.00	50.00	7.00	0	0
B. occidentalis	57	91	89.10	8.83	55.23	18.50	2.20	4.40
B. rufocinctus	64	85.9	27.98	0.90	18.54	7.30	0.10	1.10
B. ternarius	11	100	82.63	2.81	60.29	15.80	2.70	1.00
B. vagans	3	100	25.66	1.00	19.33	4.00	0.30	1.00
Total	434							
Average	31.0	95.9	62.10	3.53	35.22	10.45	1.46	5.11

Table 4. *Parasitus* deutonymphs collected from spring bumblebee queens.

Psithyrus or *Bombus* species	*Psithyrus* and *Bombus* queens		Number of deutonymphs					mean number *Parasitus* per queen	range
	total collected	% with deutonymphs	*P. hobbsi*	*P. favus*	*P. perthecatus*	*P. inquilinobombus*	unidentified		
B. appositus	24	20.4	0	0	1	0	4	0.21	0-1
B. bifarius	114	23.7	0	36	21	1	72	1.12	0-15
B. californicus	27	22.2	0	11	5	0	1	0.63	0-8
B. flavifrons	11	9.1	0	0	1	0	0	0.09	0-1
B. frigidus	35	17.1	0	4	4	0	8	0.46	0-9
B. huntii	4	50.0	1	0	2	0	0	0.75	0-2
B. melanopygus	2	50.0	0	1	0	0	0	0.50	0-1
B. mixtus	4	0	0	0	0	0	0	0	0
B. nevadensis	5	20.0	0	1	1	0	0	0.40	0-2
B. occidentalis	60	31.6	1	76	13	0	17	1.78	0-50
B. rufocinctus	45	20.0	0	6	1	0	4	0.25	0-2
B. ternarius	12	25.4	0	3	0	0	0	0.25	0-1
B. terricola	3	60.6	0	3	1	0	0	1.33	0-2
P. insularis or *P. fernalde*	93	19.4	1	20	11	1	0	0.35	0-7
P. suckleyi	62	22.6	0	18	5	0	3	0.42	0-5
Total	497		3	179	66	2	109	0.72	0-50

queens not carrying a pollen load and field collected workers. When queens and workers were combined the C. D. (Coefficient of Dispersion) was 3.798, and when only queens were used the C. D. was 3.372. Thus, there appears to be a tendency for the deutonymphs to congregate on queens. Even among the queens some clumping is indicated. The numbers in Table 4 indicate a tendency for *P. perthecatus* and *P. favus* to be more numerous on *B. occidentalis* and *B. bifarius* queens, while in the nests *Parasitus* seems more abundant with *B. frigidus, B. occidentalis* and *B. bifarius.*

PHORESY AND DISPERSAL

The deutonymph is the phoretic stage in *Parasitus.* Deutonymphs were found on the bee's metathorax and propodeum. They attach themselves to the base of the pile with their chelicerae (as do other phoretic deutonymphs of *Parasitus* on other insects (Kühnelt 1950)). If their numbers are great, they will also crowd around the neck. The mites are easily excited, and if disturbed will run over the entire body, but seldom leave the bee.

The importance of phoresy to acarine evolution is indicated by its appearance several times in three major groups: Mesostigmata, Prostigmata, and Astigmata (Cross and Bohart 1969). Phoresy allows mites a means of attaining new resources when such resources are widely dispersed.

Dispersal occurs before mating. As Mitchell (1970) determined for any bisexual mite dispersing before mating (assuming equally numerous sexes and equal probabilities of dispersal), four mites of a species must meet 87.5% of the time to include one of each sex, assuming that males and females are necessary to start a population. The sex ratio for the *Parasitus* species was determined for adults in *Bombus* nests (Table 5). In none of the species was a 1:1 ratio shown. When both years are considered, all species of *Parasitus* show more females than males. A higher percentage of females would increase the number of eggs laid, and thus increase the number of deutonymphs produced for dispersal. With females more numerous than males, the number of four mites necessary to include both sexes 87.5% of the time would have to be raised. Only 19 of 112 (17%) queens caught in the spring which were carrying *Parasitus* deutonymphs had four or more mites, 59.8% of these spring queens carried only one *Parasitus* deutonymph. Seventy-eight percent of the 434 nests sorted had two or more species of *Parasitus.* These two facts indicate that the mites do not depend entirely on the establishing queen for dispersal.

The highest number of *Parasitus* deutonymphs found on one bee in the study area was 50, but there is a report of 106 on a single bumblebee queen (Skou, Holm, and Haas 1963). A *B. sylvicola* Kirby queen sent to me from McConnell River Northwest Territories, Canada, collected by K. MacInnes on June 18, 1970, had 104 *P. favus* and 10 *P. perthecatus.* A *B. po-*

Table 5. Sex ratio for adult *Parasitus* species in *Bombus* nests.

Parasitus species	1970 no. mites	1970 % ♂	1971 no. mites	1971 % ♂	total no. mites	total % ♂
P. hobbsi	337	54	842	42	1179	45
P. fimetorum	337	48	489	32	826	39
P. favus	1388	54	2462	40	3850	44
P. perthecatus	353	52	675	36	1008	40
P. inquilinobombus	110	32	298	34	407	33

TABLE 6. *Parasitus* on *Bombus* and *Psithyrus* females removed from established *Bombus* nests in 1970, 1971.

Species	No. of Bees	% of Bees with *Parasitus*	Total No. of *Parasitus* from all queens
Bombus	34	2.65	1
P. insularis	246	9.76	37
P. suckleyi	43	9.30	4
P. fernaldae	21	0	0

laris Curtis queen from Devon Island, Northwest Territories, Canada, collected by J. R. Ryan, had 211 *P. perthecatus* and 210 *P. favus*. In southern Alberta the average number of deutonymphs found on bumblebees having *Parasitus* is 3.2 (range 1-50) for spring collected queens and 3.0 (range 1-10) for field collected workers. Only one of the 99 *Bombus* males collected in the field had *Parasitus* deutonymphs. Clearly one must seek alternative means of introduction of mites into *Bombus* nests.

Deutonymphs occur on the bees and in the nests throughout the season. Generally they do not stay on a queen long once she enters a prospective nest and starts to rearrange nesting material. Twenty-four queens carrying pollen were collected (indicating they had already established a nest), but only two of these (8.33%) had phoretic *Parasitus* deutonymphs. Also conspecific queens and *Psithyrus* removed from nests had few mites (Table 6). However, deutonymphs do leave the nest after establishment. Not only were queens with pollen loads, *Psithyrus* and conspecific queens from nests sometimes carrying deutonymphs, but also 8.05% of the workers collected in the field had attached deutonymphs. A deutonymph on a bumblebee that is actively gathering pollen and nectar could be left on a flower and picked up later by another bumblebee. *Parasitus* deutonymphs were collected from flowers of *Hydrophyllum capitatum* Douglas on the fourth and sixth of June 1970, and *Arctostaphyllus uva-ursi* (Linnaeus) Sprengel on the 27 May 1970, both in the area foraged by bumblebees. Stebbing (1965) reports a *Parasitus* deutonymph being accidentally collected on flowers which were to be used for pollen slides. Banks (1919) reports *P. bomborum* (syn. of *P. fucorum*) from *Bombus* and from catkin of *Salix* in the Northwest Territories, Canada. Other flowers commonly visited by bumblebees, 100 *Taraxacum officinale* Weber, *Anemone patens* Linnaeus, and 130 *Dodecatheon pauciflorum* (Durand) Greene, were collected and searched for deutonymphs, but none were found. Possibly the length of time a mite remains on a flower, before a bumblebee revisitation, is short. Thus mites not on the original nest establishing queen could be introduced into the nest.

Worker bees in the study area were observed to enter nests other than their own on several occasions. If these workers were carrying deutonymphs from their original nest, they could be added to the population in the new nest.

Psithyrus, an obligate parasite of *Bombus*, carries the same species of mites. *Psithyrus* females invade the nests of the bumblebees and lay their eggs, later to be reared by the bumblebee workers. *Psithyrus* emerges from hibernation in late May and June and seeks out bumblebee colonies. They often enter and later leave nests with few or no workers, but they may pick up mites and carry them to another nest, or may leave mites. A *Psithyrus* female attempting to enter a *Bombus* nest with workers must be accepted by the colony before she can stay. She may enter several times for brief periods of crawling around the nest or taking nectar from the honey pot. Such a *Psithyrus* has been observed going into a nest and remaining as long as 10 minutes, or may even spend the night in a nest which she does not parasitize (Richards 1928). If she remains in the nest, her load of mites will be added to those already in the nest. Even if she leaves the nest, the number of brief visits allow the deutonymphs time to get on or off her. More than one *Psithyrus* female may find the same *Bombus* colony. In two cases 14 *Psithyrus* females were taken from single bumblebee colonies in 1971. At the end of the season deutonymphs may leave the nest both on new *Bombus* queens and *Psithyrus* females.

Also probably important in introducing mites are the excess of *Bombus* queens. Hobbs (1965, 1967b) describes incidences of superseding queens. As in the case of *Psithyrus,* mites might leave these queens and become part of the nest's population, attach to a queen and be carried away if she leaves.

Some bumblebee queens have been observed to enter a domicile, camouflage the entrance, rearrange the nesting material and drop their mites in the nest. Shortly thereafter such a queen may abandon the nest. Abandoned nests, containing mites, can later be reoccupied by other bumblebee queens which then may be parasitized. During May and June, 1971, twelve such abandoned nests were investigated. The number of *Parasitus* in these nests ranged from one to fourteen and averaged four per nest. Four of these nests were later occupied by other bumblebee queens, which established broods. Nests are also sometimes abandoned after some brood development and in some cases these same nests were used by another queen to rear her brood. If the time period is not too great between successive brood establishments, the deutonymphs from the first queen could survive to become part of the population of mites in the colony of the second queen.

During brood-decline, some unknown factors (i.e., decreased worker population, increased temperature, humidity fluctuations, appearance of sexuals, type and amount of food being foraged, or combinations of the above) cause the deutonymphs to attach enmass to the bees which leave the nest. In declining nests, mites are seen crawling over the cotton through which the bees will crawl in leaving the nest. Deutonymphs use the first pair of legs to locate the bumblebees. The deutonymphs crawl quickly up the leg of any bee contacting them. They more or less indiscriminately attach to workers, males, and queens, but there is some tendency to congregate in greater numbers on queens. The percent of the total number of bumblebees collected from fall nests with *Parasitus* is 15.9 for queens, 8.66 for workers and 12.45 for males. In contrast, 22.16% of the spring queens collected were infested and only one in 99 field-collected males had deutonymphs. Possibly, queens collected directly from nests had not yet obtained deutonymphs. When a queen with no mites was placed in nests where deutonymphs were actively searching for hosts, seven to ten mites crawled onto the queen within 30 seconds. The difference between numbers of mites on field collected and nest males indicates that deutonymphs attaching to males are repelled by some stimulus and leave, either while the males are still in the nest or when visiting flowers. Deutonymphs that remain on workers and males die when these bees die at the end of the flight season. Mites remaining in the nest also die. Thus selection would favor a mechanism by which the deutonymphs recognize queens.

Many insect associates are found in bumblebee nests. These insects may be eaten by other mites in the nest and may

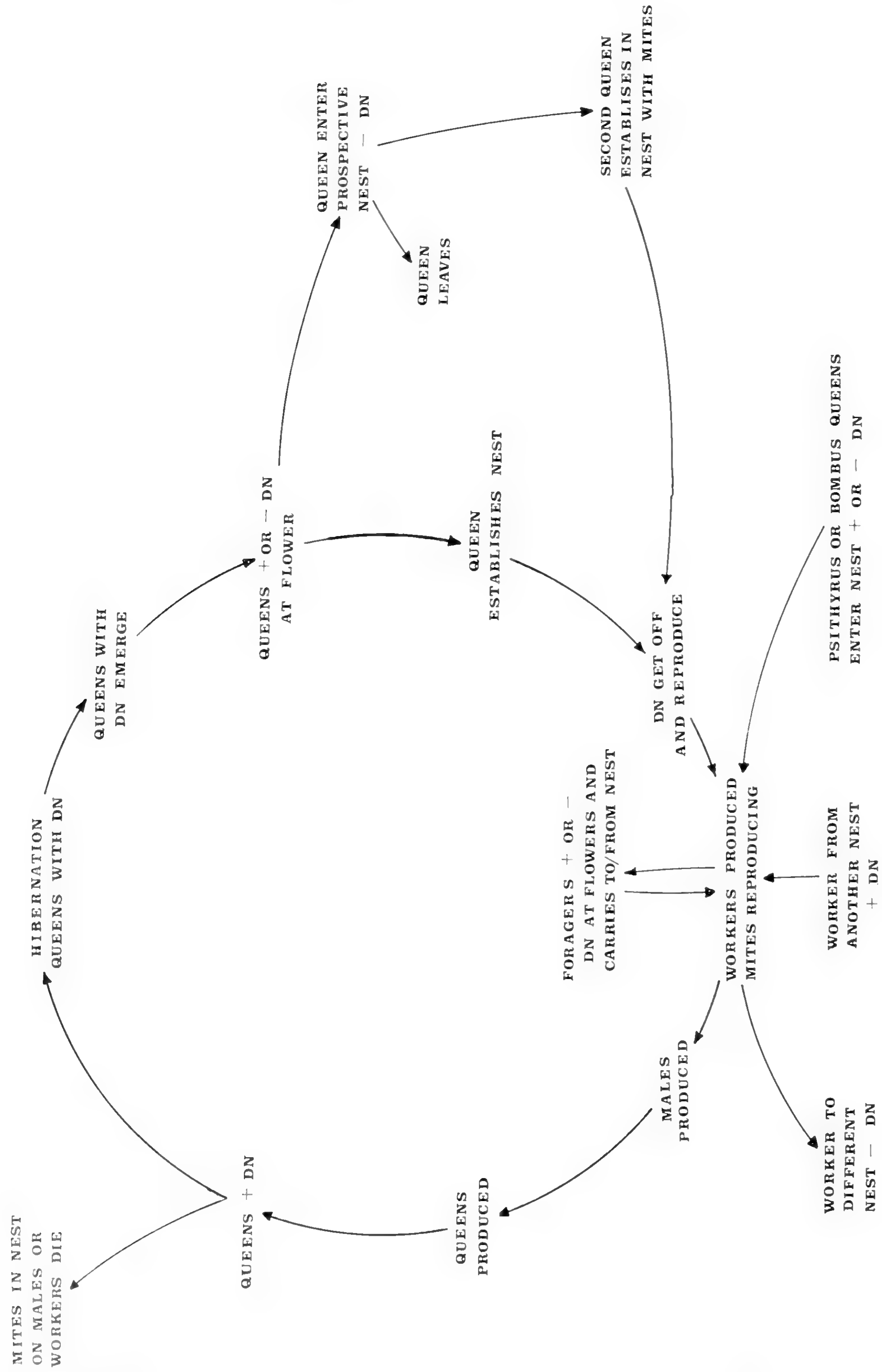


FIG. 6. Various mechanisms by which mites may be gained (+) or lost (−) by a *Bombus* nest.

influence the population of all the mites by providing a food source or introducing predators or competitors. A summary of the various mechanisms by which mites may be gained or lost by the population in a nest is given in Fig. 6.

P. fimetorum was found in 26.1% of the nests sorted. It has not to my knowledge been reported previously from bumblebee nests. Holzmann (1969) studied the deutonymphs and notes that they can live up to six months on little food, are quick moving, and have been found on dung-beetles of the genera *Aphodius, Geotrupes,* and *Hister*. This species is known to be common in Europe. It was collected in the soil in Poland by Micherdzinski (1969) and in the Swiss Alps by Schweizer (1949). Costa (1963) reports collecting it from nests of voles and on *Copris hispanus* (Linnaeus) (109 deutonymphs on one beetle) in Israel. It is not known how *P. fimetorum* gets into the bumblebee nests in Alberta. Perhaps they wander in from the soil or are carried in by beetles which enter the nests. They were never collected on bumblebees, and were not found in six soil samples. They have been collected in above ground domiciles, which suggests that at least some are carried into nests by some insect. They were more common in surface nests than in subterranean or above ground nests, and were not common in any of the five natural nests (four of which were underground and one on the surface).

SCUTACARUS ACARORUM ON *PARASITUS*

During field observations and later during studies of mite species composition from nests, a small mite, *Scutacarus acarorum* (Goeze, 1780), was often seen attached to *Parasitus*. This species has been previously reported from *Bombus* by Cross and Bohart (1969), Husband (1968), Karafiat (1959), and Kühnelt (1950). Hughes (1959) shows a picture of a *Parasitus fucorum* deutonymph with a scutacarid attached to its leg. *S. acarorum* is known from Germany, Italy, England, Mongolia, North America and South America. Cross and Bohart (1969) state that they become progressively less frequent on all *Bombus* species at lower latitudes, but Husband (personal communication, 1974) says this is due to a paucity of bumblebees at lower altitudes, both in numbers and species of the bees.

These mites fasten themselves to their host with the claw complex on the first pair of legs. In southern Alberta these mites were commonly found attached to the deutonymphs of *Parasitus favus* and *P. perthecatus,* but a few were also found on males of *P. favus,* females of *P. perthecatus,* deutonymphs of *P. hobbsi,* and females of *P. inquilinobombus* and one on a macrochelid male. An *S. acarorum* was also found on a field-collected *B. occidentalis* queen. *S. acarorum* was usually found attached to the setae of the legs, but also attaches to setae on the dorsum of the deutonymphs. *S. acarorum* was found on *Parasitus* spp. in 17% of 424 of the bumblebee nests. In these nests 24% (62 of 258) of the deutonymphs of *P. favus* and 33.9% (21 of 62) of the deutonymphs of *P. perthecatus* had *S. acarorum* attached to them. The number of *S. acarorum* on deutonymphs ranged from 1 to 13. A female of *S. acarorum* attached to a deutonymph of *Parasitus* in culture remained attached until the deutonymph died. It then crawled off and remained in the culture eight additional days. *Scutacarus* uses the *Parasitus* and the bumblebees phoretically. If they use the host for anything else, it is not known. Only females of *S. acarorum* were encountered.

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THE UNIVERSITY OF KANSAS
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THE MECOPTERA OF INDIA AND ADJACENT REGIONS

By

MICHAEL K. RUST and GEORGE W. BYERS

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The Mecoptera of India and Adjacent Regions[1]

By Michael K. Rust and George W. Byers

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ABSTRACT

Six species of *Bittacus,* 21 of *Neopanorpa* and 3 of *Panorpa* are described, compared, illustrated, and differentiated in taxonomic keys. The following new species are described: *Bittacus nodosus, Neopanorpa denticulata, N. echinata, N. gibbosa, N. indica* and *N. ochrura.* Previously unknown sexes of 5 species based on single holotypes are described and illustrated. *N. effusa* (Navás) and *N. furcata* (Hardwicke) are removed from *Leptopanorpa* to *Neopanorpa.* The geographical distribution of Mecoptera in the Indian subcontinent is correlated with elevation, rainfall, forest cover and other ecological factors, and zoogeographical relationships are discussed.

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[1] Contribution no. 1607 from the Department of Entomology, The University of Kansas, Lawrence, Kansas 66045.

INTRODUCTION

Accounts of insects of the order Mecoptera of the Indian subcontinent,[2] primarily species descriptions, have been published occasionally over the past 150 years. Of the 21 species so far described, many are still represented by single holotypes or a few syntypes, and little or nothing is known about their distribution. It is possible that the ranges of several Indo-Chinese and Chinese species extend into the Indian region.

Five previously unknown species of *Neopanorpa* and one of *Bittacus* are described in this paper. In addition, the previously undescribed sexes (one female, four males) for five species heretofore known only from single holotypes are described and illustrated. Two species previously assigned to *Leptopanorpa* have been transferred to *Neopanorpa*. It is our hope that this paper will serve primarily as a basis for future research on Mecoptera in the Indian region, especially since our survey has been so limited. In addition to those already mentioned, we have examined several specimens of undescribed species of *Neopanorpa* and *Bittacus* that have not been included because the males were badly damaged or only females were available.

Three species of *Panorpa* reported from Tibet, but probably from western China are discussed and illustrated to clarify the original locality data and to provide more useful illustrations of the types. We have examined an undescribed species of *Panorpa* from northern Burma, and it seems probable that the range of *Panorpa* extends into the hills of eastern Assam.

On the basis of wing pattern and genitalic characters of both males and females, three of the species of *Neopanorpa* form a compact group. We have called this the *appendiculata* group, after the oldest named species included. The members are: *appendiculata, salai,* and *indica* n. sp. Similarly, another four southern Indian species form a closely related group, which we have called the *denticulata* group, after the most abundant included species. Its members are: *denticulata* n. sp., *hirsuta, echinata* n. sp., and *zebrata*. The other species of *Neopanorpa* cannot yet be arranged in useful taxonomic groups.

The most extensive collection of Indian Mecoptera is in the Snow Entomological Museum, University of Kansas. Three additional collections from the Indian region have been examined. They are from the British Museum (Natural History), London, loaned by Mr. Peter H. Ward, the Illinois Natural History Survey, Urbana, Illinois, loaned by Dr. L. J. Stannard, and the Naturhistorisches Museum, Basel, loaned by Dr. W. Wittmer. We also wish to thank Mr. P. Susai Nathan for his help in locating several of the collection sites.

Unfortunately, we have not been able to obtain on loan any specimens from the various institutions in India, Pakistan or adjacent countries. We are not aware of the extent to which this has limited our investigation.

Support for this study, through grants GB-30837 and GB-7045X from the National Science Foundation, is gratefully acknowledged.

HISTORICAL REVIEW

The first record of Mecoptera from the Indian subcontinent was the description of *Neopanorpa furcata* by Hardwicke (as *Panorpa*) in 1825. Westwood's description of *Neopanorpa appendiculata* (1846, as *Panorpa*) was followed by the description of *Bittacus indicus* by Walker in 1853. Thirty-two years later Gerstaecker (1885) described *Bittacus latipennis*.

Between 1908 and 1935, Navás described nine additional Indian species, of which seven are still considered valid. He used the generic names *Aulops* Enderlein and *Campodotecnum* Enderlein for the species *suffusa* and *effusum* respectively. *Aulops suffusa* Navás was synonymized by Esben-Petersen (1915) with *Neopanorpa nipalica* Navás; and *Campodotecnum effusum* Navás was transferred to *Leptopanorpa effusa* by Esben-Petersen (1915) (but we consider it a species of *Neopanorpa*). The other species were *Neopanorpa ocellaris* (1908, as *Panorpa*),

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[2] The Indian subcontinent, as used here, includes Assam, Bangladesh, Bhutan, Sri Lanka (Ceylon), India, Nepal, Pakistan and Sikkim.

Panorpa stigmalis (1908), *Panorpa davidi* (1908), *Neopanorpa nipalica* (1910, as *Panorpa*), *Neopanorpa salai* (1929), and *Neopanorpa benaci* (1935).

Needham (1909) added two new species, *Neopanorpa sordida* and *N. fenestrata* (both as *Panorpa*). In 1915, Esben-Petersen transferred most of the Indian species described as *Panorpa* into the genera *Neopanorpa* and *Leptopanorpa.* He presented no evidence justifying the synonymy of *Aulops suffusa* Navás with *Neopanorpa nipalica* Navás, and he agreed with Navás' earlier expectation that the female type of *P. davidi* was in fact a new species, *P. guttata.* In addition, he described *Neopanorpa cornuta, N. flava,* and *N. zebrata.* In his world monograph of the Mecoptera (1921), Esben-Petersen redescribed and illustrated most of these species.

Since Esben-Petersen's monograph, six further new species have been described. These are *Bittacus henryi* (Kimmins, 1928), *Neopanorpa hirsuta* (Crampton, 1931, as *Panorpa*), *N. contracta* (Cheng, 1954), *Bittacus taraiensis* (Penny, 1969), *Neopanorpa chillcotti* (Byers, 1971) and *Neopanorpa ramulata* (Byers, 1975).

The following species are recognized in this investigation.

BITTACIDAE:
- *Bittacus henryi* Kimmins
  - *indicus* Walker
  - *insularis* Esben-Petersen
  - *latipennis* Gerstaecker
  - *nodosus* n. sp.
  - *taraiensis* Penny

PANORPIDAE:
- *Neopanorpa appendiculata* (Westwood)
  - *benaci* Navás
  - *chillcotti* Byers
  - *contracta* Cheng
  - *cornuta* Esben-Petersen
  - *denticulata* n. sp.
  - *echinata* n. sp.
  - *effusa* (Navás)
  - *fenestrata* (Needham)
  - *flava* Esben-Petersen
  - *furcata* (Hardwicke)
  - *gibbosa* n. sp.
  - *hirsuta* (Crampton)
  - *indica* n. sp.
  - *nipalica* (Navás)
    - syn. *suffusa* (Navás)
  - *ocellaris* (Navás)
  - *ochrura* n. sp.
  - *ramulata* Byers
  - *salai* Navás
  - *sordida* (Needham)
  - *zebrata* Esben-Petersen
- *Panorpa davidi* Navás
  - *gutatta* Navás
  - *stigmalis* Navás

MATERIALS AND METHODS

Dissections of male and female genitalia were preceded by removing the posterior abdominal segments from the specimen and gently boiling them for one to two minutes in water. In several cases, it was necessary to remove the male's hypovalves in order to examine the aedeagus. This was accomplished by carefully cutting the hypovalves and ninth tergum apart from the basistyles. To remove the genital plate of the female, it was necessary to make an incision through the pleural membrane on each side of segments 7-8. The genital plate is usually secured by tough membranous tissue, and care must be taken to prevent damage to it when this tissue is cut.

To soften pinned specimens for dissection or to be placed in fluids, a dilute solution of trisodium phosphate was used. Specimens should not remain in the trisodium phosphate solution over 24 hours, or the membranes disintegrate and only the sclerotized portions remain. Softened specimens should be thoroughly rinsed in water and placed in alcohol.

To photograph the wings, it was often necessary to remove them. A relaxing jar was used to soften the specimens, and the wings were removed with a scalpel, mounted between glass slides and photographed.

Drawings and body measurements were made with the aid of a camera lucida. Considering the variable length of the abdomen due to the amount of abdominal contents at preservation, the method of preservation, and position, the recorded measurements of body length are at best approximations.

In descriptions of the genital plates of females, total length is measured in ventral aspect. In many species, total length is from the anterior apices of the apodemes to the posterior apices of the arms of the distal plate. The length of the arms is measured from the apices to a line perpendicular to the axial portion at its junction with the arms' inner margin (Fig. 70). Length of the axial portion is from posterior apex to apices of the apodemes. The length of the apodemes is measured along the mid-line from the anterior edge of the basal plate to the apices of the apodemes.

The total length of the male genital bulb in ventral aspect is the distance from the base of the bulb to an imaginary line extending through the most distal points on each dististyle (in a closed position). Hypovalves are occasionally compared to length of basistyles, which is measured from the base of the basistyles to a line connecting the most distal points on both basistyles.

Approximately 450 specimens were examined. Most were from South India (Nilgiri Hills), and collections from other parts of the Indian region were small and from scattered localities. Of these 450 specimens, 284, 24, and 39 represented *Neopanorpa denticulata, N. hirsuta,* and *N. appendiculata,* respectively. The remaining approximately 100 specimens represented about 20 species.

THE INDIAN TOPOGRAPHY AND CLIMATE

The Indian subcontinent has a tremendously diverse topography, ranging from sea level to the highest mountain ranges in the world, and climatic pattern, varying from deserts to tropical rain forests. The central anchor-shaped mountain range of Ceylon ascends from the coastal plain to summits over 5000 feet. Extending north from Cape Comorin to Bombay along the western coast of India, the Western Ghats rise sharply and descend to the Deccan Plateau. Separating the Deccan Plateau and some outlying uplands (Vindhya Range, etc.) from the foothills of the Himalaya is a broad lowland area (the Indo-Gangetic Plain) extending from the valley of the Indus, across the Indian Desert and eastward to the Khasi Hills of Assam. Vast areas of Nepal, Sikkim, and Bhutan are in the foothills of the Himalaya.

The northeast monsoonal air mass flows southward and southeastward from a continuous high pressure region near the Hindu Kush. As the air mass flows over India, it is continuously diverted from the Bay of Bengal across southern India by the Coriolis effect. Beginning in December in the northern provinces, the monsoon continues until February. Commonly referred to as the cold season, this period is characterized by generally dry, cool air resulting in lower maximal and minimal temperatures.

With the termination of the northeast monsoon, a warming trend occurs from March until May in most of the Indian subcontinent. This period is characterized by clear skies and warm temperatures. In the northeastern provinces of India, violent storms result when dry land air meets humid sea air; these storms provide substantial rainfall that enhances agriculture.

Originating over the Indian Ocean in a zone of high pressure, the wet southwestern monsoonal air mass flows northeastward. The beginning of the wet monsoon in Ceylon is around May; the air mass progresses northward slowly and reaches Karachi, Pakistan, about 15 July. The physical relief and plant cover of India and Burma and the upper wind currents are influential in diverting the winds through Assam, the northeastern provinces of India, and the Himalayan foothills. These regions receive about 25-30% of their annual rain in July, when it normally rains at least 20 days. As the air mass slowly withdraws to the sea, there is a transitional period of cool, dry weather during October and November.

Along the western slopes of the Western Ghats, there is a substantial amount of rain (80 or more inches annually), supporting tropical evergreen forests (fig. 1). The eastern slopes and plateau receive only about 40 inches of rain annually and are covered predominantly by tropical dry deciduous and thorn forests. The eastern coast of southern India consists of many fertile delta areas now under heavy culti-

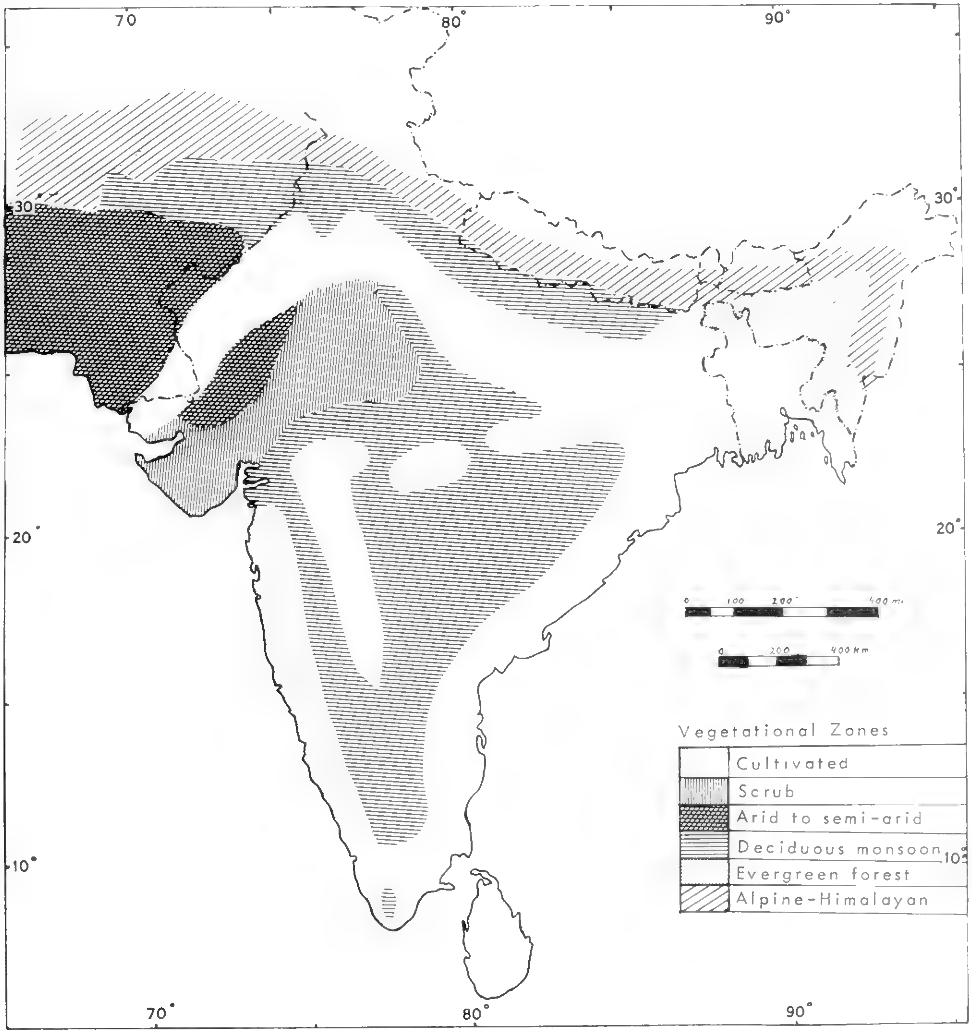


FIG 1. Vegetational zones of India and adjacent regions.

vation. In a very similar pattern, Ceylon is divided from west to east into climatic and vegetational zones.

The lowlands of western India and Pakistan do not receive much rain (0-10 inches in desert areas, up to 20 inches per year in western India) and are covered with semi-arid and arid vegetation. In sharp contrast, mid-central and mid-eastern India receive from 30 to 75 inches of rain annually and the area is intensely cultivated, especially the Ganges River basin. The higher plateaus are covered primarily by dry, tropical deciduous forests.

The lowlands and river basins of Assam and Bangladesh receive about 60 inches of rain annually, whereas the plateaus of Assam receive between 100 and 200 inches annually. Some areas receive considerably more rain, for example, Cherrapunji, Assam, about 428 inches. The forests in these areas are primarily tropical evergreen.

As elevation increases from the foothills into the Himalaya, the temperate forests change to coniferous forests at about 12,000 feet, and these in turn give way to alpine meadows and tundra on the southern slopes of the mountains at about 15,000 feet.

DISTRIBUTION OF MECOPTERA IN THE INDIAN REGION

The climatic zones, topography, and natural vegetational zones (figs. 1, 2) can be considered together in forming a general picture of India with respect to Mecoptera and their distribution. The Shillong Plateau of Assam and the Western Ghats are similar in that they are covered primarily by tropical evergreen forests, and characterized by large seasonal rainfalls and cool temperatures. More than half the described species of Indian *Neopanorpa* are from these areas. The other areas in which *Neopanorpa* has been collected are the deciduous monsoonal and dry tropical forest zones of the Himalayan foothills. The vegetation of these areas is stratified according to elevation. The exact environmental parameters important for the survival of *Neopanorpa* are not known.

There are no records of *Neopanorpa* from central India. Most of that area is agricultural and moreover lacks the combination of climatic, topographical, and vegetational conditions found in either northern or southern India. Along the northern edge of the Deccan Plateau, the forests are primarily of the tropical deciduous type, and possibly *Neopanorpa* occurs in these areas.

In southern India, the majority of the specimens of *Neopanorpa* were collected in early May, during the transitional period between monsoons. The remaining specimens were collected from late August through October, which is slightly prior to the termination of the southwest monsoon. In sharp contrast, the majority of specimens collected in northern India were taken from late July through September. In both of these areas and seasons, *Neopanorpa* was collected from 700 feet to about 7,000 feet.

Only *Bittacus* has been reported from Sri Lanka (Ceylon). From the few available specimens, it appears that *Bittacus* also emerges prior to the termination of the wet monsoon. All four Singhalese specimens were taken at elevations under 500 feet. Ceylon has a dense human population and the lowland areas are intensely cultivated. Destruction of suitable habitat has probably severely limited the recent distribution of *Bittacus* on Ceylon.

The apparent distribution of *Bittacus* is very different from that of *Neopanorpa*. The elevations of areas (fig. 2) in which *Bittacus* has been collected in India range from nearly sea level to 1400 feet. In general, these areas are warmer and drier than those in which *Neopanorpa* has been collected. There is, however, a lowland species of *Neopanorpa* (undescribed) from Nepal, and the type locality of *B. latipennis* is Darjeeling, India. The ranges of some North American species, such as *B. strigosus* Hagen and *B. stigmaterus* Say, are over a thousand miles wide, so it is possible that some of the western Chinese species may extend into Assam and along the Himalayan foothills.

There are no records of *Panorpa* in the Indian subcontinent. Within a hundred miles of the northeastern border of Assam, however, in the mountains of Sikang, China, there are ten species of *Panorpa* (Cheng, 1957). Only a single species is known from Yunnan Province, and there is an undescribed species in northern Burma. Since some species of *Panorpa,* such as the North American *P. helena* Byers, are wide-ranging, it seems that *Panorpa* may extend westward into the mountains of Assam and the Himalayan

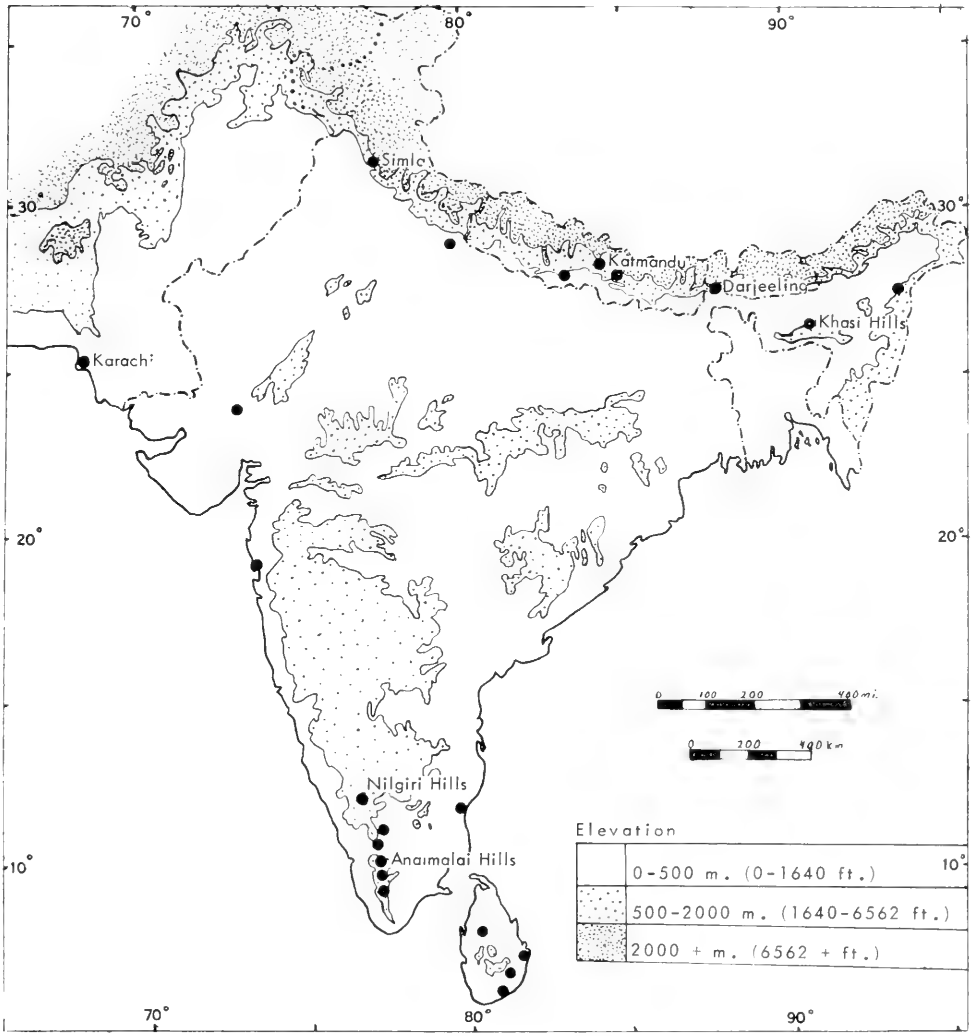


FIG. 2. Elevational map of India and adjacent regions. Black circles indicate localities where Mecoptera have been collected. See accompanying list for details.

foothills. *Panorpa* has never been collected there, however, due possibly to the lack of collecting or to its absence for ecological reasons.

TAXONOMY OF THE GENUS *BITTACUS*

Since the head and thorax other than the wings are rarely used for taxonomic purposes, they have been omitted here. Setty (1940) and Hepburn (1969, 1970) discussed and illustrated these body regions in detail. Otanes (1922) and Matsuda (1965) provided a somewhat more generalized discussion of the head in Mecoptera. Storch and Chadwick (1968) investigated the thorax of *Bittacus strigosus* Hagen of North America.

WINGS: The color, shape, and venation of the wings (fig. 3) are extensively used in the taxonomy of *Bittacus*. The veins include the costa, a two-branched subcosta, a five-branched radius (R_2 sometimes further branched), a four-branched media, a two-branched cubitus, and three anal veins (3A very short). Both fore and hind wings have similar shape, but the fore wings are longer (by one or more mm.). The only significant differences in venation between the fore and hind wings are that the basal fusion of veins Cu and M is longer in the hind wings, and Cu_2 and 1A are partly fused in the hind wings, not independent as in the fore wings. The color of the wing membrane varies from clear to yellowish or tinged with brown. The apical wing margin may be bluntly rounded or more pointed, often a taxonomic character.

In many species, the position of certain cross-veins may be diagnostic, especially the apical and subcostal cross-veins. The number of pterostigmal cross-veins (fig. 3, Pcv) between veins R_1 and R_{2+3} has often been used for taxonomic purposes, but since the number of cross-veins may vary within an individual specimen, this character is not always reliable. The position of the subcostal cross-vein (Scv) in relation to the origin of the radial sector (ORs) and the first fork of the radial sector (FRs) is a taxonomically useful character, but the position of the Scv may vary. In many species, there is an apical cross-vein (Av) between Cu_2 and the distal end of 1A near the hind margin of the wing; the presence or absence of this cross-vein appears to be a reliable taxonomic character.

ABDOMEN OF THE MALE: Many taxonomic characters are found on segments 9-11 (Tjeder, 1956). The general shape and the projections of the epiandrial lobes of the ninth tergum (figs. 5, 8) vary considerably between species and are usually diagnostic. The ninth sternum is not noticeably modified and is rarely included in descriptions. The basistyles are fused basally and extend posteriorly beneath the ninth tergum; their shape, size, and hairiness may be taxonomically useful. The diststyles, one on the posterodorsal apex of each basistyle, are small compared to the basistyles. Lobes (penunci) at the base of the aedeagus and the shape of the apical portion of the aedeagus are taxonomically useful in bittacids generally. However, in the Indian species, the base of the aedeagus is not modified and lobed as it is, for example, in some of the Chinese species. The proctiger, or combined tenth and eleventh segments, is usually small and inconspicuous, but in some species it is enlarged and extremely modified and extends dorsad between the epiandrial lobes. The single-segmented cerci are rarely important in taxonomy.

ABDOMEN OF THE FEMALE: In earlier descriptions, the female genitalia were almost completely ignored, but Tjeder (1956) based several descriptions of African species on female holotypes, using such characters as degree of sclerotization of the antecosta of the posterior abdominal segments, subgenital plate, spermatheca and its duct, and cerci. These characters have not been thoroughly investigated, and nothing is known concerning their variation in Indian bittacids. When possible, these structures have been included in the descriptions in this paper.

The subgenital plate is below the eighth and ninth terga. The shape, hairiness, and degree of fusion of the sclerites of the subgenital plate appear to be reliable taxonomic characters. The supra-anale and subanale (tergum and sternum of the eleventh segment) often have characteristic posterior margins. The trichobothria of the cerci may also be used for taxonomic purposes (Tjeder, 1956). The spermatheca, which may be diagnostic of the species, is usually within segment 7 a little anterior to the subgenital plate. The width and degree of sclerotization of the posterior abdominal antecostae have also been used in taxonomy.

Key to the Indian Species of Bittacus

The males of *B. indicus* and *insularis* and the females of *B. taraiensis* and *nodosus* are unknown. The sex of the holotype of *latipennis* is unknown.

1 Vein 1A extends to or beyond level of FRs 2
Vein 1A extends at most to midpoint between levels of ORs and FRs 3

2(1) Scv one-fourth distance from ORs to FRs; proctiger of male large, directed dorsad between epiandrial lobes .... *taraiensis*
Scv midway between ORs and FRs .... *indicus*

3(1) Vein 1A joins hind margin opposite level of ORs; Scv before FRs; fore wing 14-16 mm 4
Vein 1A joins hind margin midway between ORs and FRs; Scv variable; fore wing over 17 mm 5

4(3) Scv midway between ORs and FRs; Cu_2 joins hind margin opposite level of fork of M_{3+4}; epiandrial lobes of male stout, about twice as long as wide, with numerous spines at apex of each .... *insularis*
Scv slightly before FRs; Cu_2 joins hind margin slightly proximal to level of fork of M_{3+4}; (male unknown) .... *henryi*

5(3) Scv midway between ORs and FRs to slightly distal of FRs; Sc joins costal margin proximal to level of Cu_1; epiandrial lobes of male stout, about twice as long as wide, with four or five spines on small dorsal protuberance at apex of each .... *nodosus*
Scv distal to FRs; Sc joins costal margin before level of Cu_1, opposite level of Cu_2; (male unknown) .... *latipennis*

Descriptions of Species: Genus *Bittacus*

Bittacus henryi Kimmins

Bittacus henryi Kimmins, 1928: 395-396, fig. 1.

Unfortunately the original description was based on a single female. This species closely resembles *B. insularis* but, on the basis of the holotype, differs from it in the positions of the Scv and Sc, the length of the fore wings (*henryi* about 16.1 mm. and *insularis* about 14.8 mm.), and the more basal position of Cu_2 with respect to the fork of M_{3+4}. In *insularis,* the Scv is midway between the ORs and the FRs, and the Sc merges with the costal margin slightly distal to the FRs. In *henryi,* the Scv is nearly opposite the FRs, and the Sc merges with the costal margin barely past the FRs. Kimmins (1928) stated that the position of the FRs in relation to the fork of vein M is different in *henryi* and *insularis.* However, the position of the FRs appears to be the same in the holotypes of both species. Another difference in the wing venation is the additional cross-vein between R_2 and R_3 in *henryi,* but it is present in only three of four specimens we consider to be *henryi.* Very little is known concerning variation in Indian bittacids, and there is a strong possibility that despite the described venational differences *henryi* and *insularis* may be synonyms.

The venation, particularly the position of the Scv, of males from southern India is similar to that of *henryi*; therefore, these males are included in the following redescription, which is otherwise based on notes and drawings of the female holotype:

Head: Vertex, genae, frons, and rostrum sordid yellowish brown; two lateral ocelli slightly larger than medium ocellus; a row of long yellowish hairs on ridge across frons. Antennal scape and pedicel sordid dark brown, flagellum blackish brown with short pilosity.

Thorax: One large black spine at each side on anterior margin of pronotum. Entire dorsum, pleural regions, and coxae sordid yellowish brown. Legs yellowish brown, femora and tibiae with blackish apices; hind femora slightly enlarged in male. Wing membrane with light yellowish brown tinge, outer margins slightly darker; longitudinal veins brown, cross-veins in basal portion of wing brown, several in distal portion pale. Av absent; Scv slightly basal to FRs; two Pcv. Sc merges with costal margin slightly beyond FRs; vein 1A merges with hind margin opposite ORs.

Abdomen of Male: Terga and sterna 2-9 yellowish brown. Base of tergum 9 with transverse ridge extending distally onto epiandrial lobes. Lobes stout, with numerous spines at apices, hairs longest at bases of lobes; mesal protuberance on lower inner surface with many small spines (fig. 8). Angle of hind margin slightly acute. Diststyles short (figs. 6, 7), apices curved mesad. Cerci short, 0.8 length of basistyles. Aedeagus stout at base, tapering to a fine point.

Abdomen of Female: Terga 2-11 and corresponding sterna and subgenital plate yellowish brown. Subgenital plate bluntly rounded at apex. Cerci sub-equal in length to segment 9.

Length of Fore Wing: Female holotype, 16 mm.; male, 14.6-15.0 mm., hind wing, 13.3-13.6 mm.

Holotype: Female, Vavuniya, N. P., Ceylon, 16 December 1923; in the British Museum (Natural History), London.

In addition, we have examined the following specimens: 1 male, Pondicherry, India (no date), Maindron, in the Museum National d'Histoire Naturelle, Paris; 1 female, Yala, Ceylon, 18 December 1931, in Colombo Museum, Ceylon; 1 male, Coimbatore, Madras State, India, 1400 feet, November 1962, P. S. Nathan (figs. 5-8), and 5 males, 4 females, Coimbatore, June 1974, S. Bharathi, in the Snow Entomological Museum.

On the basis of male genital structures, this species resembles *B. nodosus* from Pakistan and certain African species, especially *B. chevalieri* Navás. The epiandrial lobes have a striking resemblance to those of *nodosus* and *chevalieri,* particularly the protuberance on the lower, mesal margin. In lateral view, the epiandrial lobes and basistyles of *henryi* are somewhat smaller but in shape resemble those of *B. sjostedti* Weele from Africa. The male genitalia suggest a closer relationship of *henryi* to several northeastern African species than to the western Chinese bittacids.

Bittacus indicus Walker

Bittacus indicus Walker, 1853: 469.

This species is known only from the holotype, from which the abdomen has been largely eaten away by dermestids or psocids. There are two eggs clinging to the remaining portion of the abdomen, which indicate that the species description was based on a female. There has been some confusion concerning the type locality; that on the label is "E. Ind." which Walker interpreted as East Indies. Esben-Petersen (1921) interpreted it to be East India, which is the more probable locality, because no other *Bittacus* has ever been collected in the East Indies.

Esben-Petersen (1921) makes reference to a type series. A second specimen with the type is labeled "East Ind." and was also part of the Saunders collection, but it does not have a type label. Vein 1A ends

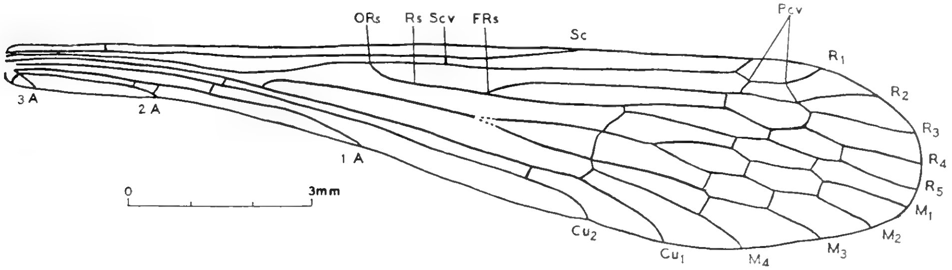
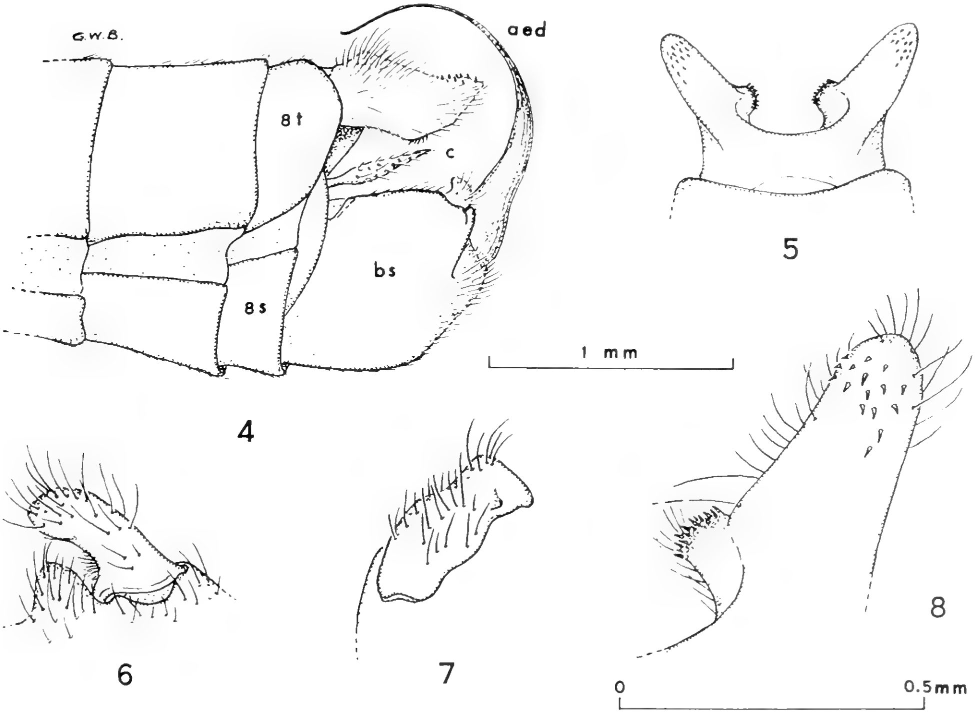


FIG. 3. Right fore wing of *Bittacus henryi* (length about 13.5 mm.); A—anal vein, Cu—cubitus, FRs—first fork of radial sector, M—media, ORs—origin of radial sector, Pcv—pterostigmal cross-vein, R—radius, Rs—radial sector, Sc—subcosta, Scv—subcostal cross-vein.



FIGS. 4-8. *Bittacus henryi* Kimmins. 4, terminal abdominal segments, male, left lateral aspect (aed—aedeagus, bs—basistyle, c—cercus, ds—dististyle, s—sternum, t—tergum); 5, epiandrial lobes, dorsal aspect; 6, right dististyle, posterior aspect; 7, right dististyle, anterodorsal aspect; 8, left epiandrial lobe, dorsal aspect. Upper scale figs. 4-5, lower scale figs. 6-8.

opposite the ORs in the front wing of this second individual, which would indicate that it is not *B. indicus.* This condition is found in *B. insularis* and *B. henryi,* but the fore wing of this second specimen is over 3 mm. longer than that of either *insularis* or *henryi.* This specimen probably represents an undescribed species, but since it is in very poor condition, the species should not be described until additional specimens are available.

The following brief redescription is based partly on notes and drawings of the female holotype:

HEAD: Dorsum pale brown, except black ocellar prominence. Rostrum shiny brown. Antennae yellowish brown, short haired, 10 mm long.

THORAX: Dorsum and pleural areas brown. Legs brown, except tips of femora and tibiae narrowly banded blackish brown. Wing membrane tinged with pale grayish brown; longitudinal veins yellowish brown in distal portion. No Av; two Pcv; Scv equidistant between ORs and FRs; end of Sc opposite end of Cu_2; end of 1A opposite FRs.

ABDOMEN OF FEMALE: Basal segments brown (terminal segments broken off).

MALE: Unknown.

LENGTH OF FORE WING: Female holotype, 19 mm.; hind wing, female holotype, 17 mm.

HOLOTYPE: Female, "E. Ind." (probably eastern India); in the British Museum (Natural History), London.

On the basis of wing venation, this species closely resembles *B. taraiensis,* but it differs slightly in that the Scv is midway between the ORs and FRs, not as proximally situated as in *taraiensis.* Another slight difference is that the end of vein 1A of *indicus* is nearly opposite FRs, not beyond it as in *taraiensis,* but this may result from differences in wing size (fore wing of *taraiensis,* 17.5-18.0 mm.; *indicus,* 19 mm.). The basal cross-vein between veins 1A and 2A of *taraiensis* is at midlength of 2A but is in the distal one-sixth of 2A in *indicus.* In two North American species of which numerous specimens were examined, *B. pilicornis* Westwood and *B. strigosus* Hagen, the position of this second cross-vein appears to be constant. In *B. stigmaterus* Say, also from North America, it is absent. Some variation occurs in *B. punctiger* Westwood from North America. The position of this cross-vein may prove to be taxonomically useful, but its reliability is still somewhat doubtful.

This species is distinct from the other Indian species, except *taraiensis,* in that vein 1A extends distally beyond the level of FRs. It seems probable that *indicus* and *taraiensis* are synonyms.

Bittacus insularis ESBEN-PETERSEN

Bittacus insularis Esben-Petersen, 1915: 234.

This Singhalese species was originally described from a single female. As stated in the redescription of *B. henryi,* there is a likelihood that these nominal species are synonyms. But several pairs of Chinese species, for example, *B. vexilliferus* Byers and *B. carpenteri* Cheng, have nearly identical wing patterns yet are readily differentiated by the male genitalia. Further species descriptions based on females only should therefore probably be avoided, at least until reliable diagnostic characters can be demonstrated.

The following brief redescription is based on drawings and notes of the female holotype:

HEAD: Vertex brown, except ocellar prominence black; rostrum brown grading to blackish brown towards apex. Antennae dark brown.

THORAX: Prothorax sordid brown. Meso- and metathorax reddish brown. Femora, tibiae, and tarsi brown grading to blackish brown at apices. Wing membrane with yellowish brown tinge, with smoky brown apical margin. No Av. End of Sc extends distally beyond FRs. Scv midway between ORs and FRs. Vein 1a joins hind margin opposite ORS. End of Cu_2 extends distally beyond first fork of M_{1+2}. Two Pcv.

Abdomen of Female: Terga and sterna brown. Subgenital plate slightly concave near mid-length; apex bluntly rounded with numerous long hairs. Cerci about .25 mm. long.

Male: Unknown.

Length of Fore Wing: Female holotype, 15 mm.; hind wing, 13 mm.

Holotype: Female, Hambantota, Ceylon, 29 November 1908, T. B. Fletcher; in the British Museum (Natural History), London.

This small species differs from the larger Indian species in having the end of vein 1A opposite the level of the ORs. In *B. latipennis* and *B. nodosus*, the Scv is distal to the FRs, not midway between the ORs and FRs as in *insularis* (and *indicus* and *henryi*).

Bittacus latipennis Gerstaecker

Bittacus latipennis Gerstaecker, 1885: 120.

Since the species was described from a single specimen from which the abdomen was absent, it is impossible to determine its sex. However, the position of the Scv distal to the FRs, the merging of vein 1A with the hind margin beyond the level of ORs, and the width of the wing should permit recognition of either sex, when *latipennis* is again discovered. The position of 1A with respect to the ORs is similar in *B. henryi* and *B. insularis*, but both of these species are smaller than *latipennis* and have the Scv located between the ORs and FRs.

Esben-Petersen (1921) adequately dealt with the general body coloration. His account of the wing venation is, however, somewhat incomplete. The following redescription is based on his photographic illustration of the holotype of *latipennis*:

Wings: Membrane with yellowish brown tinge, except for several hyaline spots; longitudinal veins brown; cross-veins in basal portion brown, paler in distal portion. Av absent. Scv dstal to FRs in fore wing, near ORs in hind wing. One Pcv. Sc extends about 2 mm. beyond end of FRs; 1A merges with hind margin slightly distal to ORs.

Length of Fore Wing: holotype, 19 mm.; hind wing 17 mm.

Holotype: Darjeeling, India, date unknown; in Zoologisches Institut und Museum, Ernst Moritz Arndt Universität, Greifswald, D. D. R. (East Germany).

This species can be easily recognized by the long, broad wings. In *B. indicus* and *B. taraiensis*, vein 1A joins the hind margin of the wing distal to the FRs, not slightly beyond the level of ORs as in *latipennis*. There is a broad-winged, undescribed species from Nepal (only one female available), but it differs from *latipennis* in having vein 1A opposite the level of the FRs, and the Scv far beyond the FRs, at the level of the end of the Cu_1.

Bittacus taraiensis Penny

Bittacus taraiensis Penny, 1969: 161-164, figs. 1-3.

This species is very similar to *B. indicus*. The only significant difference is the position of the Scv. In another Indian *Bittacus*, *B. nodosus*, the position of the Scv varies, and this would support synonymizing *indicus* and *taraiensis*. But as emphasized in the redescription of *B. insularis*, some Chinese species that have very similar wings can be recognized only from the male genitalia. Our knowledge of Indian bittacids is very incomplete.

Penny (1969) stated that *taraiensis* also differed from *indicus* in the coloration of the abdomen. Coloration is a somewhat unreliable character, often affected by method of preservation, age of the specimen when preserved, etc. The types of *taraiensis* are preserved in alcohol and the holotype of *indicus* is a pinned specimen.

The following brief redescription is derived from Penny's (1969) original description:

Wings: Membrane hyaline, stigma and adjacent cells tawny brown; distal two rows of cross-veins nearly white. Av absent, 1A extending distally beyond first fork of M. Two Pcv. Sc extends beyond FRs. Scv one-fourth distance from ORs to FRs.

Abdomen of Male: Epiandrial lobes with connecting transverse ridge at base, apices converging and curved dorsad; short, many-spined protuberance on basal, mesal margin directed mesad. Basi-styles with bluntly rounded apices. Aedeagus stout at base, tapering abruptly to fine point. Proctiger projecting dorsally between epiandrial lobes, with long hairs at apex.

Female: Unknown.

Length of Fore Wing: 17.5-18.0 mm.

Body Length: 14-16 mm.

Holotype: Male, Pant Nagar, Nainital Dist., India, 5 August 1968, L. J. Stannard; in the Illinois Natural History Survey collection, Urbana, Illinois. Paratype, 1 male, same locality and collector, 26 July 1968.

On the basis of the proctiger, this species is similar to several western Chinese species, especially *B. carpenteri* Cheng and *B. pieli* Navás, in having the 10th segment elongated and extended dorsally between the epiandrial lobes (Penny, 1969). But in *taraiensis*, the aedeagus is not lobed at the base (i.e., has no penunci) as in these species but is similar to those of *B. henryi* and *B. nodosus*. The epiandrial lobes of *taraiensis* are similar to those of some Indian and African species, especially *B. chevalieri* Navás, in having a many-spined protuberance on the inner, basal margin. The genitalia of *taraiensis* represent an intermediate form between certain western Chinese and African species.

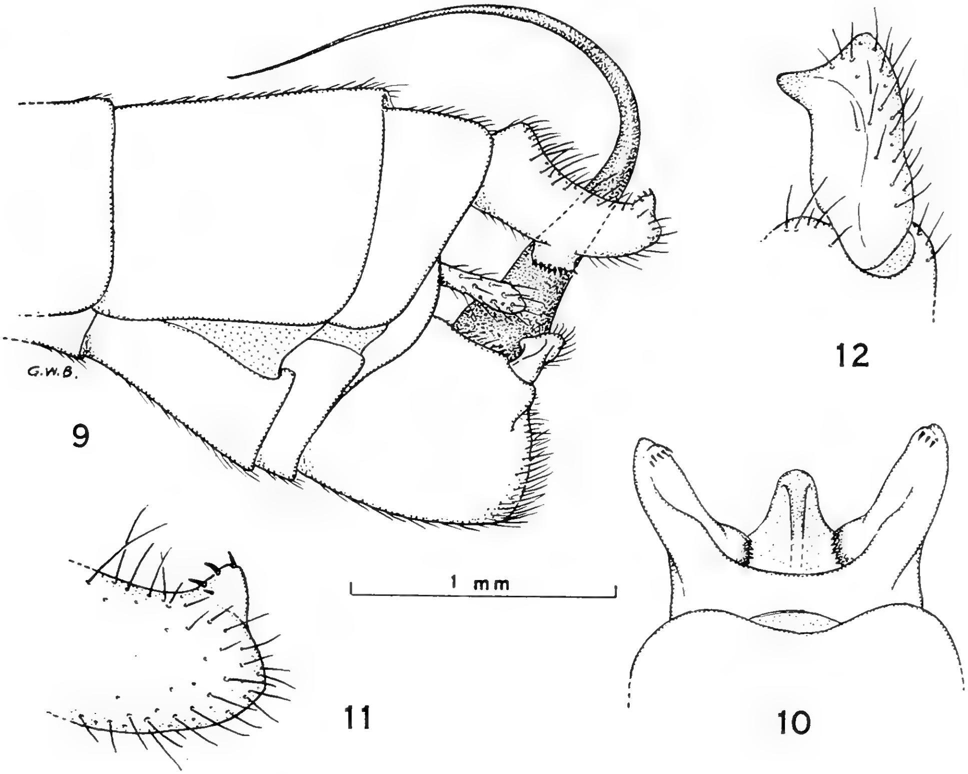
In wing venation, *taraiensis* differs from the other Indian species, except *indicus* and an undescribed species (female) from Nepal, in having 1A extending distally beyond FRs.

Bittacus nodosus, New Species

Description based on two males and one specimen of unknown sex, pinned.

Head: Vertex, frons, and genae light yellowish brown; rostrum light yellowish brown grading into dark yellowish brown at apex; maxillary palpi yellowish brown, except apical segment dark yellowish brown. Ocelli extremely large, on conspicuous black prominence with two spines posterior to median ocellus. Epistomal suture with row of hairs of uniform length. Antennal scape and pedicel light yellowish brown; flagellum light yellowish brown with 14 segments.

Thorax: Pronotum with one long black spine at each side, on both anterior and posterior margins. Several small black setae on meso- and metanotum; two short, black setae on posterior margin of metepimeron. Dorsum, pleural region, and coxae yellowish brown. Anterior surfaces of coxae with long yellowish hairs. Legs yellowish brown, except apices of tarsomeres blackish brown; hind femora not especially enlarged. Wing membrane hyaline, outer margin with faint brownish tinge; longitudinal veins and cross-veins brown. Av absent. One Pcv, except right fore wing (two), in holotype; two Pcv in all wings in paratypes. Scv opposite FRs, in left fore wing, slightly distal to FRs in right fore wing in holotype, midway between FRs and ORs in paratype; Scv basal to FRs in hind wings of both specimens. Vein 1A extends slightly beyond level of ORs. Three cross-veins between R_3 and R_4 in left fore wing of holotype, two in other wings.



Figs. 9-12. *Bittacus nodosus* n. sp. 9, terminal abdominal segments, male holotype, left lateral aspect; 10, epiandrial lobes, dorsal aspect; 11, tip of left epiandrial lobe, lateral aspect; 12, left dististyle, anterodorsal aspect. Scale figs. 9-10.

Abdomen of Male: Terga and sterna 2-9 sordid yellowish brown. Base of tergum 9 with transverse ridge extending postero-laterally onto epiandrial lobes. Lobes stout, each with 4-5 spines on small protuberance at apex (figs. 10, 11); protuberance on lower mesal margin with many spines (fig. 10). Hind margin of basistyles squarely blunt, with long hairs. Dististyles small, apex abruptly truncate forming a somewhat concave surface (fig. 12). Cerci short, about half as long as epiandrial lobe. Aedeagus stout at base, tapering to fine point.

Female: Unknown.

Length of Fore Wing: 16.0-17.3 mm. (holotype 17.3 mm.); hind wing, 14.5-16 mm. (hototype, 16 mm.).

Holotype: Male, Karachi, Pakistan, 8 October 1959, R. I. Sailer; in Snow Entomological Museum. Paratypes, 1 male, 1 without abdomen, Deesa, India (about 330 mi. E. of Karachi), 8 January 1935, G. G. Nurse; in British Museum (Natural History), London.

In wing venation, this species resembles *B. latipennis* in that the Scv is opposite or slightly distal to the FRs and vein 1A extends slightly beyond ORs. But *nodosus* differs from *latipennis* in having narrower wings (greatest width, *nodosus,* about 2.6 mm.; *latipennis,* about 4.9 mm.) and a shorter Sc. In addition, there is a second basal cross-vein between veins 1A and 2A in *latipennis,* not present in *nodosus,* and it appears from Esben-Petersen's (1921) photograph of the wings of *latipennis* that the longitudinal veins are slightly darkened at their bases.

The male genitalia of *nodosus* closely

resemble those of *B. chevalieri* Navás from Africa, and vaguely those of *B. henryi,* especially in the epiandrial lobes. The absence of penunci from the base of the aedeagus, the small, inconspicuous proctiger, and the spined protuberance on the inner, basal margin of the epiandrial lobes are characters shared by all three of these species. *B. nodosus* differs from the other two in having a short, spined, dorsal protuberance at the apex of each epiandrial lobe. The posterior margins of the basistyles are abruptly truncate, not rounded as in the African and Singhalese species. On the basis of the genitalia, *nodosus* resembles the African species more than it does either *taraiensis* or *henryi.*

SPECIES OF *Bittacus* NOT DESCRIBED.

Two bittacids that probably represent new species were examined but not described. The following brief discussion of these specimens is primarily to note their existence, their affinities with other species, and their location. Since the male genitalia provide the most reliable taxonomic characters, we have declined to base descriptions of new species on these individuals.

In the British Museum, there is a single *Bittacus* (abdomen missing) from Hadibu, Socotra Island (12°36′ N, 53°59′ E), in the Gulf of Aden about 125 miles east of Capo Guardfui, Republic of Somali. The wing venation is similar to that of *B. henryi* and *B. insularis,* but this species differs in having a clear membrane and slightly larger wings (about 16 mm. long).

Another undescribed *Bittacus,* a single female from Simra, Nepal, has distinctive wing venation. The Scv is distal to the FRs and 1A extends almost to the level of the FRs (fore wing). Since no other known species from the Indian subcontinent has such a venational pattern, this may allow recognition of the male when discovered. This specimen is in the collection of the Entomology Research Institute, Canada Department of Agriculture, Ottawa.

TAXONOMY OF THE GENUS *NEOPANORPA*

HEAD: The head of *Neopanorpa* has the large lateral compound eyes, long prominent rostrum, and three ocelli on a prominence, as commonly found in Panorpidae. In the adult, the ecdysial cleavage line is present but confined to the ocellar region (Hepburn, 1969). Two major components of the rostrum are the clypeus (anterior) and the subgenae (lateral); the elongated maxillary stipites and membranous submentum comprise nearly all of the posterior aspect. The absence of the occipital suture makes it impossible to define the exact extent of the genae and postgenae, but the subgenal suture clearly outlines the postgenal process.

In *Neopanorpa,* the antennae are long and conspicuous. The scape is subcylindrical and the pedicel nearly globular. The flagellum is usually blackish brown to black and consists of numerous (usually 35-45) finely pubescent flagellomeres. There is a whorl of six to eight slightly longer bristles near the apex of each flagellomere.

THORAX: In addition to the short hairs that cover most of the thoracic sclerites, the pronotum may possess several long setae along the anterior margin. In the meso- and metathorax, the meron is enlarged and extends nearly the length of the adjacent coxa. The legs are similar on all three thoracic segments, each having the femur and tibia of approximately equal length, and two long spurs at the apex of the tibia. The basitarsus is approximately equal in length to the other four tarsomeres combined. Usually amber colored, the pre-tarsal claws have five pectinations.

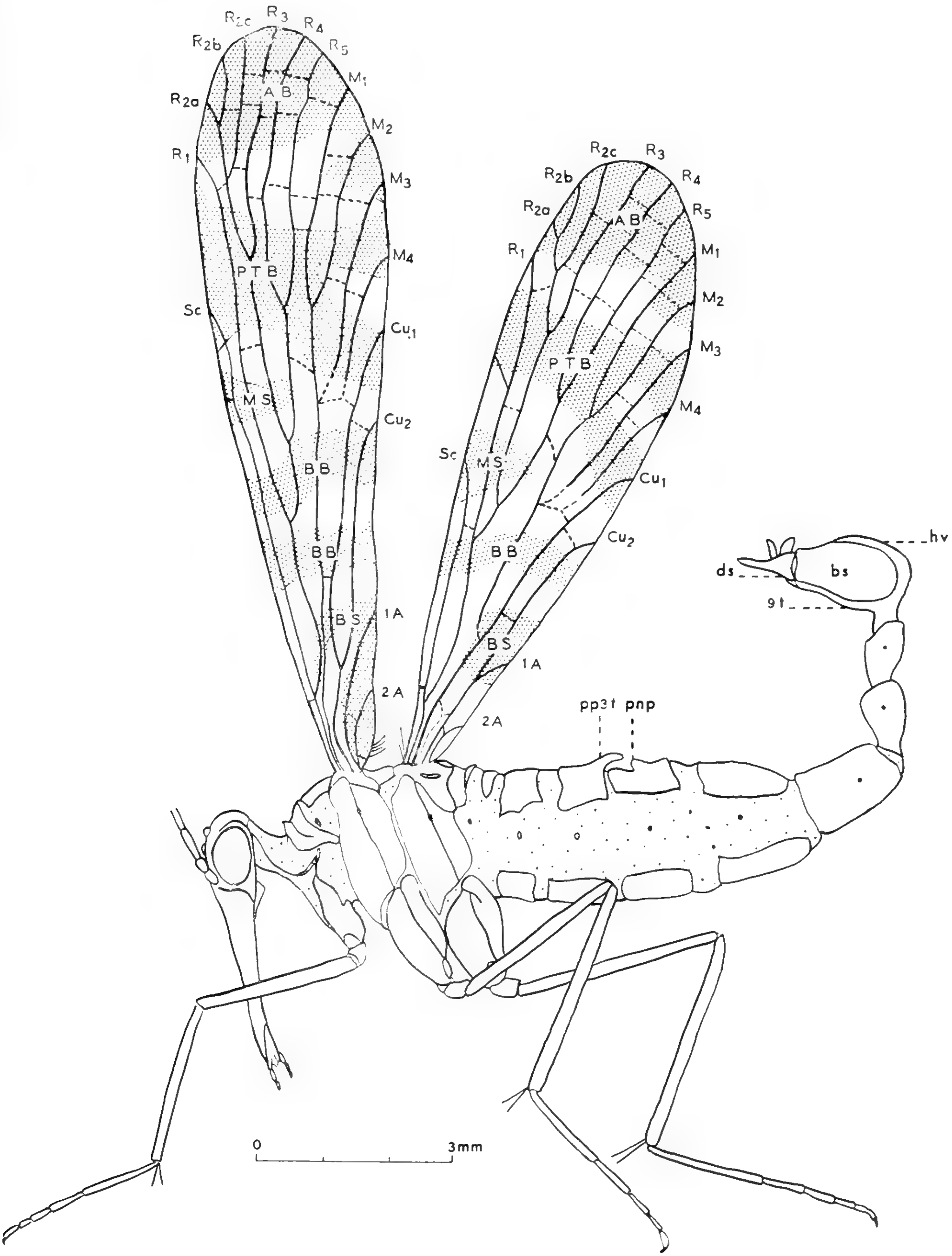


Fig. 13. Left lateral aspect of male of *Neopanorpa denticulata* n. sp. A—anal vein, AB—apical band, BB—basal band, BS—basal spot, bs—basistyle, Cu—cubitus, ds—dististyle, hv—hypovalves, M—media, MS—marginal spot, pnp—posterior notal process, pp3t—posterior process of third tergum, PTB—pterostigmal band, R—radius, Sc—subcosta, t—tergum. Note that the basal band is divided, or double, in the fore wing in many individuals of this species.

WINGS: The fore wings are slightly (1 or more mm.) longer than the hind wings. On the proximal hind margin of the fore wing, there are four to eight setae which together with two long setae on the proximal costal margin of the hind wing serve to unite the wings during flight. The venation of the wing (fig. 13) consists of a costa, a subcosta, a five-branched radius, a four-branched media, a two-branched cubitus, and three anal veins. The only significant departure in the venation of the hind wing from that of the fore wing is a consolidation of anal and cubital veins, in which the cubitus forks and converges with both the media and first anal veins; the anal and cubital veins are not independent as in the fore wing. At the first fork of the media, the veins are always pale within a clear spot (thyridium). Vein 1A merges with the hind margin before the origin of the Rs, a generic character differentiating *Neopanorpa* from *Panorpa.*

The wing membrane varies from clear to yellowish brown and may be slightly to extensively marked with spots or bands. The presence or absence of these bands can often be used to differentiate species, although there is some variation within species in their size and shape. Generally, within a species of *Neopanorpa,* the background color and wing markings are somewhat reduced in the hind wings, and the dark coloration is usually more extensive in the female.

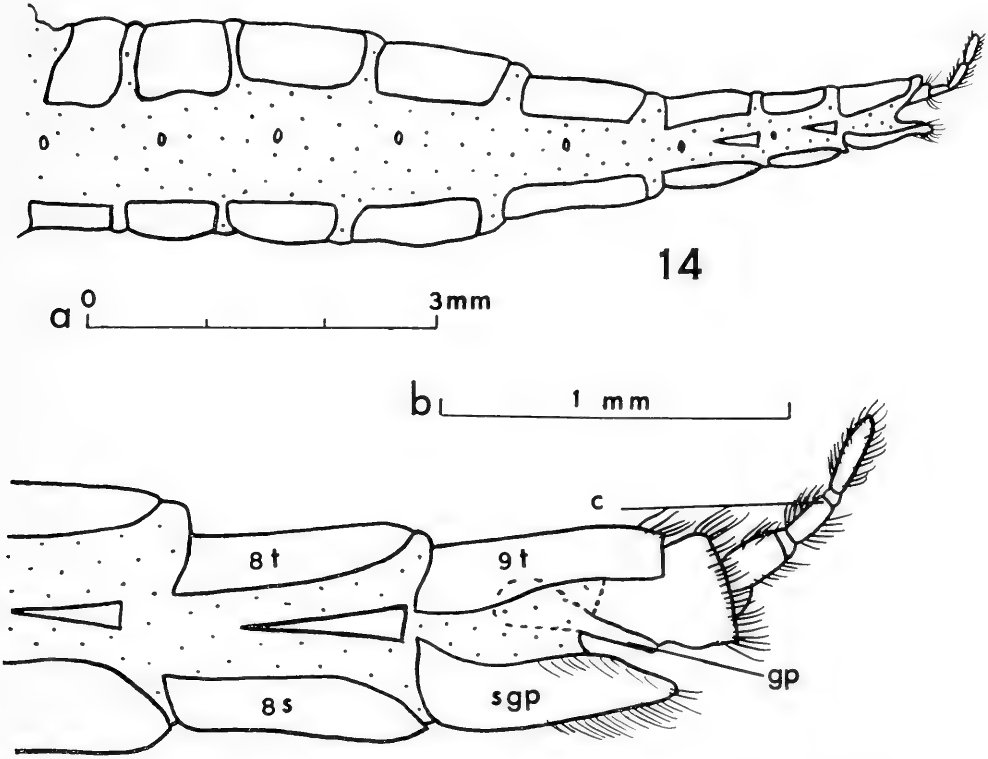
If present, the apical band is in the extreme distal portion of the wing; its proximal margin may be irregular or notched. Usually the broadest band, the pterostigmal is proximal to the apical band and has a variety of shapes depending on the species. It may be unbranched or may fork posteriorly. In several species, it is partially fused with adjacent bands. Near the costal margin in the midsection of the wing, the marginal spot may partially fuse to the pterostigmal band, basal band, or both. The basal band, in the proximal half of the wing, is often incomplete and may appear as a series of spots. In several species, the basal band is complete and may be partially fused to the marginal spot, basal spot or proximal branch of the pterostigmal band. Occasionally there is a distinct basal spot near the base of the wing; but in many heavily marked species, individual spots are difficult to discern.

ABDOMEN OF MALE: In segments 2-5, there is a large membranous pleural area between the terga and sterna. Segments 6-8 are completely sclerotized and roughly cylindrical. On the posterior margin of the third tergum, there is a sclerotized median projection (fig. 13) extending over the fourth tergum for which the terms "notoorganus", "notal organ", or "notorgan" were proposed by Crampton (1931). A small protuberance on the fourth tergum, which Crampton called the "postorganus", is a functional part of the notal organ. Mickoleit (1971) reported that in *Panorpa communis* Linnaeus from Europe the combined structure served as a mechanism for securing the female's wings during mating. This function was also recorded by Issiki (1933) and has been observed by us in several species of North American *Panorpa.* Often neglected in older species descriptions, the shape and length of the notal organ differ from species to species.

In a few species of *Neopanorpa,* the fifth and sixth terga are modified with projections or protuberances that are excellent taxonomic characters. In several large Himalayan species, the seventh and eighth segments are elongated but are thicker than those of *Leptopanorpa.* The constricted base of the ninth segment is cylindrical; the basally fused ventral and dorsal sclerites diverge to form the hypovalves and ninth tergum respectively. Segments 10-11 are small and weakly sclerotized in Panorpidae. The single-segmented cerci are the only portion of the last two segments not normally concealed by the ninth tergum.

The genital bulb (figs. 64, 65) consists of the ninth tergum (epiandrium), ninth sternum (including the hypovalves), basally fused basistyles, dististyles, and aedeagus. At the ventromesal base of each dististyle, there is a single lobe that is usually directed mesad, but occasionally more ventrad. The shape, size, and hairiness of this lobe are useful in the recognition of many species. The basal lobe is almost always single in *Panorpa* and *Neopanorpa,* while in *Leptopanorpa* it is usually divided into two parts.

Located between the basistyles, the aedeagus (figs. 68, 69) has several structures that are useful for taxonomic purposes. The dorsal and ventral valves are on the distal margin of the axial portion of the aedeagus. In *Neopanorpa,* the dorsal valves are generally small, rounded, darkly sclerotized protuberances and relatively unimportant in taxonomy. The shape of the ventral valves varies and may be useful for taxonomic purposes. The ventral and dorsal parameres often have characteristic shapes diagnostic for the species. Arising on the proximal, ventral margin of the aedeagus beside the ventral valves, the ventral parameres extend distally, with the terminal portion having a variety of shapes. In several species, they are reduced to small knobs or hooks; in others, they are blade-shaped or filamentous. If present, the dorsal parameres are above the dorsal valves and are usually short and stout, rarely attaining the length



Figs. 14-15. Abdomen of female *Neopanorpa denticulata* n. sp. 14, left lateral aspect of entire abdomen; 15, left lateral aspect of terminal segments (c—cercus, gp—genital plate, s—sternum, sgp—subgenital plate, t—tergum). Scale a— fig. 14; b— fig. 15.

and bizarre shapes of the ventral parameres. Extending laterally from the midsection of the aedeagus, the lateral processes are generally short and somewhat triangular, in *Neopanorpa*. In several species, they are fused with the dorsal parameres, the two structures together modified into long blades.

ABDOMEN OF FEMALE: In segments 2-8 (fig. 14), there is a large membranous pleural area separating the terga and sterna. A wedge-shaped sclerite (laterotergite) is situated on each side in the pleuron of the distal half of segments 7-8 in many species. In other species, these sclerites are absent, but hairs outline their position. The subgenital plate is considered to be formed of extensions of the eighth sternum, and the genital plate is the highly modified ninth sternum (Byers, 1954). Rarely visible from the outside, the genital plate (fig. 70) consists of three parts that are variously developed in different species. The distal and basal plates extend laterally from a central body or axial portion. The arms of the distal plate extend posteriorly and are occasionally visible without dissection. There are in most species two divergent apodemes at the anterior end of the axial portion, serving as sites of muscle attachment. The shapes of the subgenital plate and, more importantly, the composite genital plate are useful in the recognition of species. Segments 10-11 are greatly reduced in size as compared to the more anterior segments. Usually blackish brown to black, the two-segmented cerci are covered with many short hairs. The eleventh segment, situated below the cerci, has only weakly developed sclerites.

KEY TO MALES OF INDIAN SPECIES OF THE GENUS *Neopanorpa*

The males of *flava, ocellaris,* and *benaci* are unknown, and not enough is known about the males of *fenestrata* and *sordida* to determine accurately where they should be placed in the key. Both *fenestrata* and *sordida* should be located somewhere after couplet six.

1	Posterior half of sixth abdominal segment greatly modified, either conspicuously thickened and humped dorsally, or with slender projections	2
	Posterior half of sixth segment not so modified	4
2(1)	Sixth abdominal segment with thick dorsal hump; seventh segment bearing long dorsal hairs; ninth tergum with median, setose projection near mid-length (fig. 118)	*gibbosa*
	Sixth abdominal segment not thickened and humped dorsally; seventh segment without long hairs; ninth tergum without median projection near mid-length	3
3(2)	Projections from sixth abdominal segment more than half length of segment (fig. 43); dististyles shorter than basistyles (fig. 40); wings 12-13 mm. long	*cornuta*
	Projections from sixth abdominal segment much shorter than half length of segment (fig. 57); dististyles much longer than basistyles (fig. 58); wings 15-17 mm. long	*furcata*
4(1)	Posterior process of third abdominal tergum extends beyond posterior margin of fifth tergum	5
	Posterior process of third tergum extends at most to posterior margin of fourth tergum	6
5(4)	Hypovalves each with single mesal projection (figs. 17, 19)	*appendiculata*
	Hypovalves each with one mesal and one ventral, subapical projections (figs. 82, 86)	*salai*
6(4)	Wing membrane with strong yellowish tinge	7
	Wing membrane not yellowish, with hyaline to brownish gray tinge	8
7(6)	Hypovalves widely divergent at base, converging somewhat at tips (fig. 28); basal lobe of dististyles broad, thick blade with convex ventral surface	*chillcotti*
	Hypovalves not widely divergent at base, apical half of each deflected ventrad (figs. 48, 49); basal lobe narrow	*effusa*
8(6)	Wings unmarked except for stigmal spot, or only weakly patterned	9
	Wings distinctly marked with bands, spots, or both	11

9(8) Wing membrane hyaline; hypovalves sinuate with spiny, hairy apices curved abruptly mesad (figs. 110, 112) .... *echinata*
Wing membrane with diffuse brownish gray pattern; hypovalves not sinuate, their apices not spiny 10

10(9) Hypovalves narrowly separated at base (fig. 136); aedeagus short, not extending between dististyles; ventral parameres inconspicuous, convergent apically (fig. 138) .... *ochrura*
Hypovalves separated by subcircular space at base (fig. 71); aedeagus long, extending between dististyles; ventral parameres long, projecting beyond hypovalves, divergent apically (figs. 71, 74) .... *nipalica*

11(8) Posterior process of third abdominal tergum extending entire length of fourth tergum; ventral parameres broad near base, slender subapically, widened at apex (figs. 36, 39) .... *contracta*
Posterior process of third tergum short, rarely extending beyond mid-length of fourth tergum, but never entire length; ventral parameres broader subapically than near base .. 12

12(11) Dististyles largely covered with long, dense black hairs, especially near mid-length, their apices glabrous; hypovalves slender, sinuate (fig. 64) *hirsuta*
Dististyles without long dense black hairs near mid-length, with hairs longest on basal lobe; hypovalves not sinuate 13

13(12) Hypovalves thickest at level of basal separation, tapering toward apices, widely separated basally (as fig. 129) .... *indica*
Hypovalves wider near mid-length than at level of basal separation, not widely separated basally 14

14(13) Mesal margins of hypovalves entire, without lobes or spines (fig. 147); ventral parameres two-branched (figs. 145, 152, 153) .... *ramulata*
Mesal margins of hypovalves uneven, with setiferous or spinous lobes; ventral parameres unbranched 15

15(14) Mesal margins of hypovalves each with two setiferous lobes before apex (figs. 90, 96) .... *zebrata*
Mesal margins of hypovalves each with two spinous points before apex, another at apex (figs. 101, 104) .... *denticulata*

KEY TO FEMALES OF INDIAN SPECIES OF THE GENUS *Neopanorpa*

The females of *echinata* n. sp., *fenestrata, gibbosa* n. sp., and *nipalica* are unknown. Not enough is known about the female of *sordida* to include this species in the key. The genital plates of *benaci*

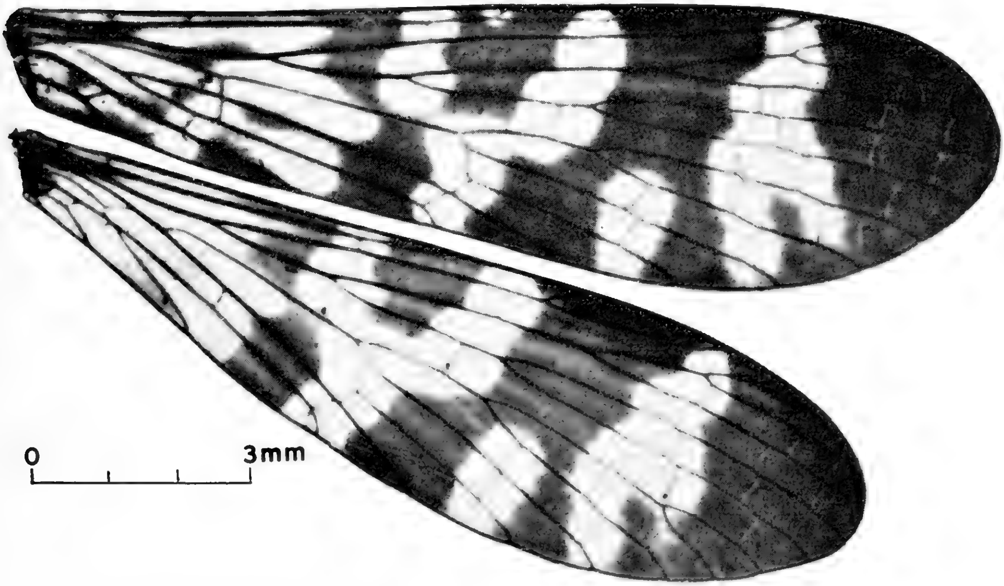


FIG. 16. *Neopanorpa appendiculata* (Westwood), male, right wings (fore wing length 13.8 mm.).

have never been examined and the position of this species in the key is based entirely on external characters.

1	Wing membrane with strong yellowship tinge	2
	Wing membrane not yellowish, hyaline to brownish gray	5
2(1)	Proximal margin of apical band oblique to costal edge of wing; proximal and distal branches of pterostigmal band subequal in width; pronotum and anterior half of mesonotum black, posterior half of mesontum and all metanotum yellowish brown	*effusa*
	Proximal margin of apical band either perpendicular to costal edge of wing or uneven and notched; branches of pterostigmal band of unequal width	3
3(2)	Genital plate broad, nearly as wide as long, its axial portion poorly developed (fig. 60); pronotum black with narrow yellowish band along posterior margin; anterior half of mesonotum black, posterior half and all metanotum yellowish brown	*furcata*
	Genital plate not nearly as broad as long, axial portion short but distinct; thoracic nota not as described above	4
4(3)	Subgenital plate deeply notched apically (fig. 32); mesonotum and metanotum sordid yellowish brown throughout, without distinct pattern; fore wing 14-16 mm. (fig. 27)	*chillcotti*
	Subgenital plate only shallowly notched apically (fig. 55); anterior two-fifths of mesonotum and anterior one-third of metanotum black, rest of both nota yellowish brown; fore wing about 18 mm. (fig. 52)	*flava*
5(1)	Distal half of fore wing heavily patterned, apical band broadly joined to pterostigmal band along hind margin	6
	Distal half of fore wing less heavily patterned, apical band not connected to pterostigmal band	7
6(5)	Apical and pterostigmal bands of fore wings with distinct included pale areas; cross-veins in apical portion of wing pale (fig. 26)	*benaci*
	Apical and pterostigmal bands without included pale areas; outermost cross-veins not pale, same color as veins in basal portion of wing	*ocellaris*
7(5)	Axial portion of genital plate less than one-half total length; basal plate and apodemes of genital plate absent	8
	Axial portion long, over one-half total length; basal plate and apodemes well developed	9
8(7)	Anterior half of mesonotum dark brown, posterior half yellowish; metanotum yellowish with dark brown semicircular spot on anterior margin; genital plate small, less than .5 mm. long (fig. 45)	*cornuta*
	Both mesonotum and metanotum black on anterior half and broadly along mid-line across posterior half; genital plate longer than .5 mm.	*ochrura*
9(7)	Apex of subgenital plate notched, plate ventrally keeled	10
	Apex rounded, plate not keeled	13
10(9)	Apodemes of genital plate long, widely divergent anteriorly (fig. 70); no basal spot in fore wings (fig. 63)	*hirsuta*
	Apodemes shorter, only slightly divergent and only shallowly separated anteriorly; basal spot in fore wings present or absent	11
11(10)	Apodemes of genital plate deflected abruptly ventrad from anterior edge of plate (fig. 155); basal spot absent from fore wings	*ramulata*
	Apodemes of genital plate deflected gradually dorsad anteriorly; basal spot in fore wings large	12
12(11)	Large clear spot in apical band; distal plate of genital plate dorso-venventrally flattened (figs. 98, 99)	*zebrata*
	Apical band without large clear spot, with notch on proximal margin; lateral margins of genital plate strongly curved ventrad (figs. 108, 109)	*denticulata*
13(9)	Apodemes of genital plate about one-third of total length (fig. 132)	*indica*
	Apodemes about one-fourth of total length	14
14(13)	Subgenital plate about 1.5 times as long as greatest width, without setae on triangular anteromedian area (fig. 23); apodemes of genital plate separated from edge of plate forward (fig. 24)	*appendiculata*
	Subgenital plate only slightly longer than its greatest width, covered with setae anteromedially (fig. 89); apodemes diverging from axis well forward of edge of genital plate (fig. 87)	*salai*

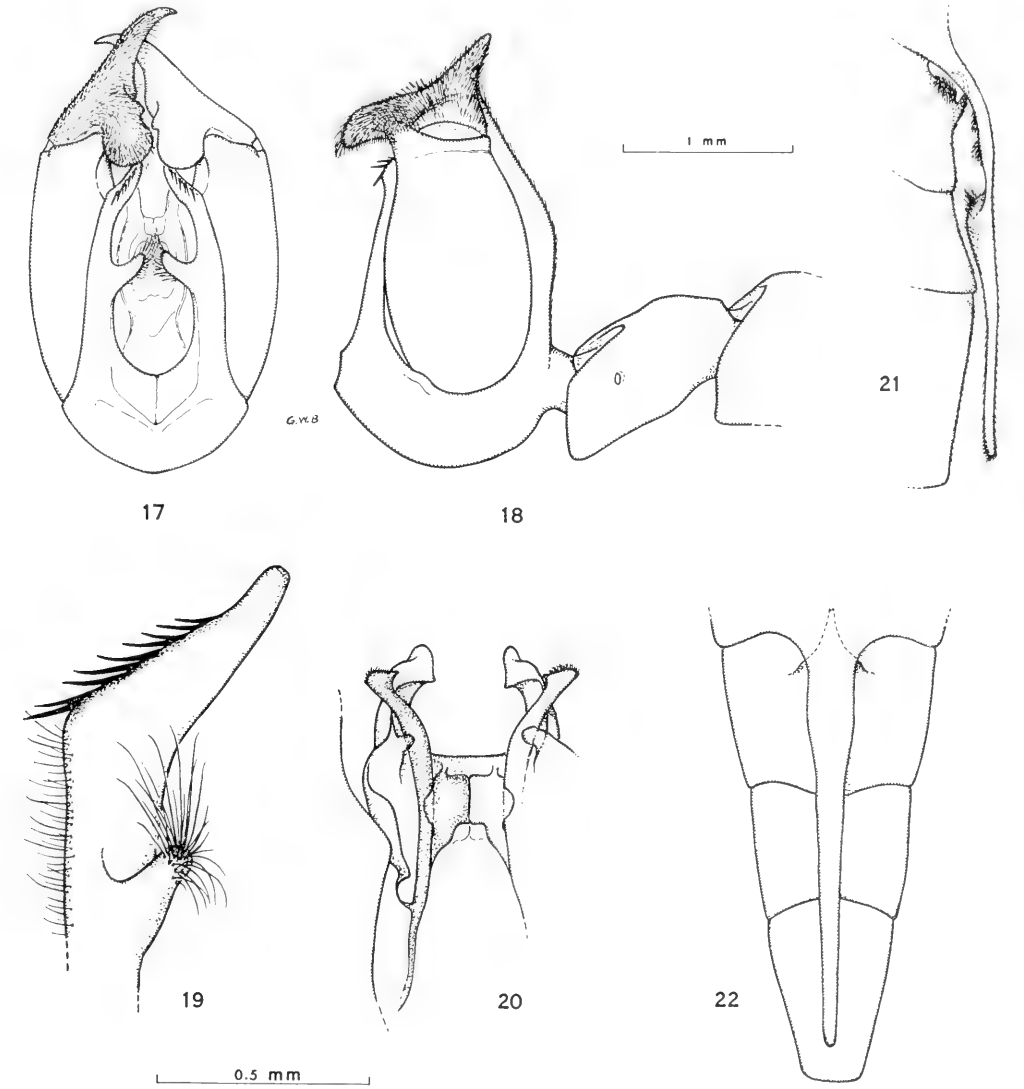
DESCRIPTIONS OF SPECIES: GENUS *Neopanorpa*

Neopanorpa appendiculata (WESTWOOD)

Panorpa appendiculata Westwood, 1846: 186.

Neopanorpa appendiculata; Esben-Petersen, 1915: 229.

Originally described as a *Panorpa,* this species was transferred to *Neopanorpa* by Esben-Petersen (1915), who pointed out that the vein 1A does not extend beyond the ORs. The redescription and photograph in Esben-Petersen's world monograph (1921) are based on a female syntype. This syntype, however, probably represents the female of *N. salai,* which species differs from *appendiculata* in having more extensive wing pigmentation, and in the male an additional projection on each hypovalve and a shorter posterior process of the third abdominal tergum.



FIGS. 17-22. *Neopanorpa appendiculata* (Westwood). 17, genital bulb, male lectotype, ventral aspect; 18, genital bulb, lectotype, right lateral aspect; 19, tip of left hypovalve, male, mesal aspect; 20, aedeagus, male, ventral aspect (part of right side omitted); 21, terga 3-6, lectotype, left lateral aspect; 22, terga 3-6, lectotype, dorsal aspect.

On the basis of wing pattern and body coloration, *appendiculata* closely resembles *N. indica,* n. sp., but the male of *appendiculata* differs in having a much longer posterior process of the third tergum and a larger mesal projection on the hypovalves. The females are not, however, as easily differentiated. Males of both species have been collected at the same locality and on the same date, together with eight females, probably all *N. appendiculata.* In the type series of *appendiculata,* there are two males of *indica* and two females with wing patterns identical to that of these males. The genital plates of these two females differ from those of the eight mentioned females in having longer apodemes and narrower distal plate. These two female syntypes of *appendiculata* are therefore tentatively included in *indica.*

The following composite redescription is based on notes and drawings of the male lectotype, 23 additional males, and 17 females:

HEAD: Dorsum, frons, and rostrum sordid yellowish brown. Scape, pedicel and basal half of first flagellomere sordid yellowish brown, antennal color then abruptly changing to black, remaining 37 flagellomeres black.

THORAX: Dorsum dark sordid yellowish brown (lectotype) to dark grayish brown. Pleural area and coxae sordid yellowish brown to grayish brown; femora and tibiae sordid yellowish brown; tarsi brownish grading to black on segments 4-5. Wing (fig. 16) membrane hyaline; markings dark smoky brown; cross-veins in distal portion pale, more basal ones brown. Apical band broad. Pterostigmal band forked posteriorly, with narrow distal branch. Marginal spot extends from costal margin to base of vein M_{1+2}. Basal band large anteriorly, constricted at vein M. Basal spot large.

ABDOMEN OF MALE: Terga 2-9 and corresponding sterna black. Posterior process of third tergum (figs. 21, 22) extending to hind margin of fifth tergum or beyond, its basal one-third broad and flattened, a broad ventral thickening near mid-length, remaining portion slender; entire process yellowish brown. Process of fourth tergum large dorsal protuberance with a narrow hooked projection directed anteriorly; protuberance covered with long black hairs. Hypovalves (fig. 17) stout, somewhat cylindrical basally; short finger-like protuberance with long hairs on inner margin in distal half, posterior margin straight, apical part deflected into interior of bulb, blade-like, with marginal row of thick black spines. Lateral margins of tergum 9 abruptly convergent in distal half, posterior margin straight. Broad hook-shaped protuberance on anterior margin of sternum 10, with long hairs on posterior margin. Cerci short, extending only to edge of ninth tergum. Diststyles about one-third length of entire bulb. Basal lobe of diststyles (figs. 17, 18) wide, bluntly rounded, directed ventrad, with long hairs on inner margin. Ventral parameres (fig. 20) thin, curved laterally in apical one-fourth, with short hairs on dorsal surface. Ventral valves of aedeagus broad, with thin lateral wings. Lateral processes broad at base, tapering to bluntly rounded point. Dorsal parameres curved ventrad, apex abruptly truncate.

ABDOMEN OF FEMALE: Terga 2-11 and corresponding sterna black. Subgenital plate (fig. 23) broad with bluntly rounded apex, with many long hairs on distal side and apex. Genital plate (figs. 24, 25) about 1.1 mm. long; posterior arms of distal plate long, about half of total length, slender, somewhat twisted at base; distal and basal plates broad, about .25 of total length, with lateral margins abruptly curved dorsad; apodemes short, about .25 of total length, with apices twice as broad as base and distinct notch on anterior margin.

Length of Fore Wing: Male, 11.0-13.0 mm. (lectotype, 11.6 mm.); female, 11.3-12.6 mm.

Lectotype: Male, Madras, date unknown; in British Museum (Natural History), London.

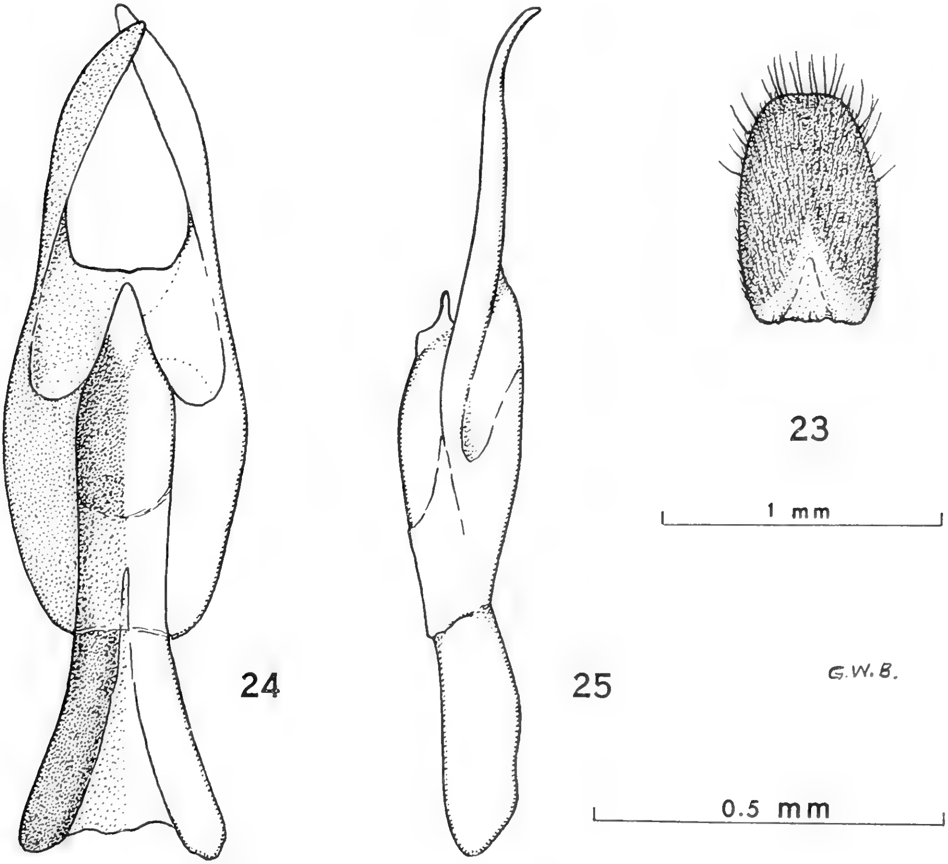
In addition to the types mentioned above, we have examined the following specimens; 9 males, 8 females, Gudalur, Nilgiri Hills, South India, 3,500 feet, September 1960, P. S. Nathan, in the Snow Entomological Museum; 14 males, 9 females, Cherangoda (1200 m.) and Singara (1100 m.), Nilgiri Hills, October 1950 and May 1954, in the Naturhistorisches Museum, Basel, Switzerland.

The similarity of hypovalves, aedeagus, and dististyles in males and the subgenital and genital plates in females are the primary characters used in grouping *appendiculata, indica,* and *salai* into the *appendiculata* group. It was called the *appendiculata* group after the first described, included species.

Neopanorpa benaci Navás

Neopanorpa benaci Navás, 1935: 97-98.

This species was originally described from the female holotype only, from Kurseong, India. The abdomen has been broken off beyond the seventh segment since being described, so nothing is known



Figs. 23-25. *Neopanorpa appendiculata* (Westwood). 23, subgenital plate, female, ventral aspect (upper scale); 24, genital plate, female, ventral aspect (lower scale); 25, genital plate, right lateral aspect.

about the genitalia. On the basis of wing pattern, *benaci* is very similar to *N. nipalica* and may be a synonym. Another male, holotype of *N. ochrura* n. sp., has a wing pattern similar to that of *benaci* but differs in having paler markings and smaller wings (about 11 mm.).

The following redescription is based on notes and drawings of the holotype and the original description:

HEAD: Vertex, frons, and rostrum black. Antennae black, about 8.5 mm. long.

THORAX: Pronotum black; anterior half of mesonotum blackish brown, posterior half brownish; metanotum blackish brown. Pleural areas and coxae pale grayish. Legs brownish. Wing pattern complex (fig. 26); membrane with a faint brownish tinge, becoming pale whitish in distal portion of wing; markings light to dark smoky brown; cross-veins in distal portion of wing pale. Apical band widely fused to pterostigmal band along hind margin, with six pale to clear spots surrounding cross-veins. Pterostigmal band complete, forked posteriorly, with a pale spot between R_4 and R_5. Marginal spot large, extending from costal margin to base of M_{1+2}. Basal band complete, constricted at vein M.

ABDOMEN OF FEMALE: Anterior segments black, posterior segments dark brown to black.

MALE: Unknown.

LENGTH OF FORE WING: Female holotype, 14.4 mm.

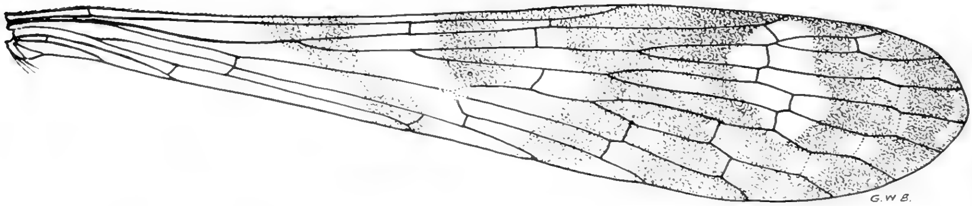


FIG. 26. *Neopanorpa benaci* Navás, female holotype, right fore wing (length about 13.9 mm.).

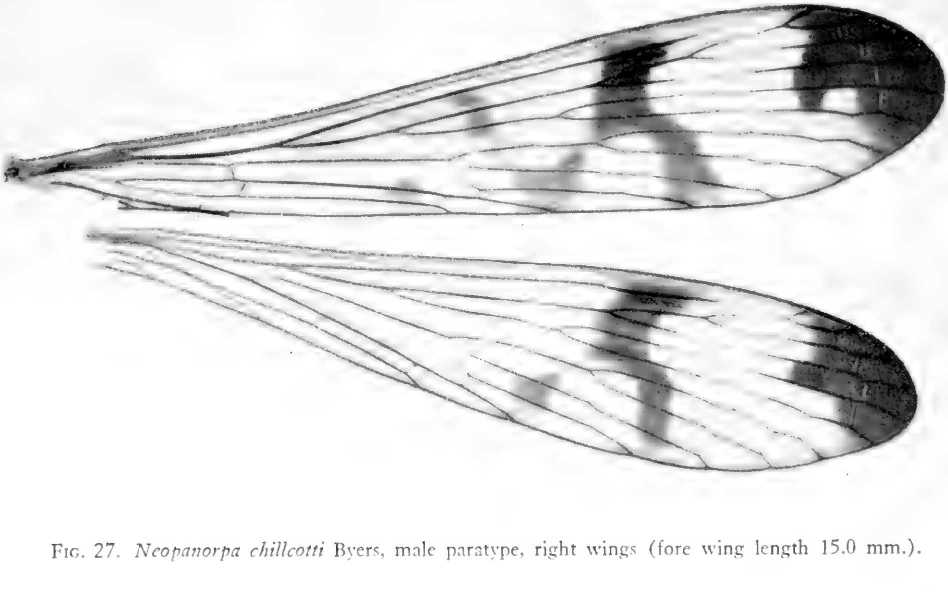


FIG. 27. *Neopanorpa chillcotti* Byers, male paratype, right wings (fore wing length 15.0 mm.).

Holotype: Female, Kurseong, India, 1932; in the Museum National d'Histoire Naturelle, Paris.

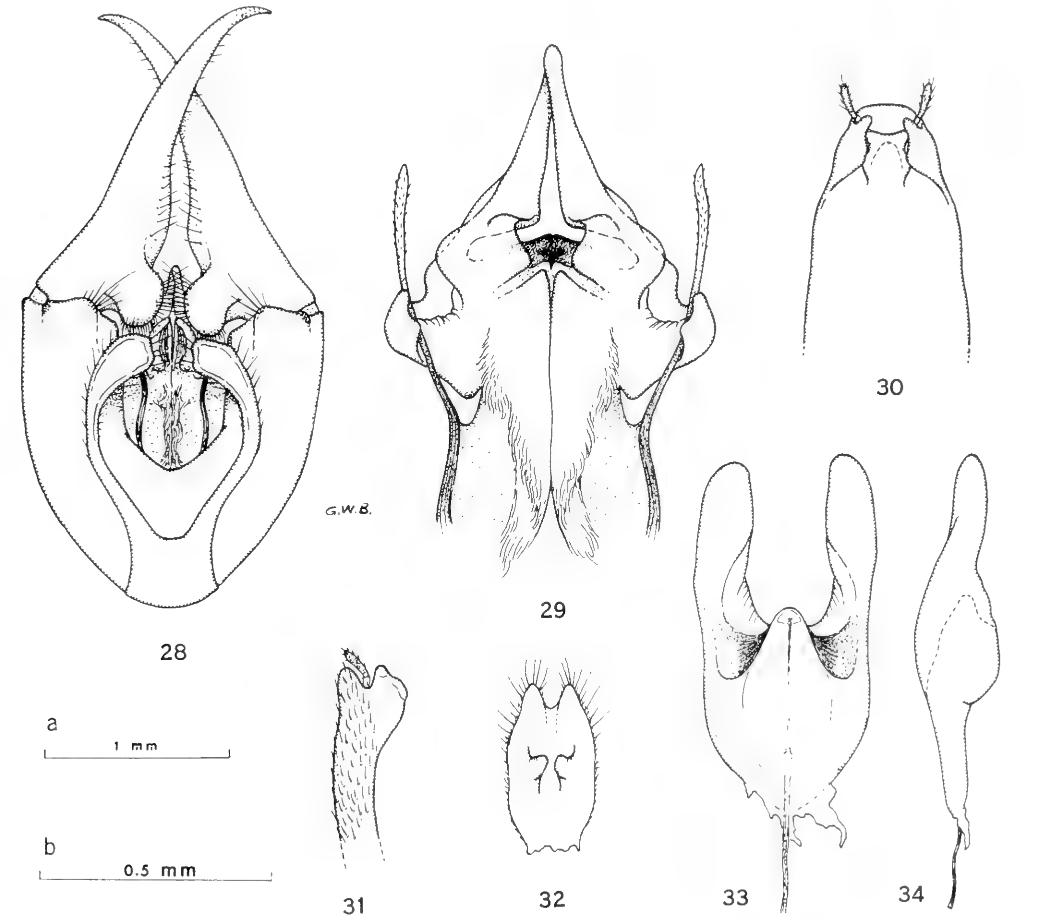
Neopanorpa chillcotti Byers

Neopanorpa chillcotti, Byers, 1971: 534-539, figs. 1-10.

Only certain diagnostic characters of this recently described Nepalese species are included in this brief redescription, to provide a basis for comparisons with other species. The following is based on the original description and reexamination of three male and one female paratypes:

Wing: (fig. 27): Membrane with strong dark yellowish tinge, markings brown. Apical band complete, its anterior proximal margin with a small projection directed posteriorly. Pterostigmal band variable, usually forked posteriorly. Marginal spot not attaining costal margin. Basal band incomplete, consisting of small spot near hind margin. Basal spot absent.

Abdomen of Male: Posterior process of third tergum extending to midlength of fourth tergum. Hypovalves (fig. 28) widely divergent at bases, convergent near apices; slender, somewhat wider in apical half. Dorsal parameres elongate,



Figs. 28-34. *Neopanorpa chillcotti* Byers. 28, genital bulb, male holotype, ventral aspect; 29, aedeagus, ventral aspect; 30, ninth tergum, ventral aspect; 31, ninth tergum, left lateral aspect; 32, subgenital plate, female, dorsal aspect; 33, genital plate, ventral aspect; 34, genital plate, right lateral aspect. Scale a—figs. 28, 30-32; b— figs. 29, 33, 34.

slender, wedge-shaped. Ventral parameres slender, with minute hairs near apices.

ABDOMEN OF FEMALE: Subgenital plate deeply notched at apex (fig. 32). Arms of genital plate (figs. 34, 35) broad and stout with bluntly rounded apices, subequal in length to axial portion. Axial portion broad, rounded anteriorly.

LENGTH OF FORE WING: Male, 14-16 mm. (holotype, 14.8 mm.).

HOLOTYPE: Male, Godavari, 10 mi SE of Katmandu, Nepal, 5,000 feet, 31 July 1967, Canadian Nepal Expedition. Holotype, allotype, and 13 paratopotypes are in the Entomology Research Institute, Canada Department of Agriculture, Ottawa, Ontario, Canada; 4 paratypes are in the Snow Entomological Museum.

Neopanorpa contracta CHENG

Neopanorpa contracta Cheng, 1953: 122, figs. 4-5, pl. 5.

Cheng's original description was based on two females from Darjeeling, India. It deals adequately with the genitalia and wing pattern, but the drawings lack precise detail. Two males, determined to be *contracta* on the basis of wing pattern and body coloration, are also included in the following brief redescription. The two males were badly damaged in transit from the Illinois Natural History Survey, but fortunately each specimen was pinned in its own sealed container so that genitalia could be associated with certainty.

HEAD: Dorsum shiny black, frons grayish brown, with a large median, shiny black spot; rostrum sordid grayish brown. Antennal scape blackish; base of pedicel blackish brown, changing abruptly to dark yellowish brown; flagellum blackish brown.

THORAX: Pronotum deep brown (holotype) to shiny blackish brown (males). Anterior half of mesoscutum and narrow band along median line to mesoscutellum blackish brown; posterolateral areas of mesoscutum light grayish brown. Metanotum similar to mesonotum. Pleural area and coxae pale grayish brown, except vertical brownish streaks on meso- and metamera. Femora and tibiae grayish; basitarsi grayish grading to black on segments 4-5, apices of tarsomeres 1-3 black. Wing membrane hyaline, markings light smoky brown. Apical band wide, with two hyaline spots in cells R_5 and M_1. Pterostigmal band complete, forked posteriorly. Marginal spot large, extending from costal margin to base of vein M_{1+2}. Basal band incomplete, reduced to small spot in males, to large spot extending from Cu_1 to hind margin in female (holotype).

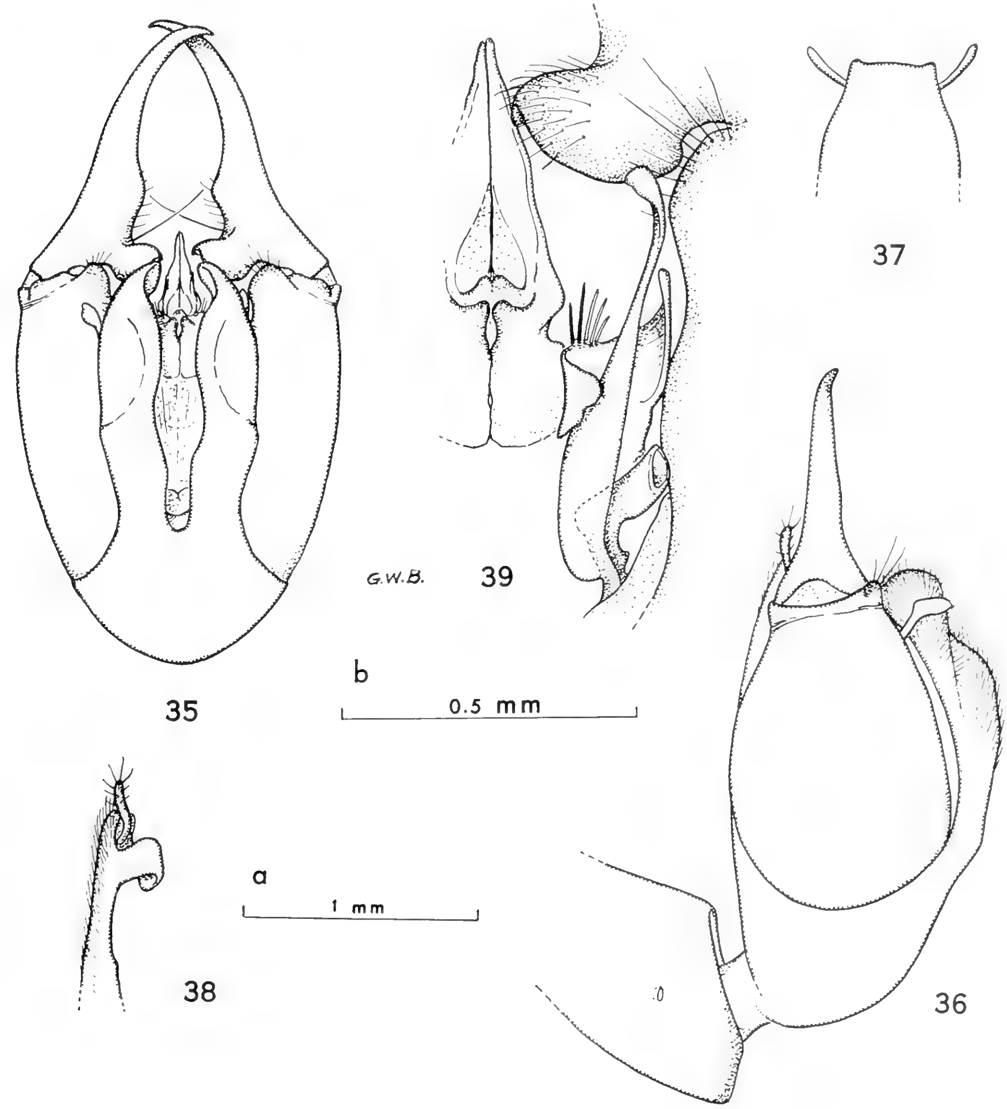
ABDOMEN OF MALE: Terga 2-3 blackish brown, 4-6 sordid grayish brown (segments 7-11 missing in one male, segment 7 in other), 8-9 sordid yellowish brown. Sterna 2-9 sordid brown. Posterior process of third tergum broadly triangular in basal half, slender in distal half, extending full length of fourth tergum, shiny black. Hypovalves (figs. 35, 36) extending to bases of dististyles, nearly uniform in width with bluntly rounded apices; distal half of each faintly sclerotized, with pale whitish tinge. Dististyles (figs. 35, 39) slender, blackish brown, outer margins concave in basal half; basal lobes directed mesad, dorsal surface shallowly concave, with long yellowish hairs at apices. Ventral parameres (fig. 39) broad at base, slender near mid-length, with apices flattened into blades; distal half of each curved ventrad. Lateral processes complex, mesal margin curved ventrad over ventral parameres, with spines along distal edge. Dorsal parameres long, contiguous, converging to a fine point.

ABDOMEN OF FEMALE: Terga 2-7 deep brown, 8-10 light brown. Subgenital plate deeply notched. Arms of genital plate long, 0.6 of total length of genital plate, twisted at base. Axial portion slightly broadened anteriorly, slightly notched.

Length of Fore Wing: Female holotype, 14.5 mm.; hind wing, 13.2 mm. Length of fore wing: Male, 14.0 mm.; hind wing, 13.2 mm.

Holotype: Female, Darjeeling, India, May 1939, T. C. Maa; in the Maa collection, Taipei, Taiwan, China. Paratype, 1 female, same collection data (Cheng collection). We have examined the following individuals: 1 male, Rangiroon, Darjeeling, India, 6,250 feet, 25 May 1966, Kamath; 1 male, same locality, 26 May 1966, Gupta; both males are in the Illinois Natural History Survey collection, Urbana, Illinois.

On the basis of the female genitalia, *contracta* superficially resembles several



Figs. 35-39. *Neopanorpa contracta* Cheng. 35, genital bulb, male, ventral aspect; 36, genital bulb, left lateral aspect; 37, ninth tergum, dorsal aspect; 38, ninth tergum, left lateral aspect; 39, aedeagus and basal lobe of dististyle, right side, ventral aspect. Scale a— figs. 35-38; b— fig. 39.

regional species of *Neopanorpa* in having a deeply notched subgenital plate and a genital plate in which the posterior arms are longer than the axial portion. The genital plate of *contracta* is similar to that of *N. appendiculata,* especially the posterior arms, but lacks the long, anterior axial portion found in *appendiculata.*

The genital bulb of *contracta* resembles that of *N. nipalica* in having long hypovalves of uniform width, long, contiguous dorsal parameres, and curved ventral parameres. However, *contracta* differs from *nipalica* in having a slightly darker wing pigmentation.

Neopanorpa cornuta Esben-Petersen

Neopanorpa cornuta Esben-Petersen, 1915: 227.

This species was originally described from eight males and ten females from the Khasi Hills, Assam. Illustrations of the male abdomen and wings (Esben-Petersen, 1921) show the sixth and seventh abdominal segments apparently in an unnatural position. In the illustration of the genital bulb, there are two forked structures (titillators), which are the ventral parameres.

N. cornuta can be recognized by its thoracic coloration and wing pattern. In addition, there are in the male two long projections on the enlarged posterodorsal margin of the sixth abdominal segment. In *N. furcata,* there are two claw-like projections, but the posterior half of the sixth segment is not enlarged in lateral aspect as in *cornuta.* The posterior half of the sixth segment of *N. gibbosa* n. sp. is enlarged, but there are no projections.

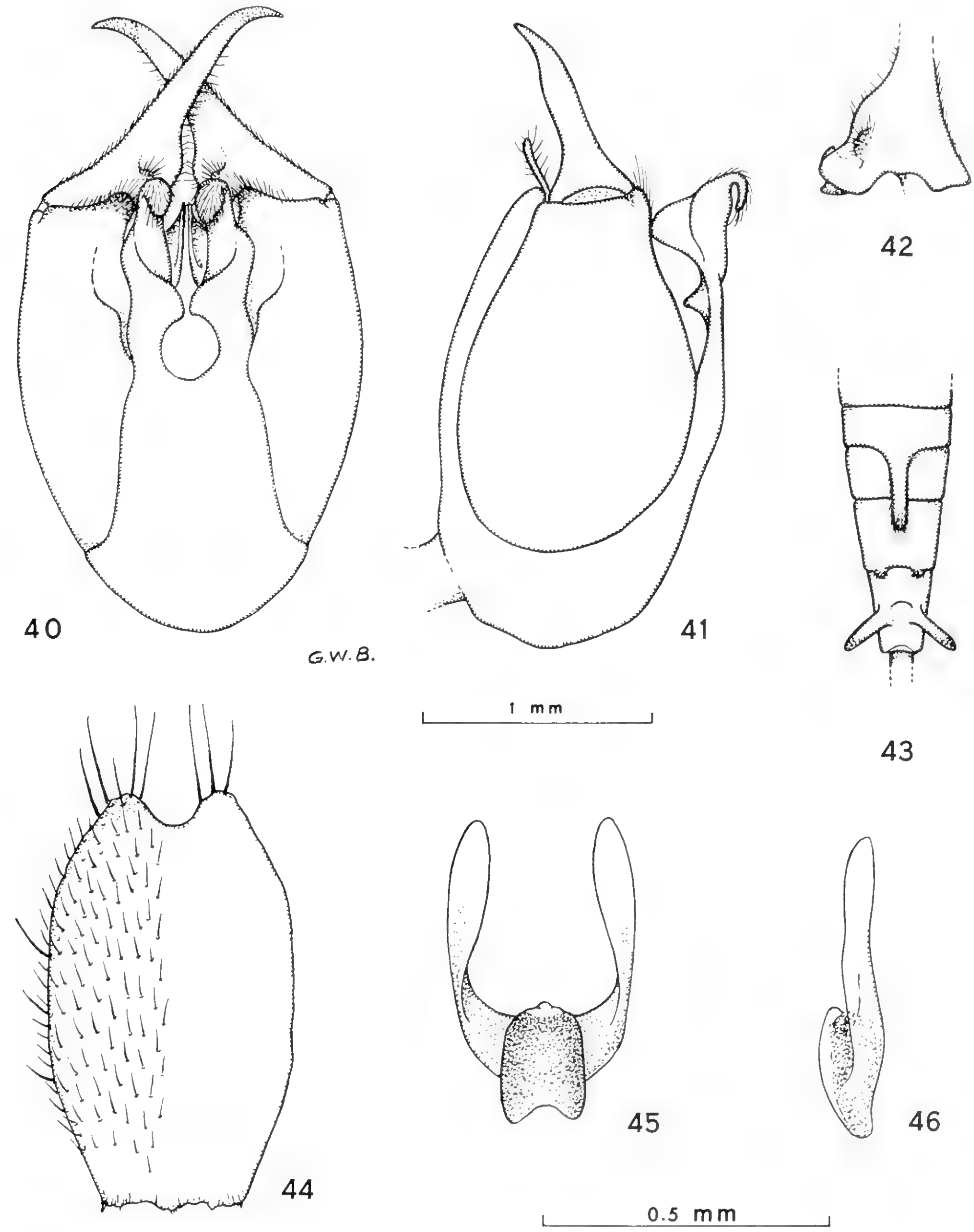
The following redescription is based on examination of the male lectotype, one male syntype from which the genital bulb is missing, two female syntypes and the original description:

Head: Vertex blackish brown, frons and rostrum yellowish brown. Antennal scape, pedicel, and proximal half of basal flagellomere yellowish brown, remaining 43 segments blackish brown.

Thorax: Pronotum black. Anterior half of mesoscutum dark brown, posterior half and mesoscutellum yellowish. Metanotum yellowish with semicircular dark brown spot on anterior margin. Pleural areas and coxae yellowish to yellowish brown. Legs yellowish, apices of tarsi dark brown to black. Wing membrane with faint yellowish tinge, markings pale smoky brown. Cross-veins in distal portion of wing whitish, in proximal portion brown. Apical band incomplete, abruptly truncate posteriorly at M_1. Pterostigmal band narrowly connected to apical band along costal margin, greatly constricted at vein R_2, forked posteriorly. Marginal spot slender, extending from R_1 to M_1. Basal band incomplete, comprising faint spot near base of Rs and wide spot extending from hind margin to Cu_2.

Abdomen of Male: Terga 2-5 dark brown; anterior half of tergum 6 dark brown, posterior half yellowish brown; segments 7-9 yellowish brown. Sterna 2-9 yellowish brown. Posterior process of third tergum (fig. 43) extends to basal one-third of fifth tergum, slender at base, cylindrical in cross-section entire length. A small protuberance on each side of posterolateral margin of fifth tergum. Posterior half of sixth tergum greatly elevated (lateral aspect), with two diverging, finger-like, yellowish brown projections abruptly blackened at apices. Hypovalves with a large dorsal protuberance at apex, smaller dorsomedian protuberance; inner margin concave in basal half (figs. 40, 41). Lateral margins of dististyles slightly concave in basal half; basal lobes directed mesad, each with a blunt, flattened tooth on anterodorsal margin and a more rounded posterodorsal tooth; adjacent ventral protuberance with stiff hairs (fig. 42). Tergum 9 terminating at base of dististyles.

Abdomen of Female: Terga brown, sterna yellowish brown. Subgenital plate deeply notched, with several long spines at apex (fig. 44). Arms of genital plate broad, 0.4 of total length. Anterior margin of



Figs. 40-46. *Neopanorpa cornuta* Esben-Petersen. 40, genital bulb, male lectotype, ventral aspect; 41, genital bulb, left lateral aspect; 42, base of right dististyle, ventral aspect; 43, third to sixth abdominal segments, male lectotype, dorsal aspect; 44, subgenital plate, female syntype, ventral aspect (lower scale); 45, genital plate, ventral aspect (lower scale); 46, genital plate, right lateral aspect.

genital plate shallowly emarginate (figs. 45, 46).

LENGTH OF FORE WING: Both male and female syntypes, 12.5-15 mm.; hind wings: 11.5-13.5 mm.

SYNTYPES: 4 males, 6 females, N. Khasia Hills (N. Khasi Hills), Assam date unknown; in the British Museum (Natural History), London; from the same locality, 2 females in the Museo de Ciencias Naturales, Barcelona, and 1 male, 1 female in the Universitetets Zoologiske Museum, Copenhagen. There is an additional male in the British Museum, the label of which reads "Assam, 1901-262." This may be one of the missing male syntypes. To prevent confusion in the future, the male syntype in the British Museum (Natural History) bearing a white label with a red circle around the word "type" is hereby designated as the lectotype.

In wing pattern, this species somewhat resembles *N. chillcotti* Byers from Nepal and *N. burmana* Byers from Burma, and closely resembles *N. gibbosa* n. sp. from Simla, India. But the wing membrane of *cornuta* is clear, not with a strong yellowish tinge as in *chillcotti,* and the wings are slightly smaller. The basal band in *burmana* is nearly complete, not consisting of two spots as in *cornuta.* The wing pattern of *gibbosa* is nearly identical to that of *cornuta* but slightly lighter in color.

Two Himalayan species, *N. gibbosa* and *N. furcata,* have the posterior part of abdominal segment 6 in the male modified, but in each the shape is diagnostic of the species and quite different from that in *cornuta.* Some undescribed species from northern Burma have hypovalves similar to those of *cornuta* but these can easily be recognized by the absence of prolongations of the sixth segment and by their distinctly yellowish seventh and eighth abdominal segments. Two Chinese species, *N. pielina* Navás and *N. mutabilis* Cheng, have deeply cleft ventral parameres similar to those of *cornuta* but are otherwise unlike *cornuta* in genitalia.

The genital plate in *cornuta* closely resembles that of several species from northern Burma (undescribed), western China, and Indo-China in having long, twisted spatulate arms and a short, stout axial portion. The deeply notched subgenital plate of *cornuta* also resembles that of many of these species.

Neopanorpa effusa (NAVÁS)

Campodotecnum effusum Navás, 1914: 429, fig. 7.

Leptopanorpa effusa; Esben-Petersen, 1921: 91-92, fig. 101.

Esben-Petersen (1921) referred to a male type specimen, but mentioned nothing of the female syntype. He was somewhat reluctant to transfer this species to *Leptopanorpa* because of the relatively short, stout seventh and eighth abdominal segments, as compared to those in other species of *Leptopanorpa,* the sessile genital segment, and the long, setose ventral parameres, not found in *Leptopanorpa.* In addition, the single basal lobe of the dististyle and the width of the wings indicate that this species is a *Neopanorpa.*

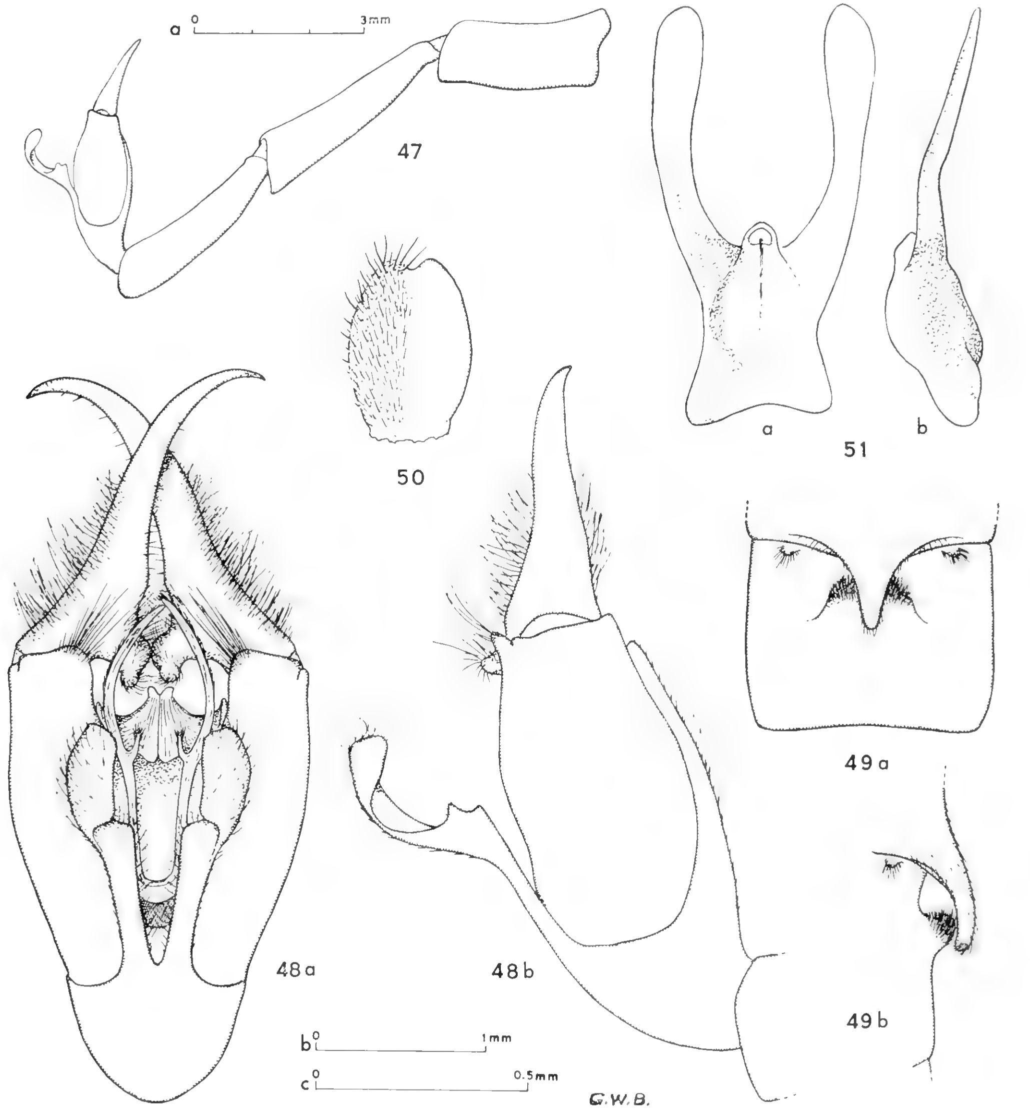
Navás' (1914) original illustrations are small and lack detail. Esben-Petersen (1921) illustrated only the fore wing of the male syntype. The following composite redescription is based in part on notes and drawings of the male syntype:

HEAD: Vertex brownish black; frons and rostrum brown; maxillary palpi yellowish brown. Antennal scape yellowish; pedicel yellowish with dark brown apex; proximal half of basal flagellomere blackish, remaining segments dark brown.

THORAX: Pronotum black. Anterior half of mesoscutum black, posterior half of mesoscutum and scutellum yellowish brown. Metanotum yellowish brown. Pleural regions yellowish brown. Legs yellowish, except distal tips blackish.

Wing membrane with strong yellowish tinge; longitudinal veins yellowish, slightly darker than membrane; markings dark brown. Apical band complete, its proximal margin oblique in posterior half. Pterostigmal band complete, forked posteriorly, with branches of sub-equal width. Basal band complete from R_1 to hind margin.

ABDOMEN OF MALE: Terga and sterna 2-6 brown, 7-9 yellowish brown. Posterior process of third tergum (figs. 49a, 49b) somewhat triangular, extending almost to mid-length of fourth tergum. Two small, hair-covered protuberances on anterior margin of fourth tergum. Seventh and eighth segments (fig. 47) each about 3.5 mm. long. Lateral and inner margins



FIGS. 47-51. *Neopanorpa effusa* (Navás). 47, terminal abdominal segments, male syntype, right lateral aspect (scale a); 48a, genital bulb, ventral aspect; 48b, genital bulb, right lateral aspect; 49a, third and fourth terga, dorsal aspect; 49b, third and fourth terga, left lateral aspect; 50, subgenital plate, female ventral aspect; 51a, genital plate, ventral aspect; 51b, genital plate, right lateral aspect.

of proximal two-thirds of hypovalves straight, distal one-third curved and arched ventrad with long hairs on ventral surface (figs. 48a, 48b). Diststyles (fig. 48a) long, nearly equal to length of basistyles; long, dense hairs on proximal two-thirds of lateral margin; basal lobes directed ventrad, not cupped, with long hairs on apices. Ventral parameres setose, slender, long, extending between bases of diststyles. Apices of ventral valves slightly divergent.

ABDOMEN OF FEMALE: Subgenital plate (fig. 50) roughly oval, its apex shallowly indented. Genital plate (figs. 51a, 51b) with short, stout axial portion, long broad arms bent angularly dorsad near mid-length, and with short, thick anterior apodemes connected by a sclerotized lamella.

BODY LENGTH: Male syntype, 21 mm.; female syntype, 12 mm.

LENGTH OF FORE WING: Male and female syntypes, 16 mm.

LENGTH OF HIND WING: Male and female syntypes, 14.5 mm.

SYNTYPES: Male and female, Sikkim, collected by Felder, date unknown; in the Naturhistorisches Museum, Wien.

In addition, the following specimen has been identified: 1 female, 87 km. N. of Phuntsholing, Bhutan, 22 May 1972, in Naturhistorisches Museum, Basel, Switzerland.

By mistake, the original identification labels of both the male and female syntypes read "*Campodotecnum falcatum* Nav., Navás S. J. det." Additional labels reading "*Campodotecnum effusum* Navás" and "*Leptopanorpa effusa* Navás, Esben-Petersen" appear to have been written by Esben-Petersen.

In wing pattern, this species resembles the other large Himalayan species in having broad apical and pterostigmal bands and the membrane strongly yellowish-tinged. The basal and distal branches of the pterostigmal band of *effusa* are subequal in width, while the distal branch is narrower in *furcata*. The basal band is nearly complete in *effusa*, not consisting of a large spot along the hind margin as in *furcata* and *flava*.

In *effusa*, the long, slender, setose ventral parameres are very diagnostic and have somewhat the appearance of those found in many species of *Panorpa*. The basal lobes of the diststyles are also unusual in that they are not cupped on either the ventral or mesal surface. Mesonotal-metanotal color pattern will differentiate *effusa* from *flava* (Byers, 1975).

Neopanorpa fenestrata (NEEDHAM)

Panorpa fenestrata Needham, 1909: 195-196, figs. 13-15.

Neopanorpa fenestrata; Esben-Petersen, 1915: 230.

Unfortunately, the male holotype could not be obtained from the Indian Museum, and Needham's original description is not very informative. Esben-Petersen (1915) transferred this species to *Neopanorpa*, but it seems that he did not examine the holotype and in his world monograph (1921) only quoted Needham's description. The genital bulb resembles that of *Neopanorpa*, but the wing venation has never been confirmed.

Needham's (1909) illustrations of the genital bulb are small and lack detail. The following is derived entirely from the original description:

HEAD: Dorsum black, lateral margins of rostrum and basal segment of antennae somewhat reddish. Antennae 11 mm. long.

THORAX: Dorsum black; pleural areas paler, somewhat reddish. Wing membrane hyaline. Apical band present. Pterostigmal band forked posteriorly. Basal band fused with marginal spot, enclosing a hyaline spot on costal margin. Basal spot present.

ABDOMEN OF MALE: Terga and sterna 2-6 black, 7-9 reddish. Posterior process of third tergum short, extending about one-third length of fourth tergum. Hypovalves long, extending beyond bases of diststyles, their inner margins contiguous in distal half; inner margins folded under lateral margins at base, forming a dorsal protuberance. Aedeagus extends between diststyles.

Length of Body: Male holotype, 15 mm.; expanse of fore wings 28 mm.

Holotype: Male, Assam, date unknown; in the Indian Museum, Calcutta.

Neopanorpa flava Esben-Petersen

Neopanorpa flava Esben-Petersen, 1915: 225-226.

This species was originally described from the female holotype only. It is one of the largest Neopanorpas known, its fore wings being 18.5 mm. long. This was probably the reason that Esben-Petersen felt that when the male was discovered the species might be transferred to *Leptopanorpa*. But *flava* has not only large but also broad wings, a long but stout abdomen, and a genital plate and bi-colored thorax that are similar to those of *N. furcata* and *N. effusa*.

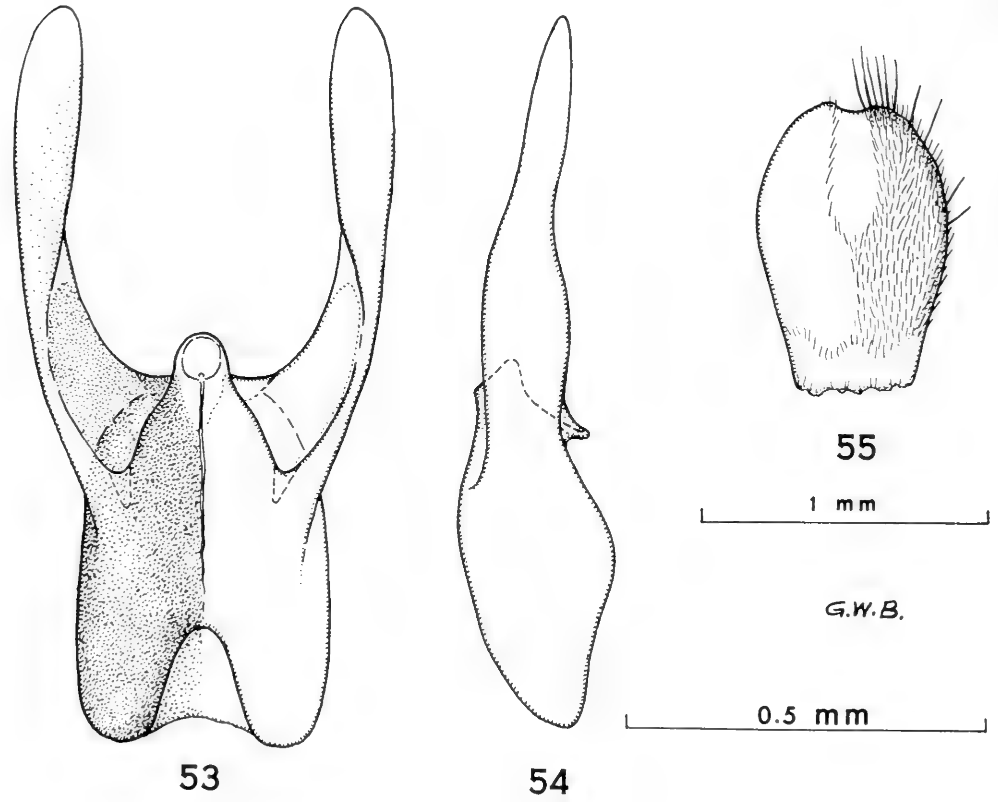
The original description dealt fairly adequately with coloration. The following composite redescription is based on notes and drawings of the female holotype and one additional female specimen:

Head: Dorsum black; frons and rostrum yellowish brown. Antennal scape, pedicel, and first flagellomere yellowish brown; remaining flagellomeres blackish brown.

Thorax: Pronotum black. Anterior two-fifths of mesonotum black, changing abruptly to yellowish brown posteriorly. Metanotum similar, except only anterior one-third to one-half black. Pleural areas, coxae, and legs yellowish brown. Wing (fig. 52) membrane with strong yellowish tinge, markings dark brown, longitudinal veins brownish through spots and bands, yellowish in uncolored membrane, cross-veins in distal portion of wing pale. Apical band complete but uneven, posterior edge deeply and broadly emarginate. Pterostigmal band complete, widely separated along costal and hind margins from apical band, greatly constricted at first fork of R_{2+3}, forked posteriorly. Marginal spot small, not in contact with costal margin (holotype). Basal band incomplete, comprising small spot near base of Rs and wide band extending from hind margin of wing almost to M. Basal spot absent.

Abdomen of Female: Terga 2-3 black-

Fig. 52. *Neopanorpa flava* Esben-Petersen, female, right wings (fore wing length 17.8 mm.).



FIGS. 53-55. *Neopanorpa flava* Esben-Petersen. 53, genital plate, ventral aspect; 54, genital plate, right lateral aspect; 55, subgenital plate, ventral aspect (upper scale).

ish brown, 3-4 blackish brown laterally, sordid reddish brown medially, 5-9 sordid reddish brown. Sterna 2-8 sordid reddish brown. Apex of subgenital plate (fig. 55) shallowly emarginate, with long brownish setae in distal one-third. Arms of genital plate (figs. 53, 54) broad, their bases arched dorsad and darkly sclerotized ventrally. Axial portion stout, its anterior apodemes short, thick, rounded at apex, the notch between them mostly closed by a sclerotized lamella.

MALE: Unknown.

LENGTH OF FORE WING: Female holotype, 18.5 mm.

HOLOTYPE: Female, Sikkim, September 1885, Bingham; in the Zoologisches Museum, Humboldt University, Berlin. Additional specimen examined: 1 female, Sikkim, R. P. Bretaudeau, 1894; in the British Museum (Natural History), London.

This species differs from the other two large Himalayan species, *N. furcata* and *N. effusa,* in having a complete apical band and wide pterostigmal band. The very striking color pattern on the mesonotum and metanotum should also prove useful in the recognition of the male when discovered.

There are five species from China and one (undescribed) from northern Burma that have very large wings (fore wings over 15 mm.) Of these species, *N. caveata* Cheng, *N. cavaleriei* Navás, and the Burmese species have markings on the wings. The wing markings of *cavaleriei* are nearly identical in shape to those of *flava*

FIG. 56. *Neopanorpa furcata* (Hardwicke), male, right wings (fore wing length 15.4 mm.).

but slightly lighter in color. The fore wings of *cavaleriei* are 16 mm. long, not as long as those of *flava* (18.5 mm.), and the membrane is nearly clear, not strongly tinged with yellow as in *flava.*

On the basis of the genital plate, *flava* resembles *N. translucida* Cheng from China in having long arms and broad axial portion, but it differs from *translucida* in not having the arms of the distal plate twisted.

Neopanorpa furcata (HARDWICKE)

Panorpa furcata Hardwicke, 1825: 132, figs. 2-6.

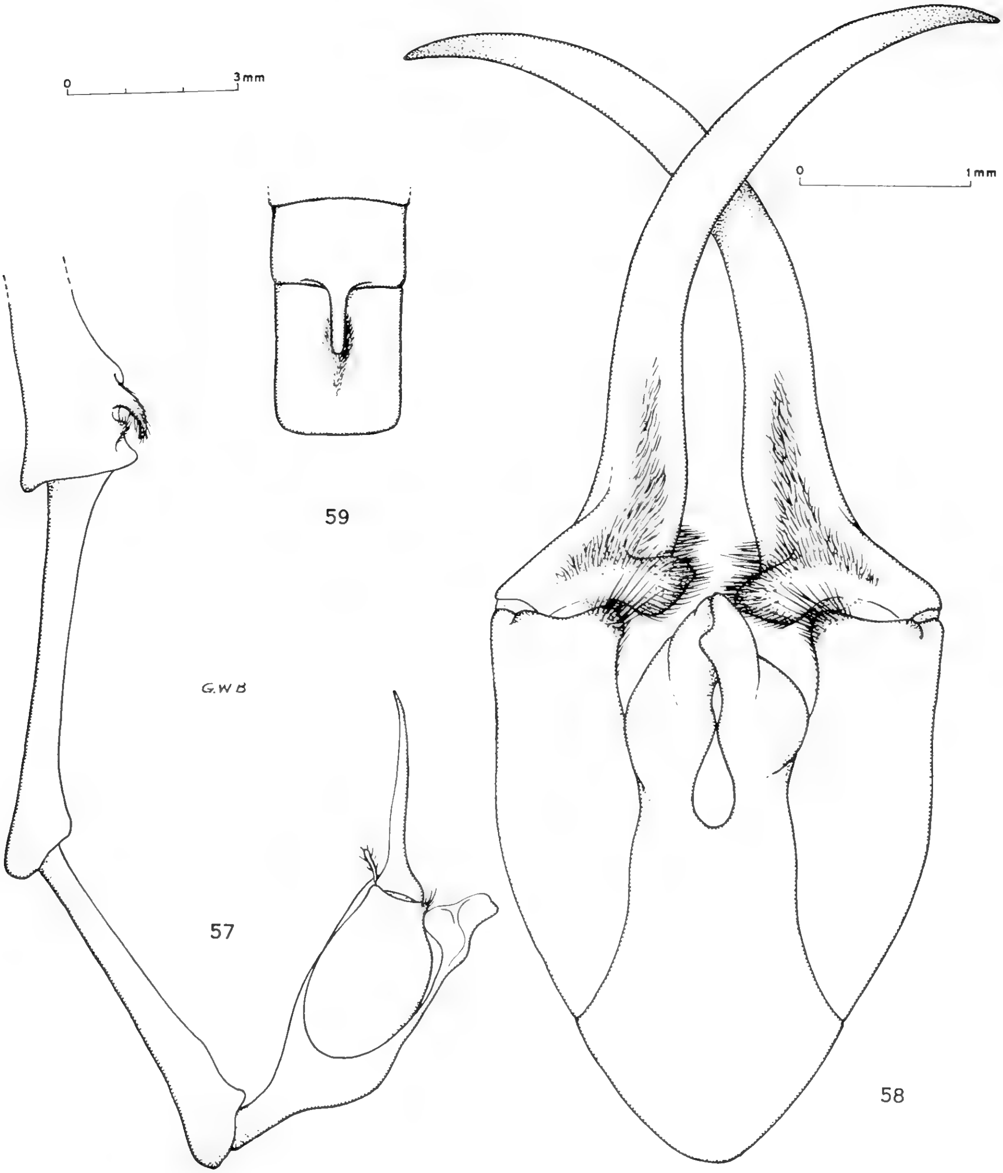
Leptopanorpa furcata; Esben-Petersen, 1915: 231.

Probably due to its wing length (19.5 mm.) and the elongate seventh and eighth abdominal segments of the male, Esben-Petersen (1915) transferred *furcata* from the genus *Panorpa* to *Leptopanorpa.* The undivided basal lobe of the dististyles, the slightly emarginate ninth tergum, the width of the wings, and the shape of the genital plate of the female, however, warrant transferring *furcata* to *Neopanorpa.*

Several inaccurate statements exist in Hardwicke's original description. Originally reported to extend the entire length of the fourth tergum, the posterior process of the third tergum is only half that length. The antennal flagella were also reported to consist of "about 52 segments." Unfortunately, the flagella are now missing from both types, but there are only 46 flagellomeres in other male and female specimens examined. Since little mention had been made of the female by Hardwicke, Esben-Petersen (1921) redescribed the female syntype and gave a brief account of the male syntype from the original description, repeating several of Hardwicke's inaccuracies.

The following redescription is a composite from the original description, Esben-Petersen's redescription, drawings of the male syntype, and study of two additional males and seven females:

HEAD: Vertex black with narrow band of yellowish brown along anterior and lateral margins; frons, genae, and rostrum yellowish brown. Antennal scape yellowish brown, pedicel blackish brown, basal flagellomere brown at base grading to black at apex, remaining segments black. THORAX: Pronotum black, except narrow yellowish brown band along hind margin. Anterior half of mesonotum black, posterior half yellowish brown to black (syntypes). Metanotum yellowish brown to grayish brown (syntypes). Legs



Figs. 57-59. *Neopanorpa furcata* (Hardwicke). 57, terminal abdominal segments, left lateral aspect; 58, genital bulb, ventral aspect (upper right scale); 59, third and fourth terga, dorsal aspect.

sordid yellowish. Wing (fig. 56) membrane with a strong yellowish tinge; longitudinal veins brownish black, except basal portion of subcosta and distal portion of radius yellowish; cross-veins paler, especially in distal portion of wing; markings dark smoky brown. Apical band complete, proximal margin nearly straight. Pterostigmal band wide, forked posteriorly, with distal branch narrow, proximal branch sub-equal in width to anterior part of band. Marginal spot small, between R_{2+3} and R_{4+5}. Basal band incomplete, a large spot extending from hind margin to cell M. Basal spot along hind margin.

Abdomen of Male: Terga and sterna

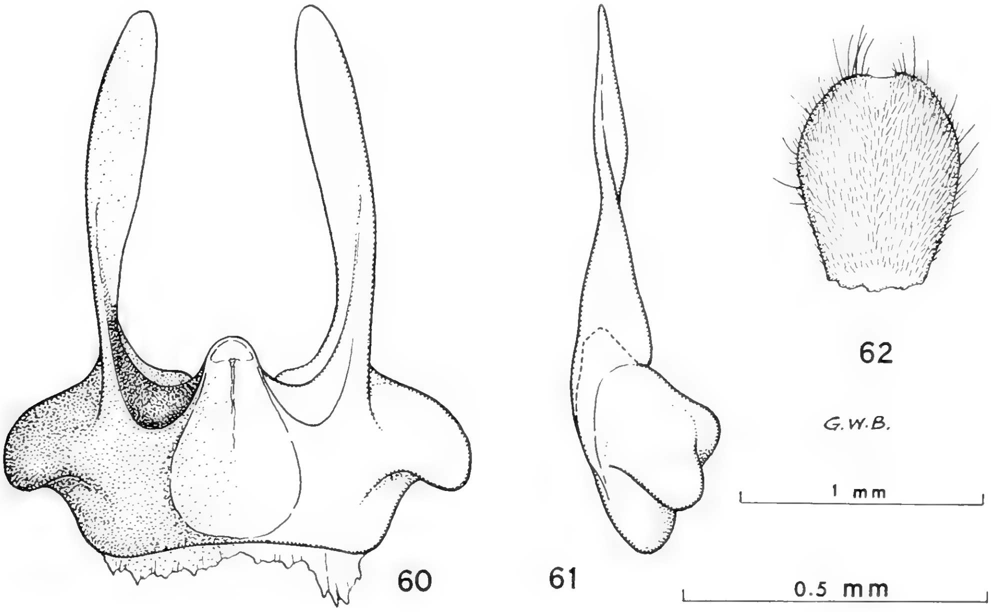
2-9 yellowish brown. Yellowish hairs along posterodorsal margin of third tergum longer than other abdominal pilosity. Posterior process of third tergum extending half length of fourth tergum, apex bluntly rounded, sides of process subparallel (fig. 59). Hairs along mid-line of fourth tergum slightly longer than other pilosity, directed cephalad. Conspicuous rounded, dorsal protuberance on posterior margin of tergum 4. Posterior margin of sixth tergum (fig. 57) with two claw-like projections with long, yellowish hairs on lateral margins; small protuberance at base of each projection densely covered with long hairs. Segment 7 about 7.5 mm. long; segment 8 about 7 mm. long; both segments abruptly more slender than preceding segments, with long hairs on anterodorsal margin. Genital bulb (fig. 58) large, about 7.5 mm. long, exceeding usual proportion to body size and wing length. Outer (lateral) margins of hypovalves (fig. 58) slightly convex; inner margins overlapped and arched ventrad in distal half; large subtriangular projection directed dorsad from mesal margin. Dististyles long, slightly over half length of bulb, slender, with outer margins concave in basal one-third; margins of basal lobe subparallel, apex truncate, lobe directed mesad, covered with long hairs.

Abdomen of Female: Terga 2-9 dark yellowish brown to blackish brown (syntype). Sterna 2-8 yellowish brown. Subgenital plate (fig. 62) slightly emarginate at apex, with long yellowish hairs on distal sides and apex. Arms of genital plate (figs. 60, 61) long, two-thirds of total length, twisted at base, spatulate at apex, with inner basal surface darkly sclerotized. Lateral margins of distal plate projecting, thickened, curved cephalad; anterior margin shallowly emarginate.

Length of Fore Wing: Male, 17.0-19.5 mm. (syntype, 19.5 mm.).

Length of Fore Wing: Female, 15.6-19.0 mm. (syntype, 19.0 mm.).

Syntypes: One male and one female,



Figs. 60-62. *Neopanorpa furcata* (Hardwicke). 60, genital plate, female, ventral aspect (lower scale); 61, genital plate, right lateral aspect; 62, subgenital plate, ventral aspect.

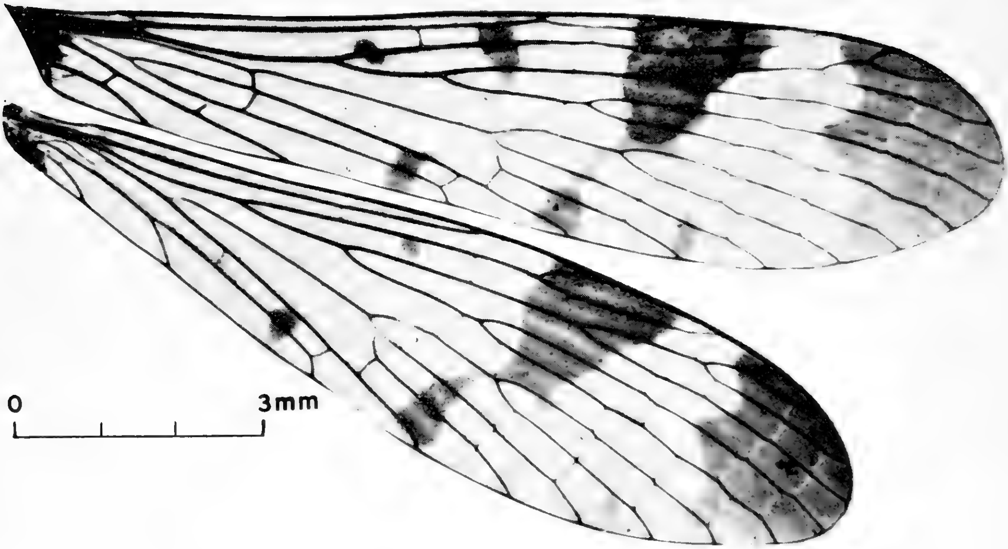


Fig. 63. *Neopanorpa hirsuta* (Crampton), male, right wings (fore wing length 12.4 mm.).

Nepal, no other data; in the British Museum (Natural History), London.

In addition, we have examined the following specimens: 1 male and 2 females, 1 mi. S of Ulleri, Nepal, 5,000-7,000 feet, 16 May 1954, J. Quinlan; 1 male and 1 female, S of Baron River, East Nepal, 11 June 1954, 7,000 feet, L. Swan; all of these are in British Museum (Natural History), London; 1 female, Namdu, Nepal, 1450 m., 18 June 1961; 2 females, Manga Deorati, Nepal, 2300-2500 m., 19 June 1961; 1 female, Solu, Nepal, 2700-2900 m., 11 June 1961; all are in the collection of Dr. H. Janetshek, Innsbruck, Austria.

On the basis of the female genitalia, this species resembles several Chinese species, especially *N. claripennis* Carpenter, in having a broad genital plate, darkly sclerotized inner, basal surface of the arms of the genital plate, and no apodemal processes. Body size and wing pattern of *furcata* are similar to those of another large Himalayan species, *N. flava,* but the genital plate of *flava* lacks the large transverse distal plate and the darkened basal surface of the arms and has a somewhat elongate axial portion.

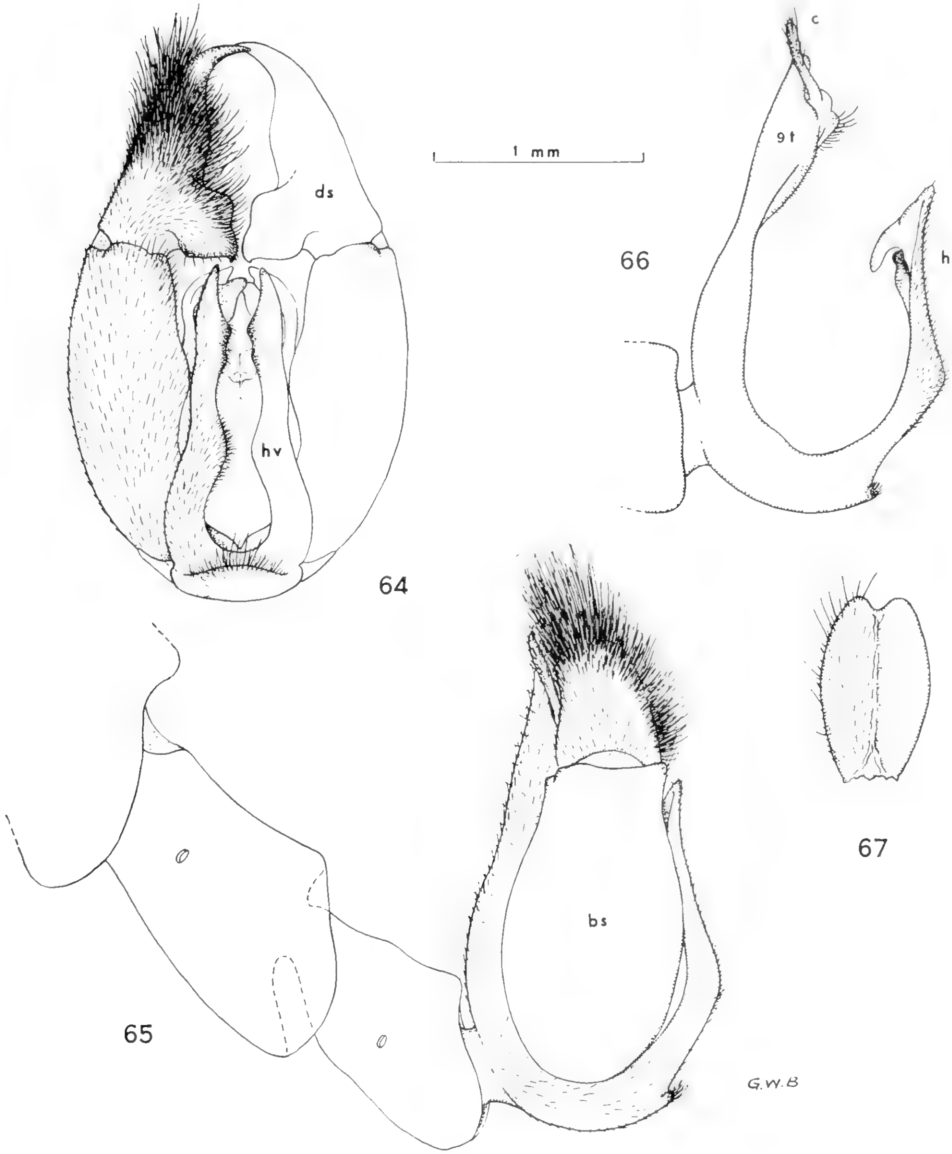
The male of *furcata* can easily be recognized by the modifications of the sixth abdominal tergum and by its genital bulb, which is over twice the size of that of most species of *Neopanorpa.* The seventh and eighth abdominal segments are extremely elongated, but they are of greater diameter than their similarly elongate counterparts in some species of *Leptopanorpa,* and the entire body of *N. furcata* is more robust than that of any typical *Leptopanorpa.*

Neopanorpa hirsuta (Crampton)

Panorpa hirsuta Crampton, 1931: 10, fig. 23.

Neopanorpa hirsuta; Carpenter, 1931: 184-185, fig. 1.

In a paper concerning the morphology and phylogeny of *Notiothauma reedi,* Crampton published a sketch of the genital bulb of an Indian species, suggesting that if it proved to be undescribed it should be called *Panorpa hirsuta.* Carpenter's (1931) redescription of this single specimen is somewhat brief, and his drawing of the genital bulb lacks certain de-



FIGS. 64-67. *Neopanorpa hirsuta* (Crampton). 64, genital bulb, ventral aspect; 65, terminal abdominal segments, male, left lateral aspect; 66, ninth and tenth segments (basistyles and dististyles removed); 67, subgenital plate, female, ventral aspect; bs—basistyle, c—cercus, ds—dististyle, hv—hypovalve, t—tergum.

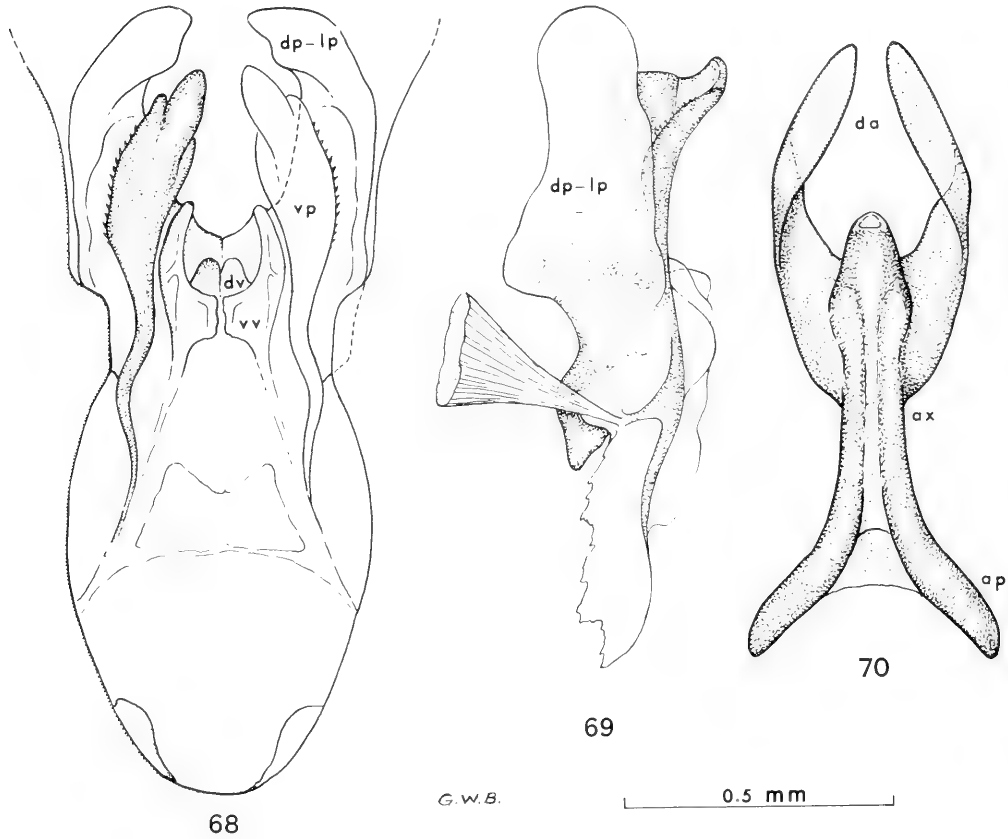
tails; in addition, the notal process is not described.

The following redescription is based on 12 males and 13 females. Eight of the females were collected together with ten males at Naduvatam in the Nilgiri Hills, in May 1958. In wing pattern and body coloration, the females agree with all known males of *hirsuta*.

HEAD: Dorsum, rostrum, and genae light reddish brown to reddish brown. Antennal scape light reddish brown; pedicel blackish brown; flagellum black, with 42-43 segments in females, 44-45 segments in males.

Thorax: Anterior edge of pronotum with short pilosity, no setae. Dorsum, pleural areas and coxae light to dark reddish brown. Femora and tibiae light reddish brown; basitarsi blackish brown grading to black on tarsomeres 4-5. Wing (fig. 63) membrane hyaline, markings light brown (holotype) to dark smoky brown; cross-veins pale in distal portion of wing, brown in proximal portion. Apical band ending posteriorly at tip of M_1 in male, at tip of M_3 in female; clear notch extending from proximal margin almost to tip of M_2 in female. Pterostigmal band wide, forked posteriorly. Marginal spot present, ending near base of M_{4+5}. Basal band incomplete. Basal spot absent.

Abdomen of Male: Terga 2-5 blackish brown to black, 6 blackish brown fading posteriorly and laterally to light reddish brown. Posterior process of third tergum (notal organ) half length of fourth tergum, bent downward over process of fourth tergum. Basistyles deeply separated. Hypovalves (figs. 65, 66) extend full length of basistyles, with distinct transverse ridge at base, lateral margins slightly convex at base and near midlength; hook-shaped dorsal protuberance at apex lightly sclerotized, nearly trans-



Figs. 68-70. *Neopanorpa hirsuta* (Crampton). 68, aedeagus, ventral aspect; 69, aedeagus, left lateral aspect; 70, genital plate, female, ventral aspect; ap—apodemal process, ax—axial portion, da—distal arms, dp-lp—fused dorsal parameres and lateral processes, dv—dorsal valve, vp—ventral paramere, vv—ventral valve.

parent. Tergum 9 extends nearly entire length of bulb, some hairs perpendicular to surface (fig. 64). Tenth sternum with long hairs. Cerci pale at base gradually darkening apically. Dististyles densely set with long black hairs, only tips exposed; basal lobe directed mesad; prominence at dorsal base of lobe bearing tuft of stout black hairs. Aedeagus (figs. 68, 69) elongate, lateral processes and ventral parameres becoming wide, inwardly concave blades, toward apex. Outer lateral margins of ventral parameres with short, thick pale hairs. Lateral processes and dorsal parameres fused, longer than ventral parameres.

ABDOMEN OF FEMALE: Terga 2-6 blackish brown to black, 7-10 dark reddish brown, cerci black. Sterna 2-6 blackish brown to black, 7-8 dark reddish brown. Subgenital plate (fig. 67) deeply notched and ventrally keeled. Arms of genital plate (fig. 70) long, blade-like, twisted 180°, with tips narrowly rounded. Anterior axial portion of genital plate forming two strongly divergent, large apodemes.

LENGTH OF FORE WING: Males, 11.0-14.0 mm. (holotype, 14.0 mm.).

LENGTH OF FORE WING: Females, 11.4-12.1 mm.

HOLOTYPE: Male, Mysore, India, date unknown; in the Museum of Comparative Zoology, Harvard University.

In addition to the holotype, we have seen the following specimens, all collected in South India by P. S. Nathan: 2 males, Chembra Peak area, Kerala State, 3500 feet, May 1970; 10 males, 8 females, Naduvatum, Nilgiri Hills, 6000 feet, May 1958; 1 female, Devala, Nilgiri Hills, 3200 feet, October 1960; 2 females, Gudalur, Nilgiri Hills, 3500 feet, September 1960; all in the Snow Entomological Museum; 1 female, Cherangoda, 1200 m., Nilgiri Hills, November 1950, 1 female, same locality but without date, both in Naturhistorisches Museum, Basel.

This species is aptly named. Males may be recognized from all other species of *Neopanorpa* by the long, dense hairs on the dististyles. The long, narrow, sinuate hypovalves with the dorsal protuberance at the apex are also diagnostic. On the basis of wing pattern, this species closely resembles *N. cantonensis* Cheng from Kwantung, China, but differs in not having a basal spot. The genital plate of the female holotype of *cantonensis* differs from that of *hirsuta* in not having anterior apodemes or a large basal plate.

The aedeagus of *hirsuta* superficially resembles that of other southern Indian species in having long, blade-like ventral parameres and fused dorsal parameres and lateral processes. The short, thick, pale hairs on the outer margin of the apically lobed ventral parameres are diagnostic of *hirsuta*. The aedeagus of *hirsuta* also differs from those of *N. zebrata* and *N. denticulata* in lacking the large mesal extensions of the fused dorsal parameres and lateral processes.

Neopanorpa nipalica (NAVÁS)

Panorpa nipalica Navás, 1910: 288, fig. 1.
Aulops suffusa Navás, 1914: 427, fig. 5.
Neopanorpa nipalica; Esben-Petersen, 1915: 230.

Esben-Petersen (1915) transferred this species from *Panorpa* to *Neopanorpa* and synonymized *Aulops suffusa* with it without stating the reasons. Navás had described *Aulops suffusa* from a single male that was somewhat teneral and badly mashed, especially part of the genital bulb. The wing coloration and processes on the third and fourth abdominal terga of these two male holotypes are nearly identical (figs. 77, 78). Even though the genital bulb of the type of *suffusa* is badly damaged, the shapes of the hypovalves, dististyles, and parts of the aedeagus are recognizable and are very similar to the corresponding structures in *nipalica*.

Esben-Petersen's (1921) redescription of *nipalica* deals adequately with body coloration and wing pattern; however, the process of the third abdominal tergum and the genital bulb were not described in detail. The genital bulb of the male holotype of *nipalica* has not been dissected, and the hypovalves conceal most of the aedeagus. The following redescription is based on examination of the holotypes of *nipalica* and *suffusa* and one additional male specimen:

Head: Antennae about as long as fore wing, comprising scape, pedicel, and 45-46 flagellomeres.

Thorax: Dorsum blackish brown. Wing membrane tinged with brownish gray, unmarked except for light brownish stigma.

Abdomen of Male: Terga 2-9 black, corresponding sterna yellowish brown. Posterior process of third tergum (figs. 76, 77, 78) slender, with apex bent downward, extending nearly entire length of fourth tergum. Dorsal process of fourth tergum mid-length of segment in type of *suffusa,* slightly further caudad in type of *nipalica*. Hypovalves (figs. 71, 72) extend to base of dististyles, lateral margins straight, apices bluntly rounded; inner margins concave in basal one-fourth, separating gradually in distal half. Basal portions of dististyles blackish; basal lobe directed mesad, cupped on dorsal surface; tips of dististyles directed slightly dorsad (lateral view). Aedeagus (fig. 74) with long conspicuous dorsal parameres; ventral parameres slender, somewhat bulbous at apices (fig. 75), which project from genital chamber (fig. 72).

Female: Unknown.

Length of Fore Wing: Male, 12.8-13.8 mm. (holotype, *nipalica,* 12.8 mm.).

Holotype: Male, Sikkim, 1890, Harmand; in the Museum National d'Histoire Naturelle, Paris. Additional specimens examined: 1 male (holotype of *suffusa*), Sikkim, H. Fruhstorfer, in the Naturhistorisches Museum, Wien; 1 male, Darjeeling, Rangiroon, India, 6250 feet, 25 May 1966, Kamath, in the Illinois Natural History Survey collection, Urbana, Illinois.

If the female is similar to the holotype in color, the unmarked wings, black dorsum of the thorax and abdomen and yellowish brown sterna should permit its recognition when discovered. There are several species from the Himalayan region known only from female holotypes, but these differ from the holotype of *nipalica* in having distinct wing markings. On the basis of wing markings, the male of *nipalica* from Darjeeling is closely similar to the female holotype of *N. benaci*. There is a possibility that *benaci* is a synonym.

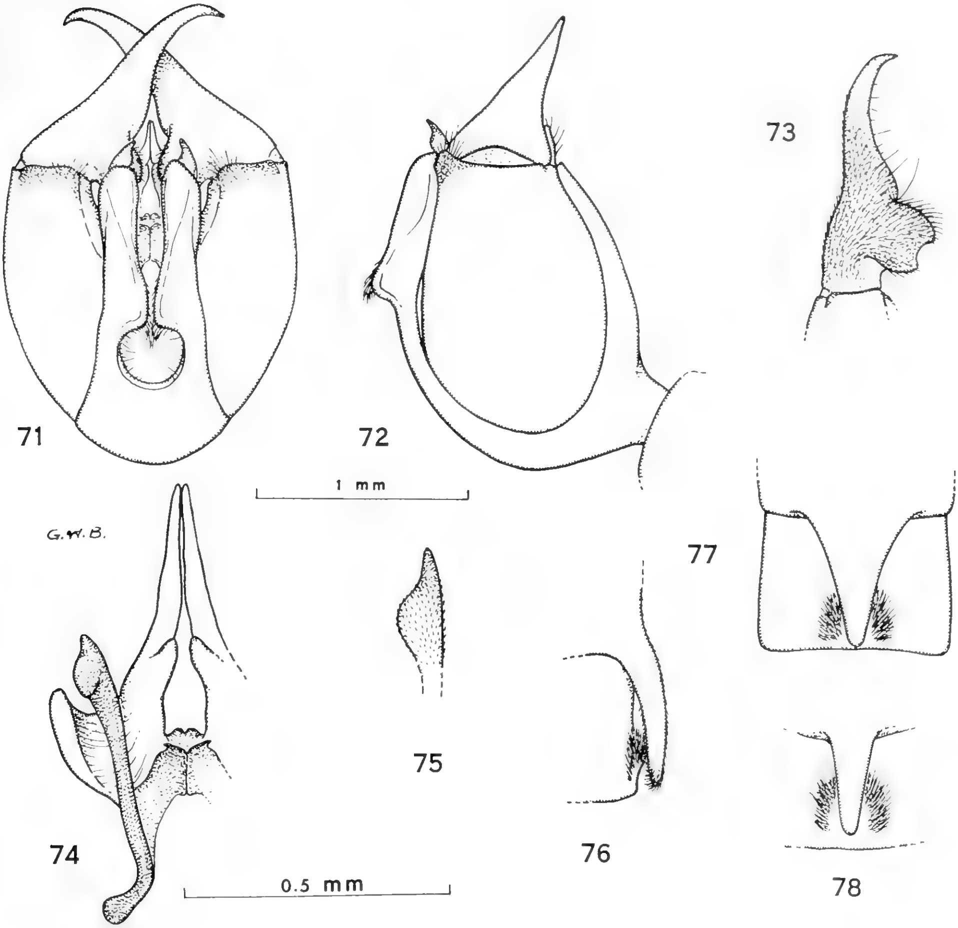
The genital bulb of *nipalica* superficially resembles that of *N. claripennis* Carpenter from China, but the hypovalves of *claripennis* are slightly wider and the notal organ of *claripennis* is short and semicircular in shape, not long and narrow as in *nipalica*. The dorsal parameres of *claripennis* are not as long or narrow as in *nipalica,* and the ventral parameres of *claripennis* are short and filamentous. Several clear-winged species (undescribed) from northern Burma have hypovalves similar to those of *nipalica* but differ in having distinctly yellowish seventh and eighth abdominal segments.

Neopanorpa ocellaris (Navás)

Panorpa ocellaris Navás, 1908: 417.
Neopanorpa ocellaris; Esben-Petersen, 1921: 82-83, fig. 92.

This species is known only from the female holotype from Sikkim. In his redescription, Esben-Petersen (1921) dealt adequately with general body coloration and improved the illustration of the wing characters.

The terminal segments of the female holotype were dissected and the following



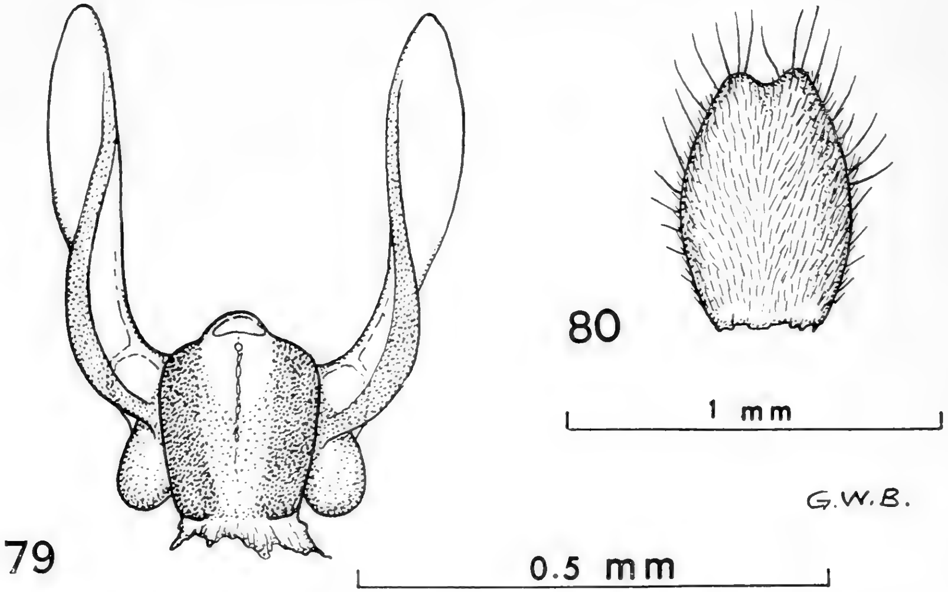
Figs. 71-78. *Neopanorpa nipalica* (Navás). 71, genital bulb, holotype of *nipalica*, ventral aspect; 72, genital bulb, holotype of *nipalica*, right lateral aspect; 73, left diststyle, holotype of *suffusa*, ventral aspect; 74, aedeagus, male, ventral aspect (lower scale); 75, tip of right ventral paramere, male, lateral aspect (lower scale); 76, third and fourth terga, holotype of *suffusa*, left lateral aspect; 77, third and fourth terga, holotype of *suffusa*, dorsal aspect; 78, third and fourth terga, holotype of *nipalica*, dorsal aspect.

brief redescription is based on the notes and drawing this specimen:

Head: Dorsum shiny black; rostrum shiny black, except lateral margins reddish brown. Antennal flagella missing.

Thorax: Dorsum shiny black. Pleural areas and coxae pale grayish brown, except a lateral black stripe on each coxa. Femora and tibiae yellowish brown, except apices of tibiae brown; tarsi light yellowish brown at base, grading to brown at apex. Wing membrane hyaline; markings dark smoky brown. Apical band complete, unusually wide. Pterostigmal band wide, forked posteriorly, distinctly fused to apical band along costal and hind margins. Marginal spot broadly fused to proximal fork of pterostigmal band. Basal band complete, unusually wide. Basal spot large, extending from costal margin to Cu_2.

Abdomen of Female: Terga 2-11 shiny black. Sterna 2-8 pale grayish brown. Apex of subgenital plate slightly notched



FIGS. 79-80. *Neopanorpa ocellaris* (Navás). 79, genital plate, female holotype, ventral aspect (lower scale); 80, subgenital plate, ventral aspect.

(fig. 80). Arms of genital plate twisted, spatulate (fig. 79). Axial portion of genital plate short, thick, with large rounded lobes at base on each side, giving it a broadly triangular shape.

MALE: Unknown.

LENGTH OF FORE WING: Female holotype, 14 mm.; hind wing 13 mm.

HOLOTYPE: Female, Sikkim, 1890, Harmand; in the Museum National d'Histoire Naturelle, Paris.

When the male is discovered, the pattern of the wing markings, the uniformly shiny black dorsum of the thorax, and the black abdomen should permit recognition. On the basis of broad, interconnected

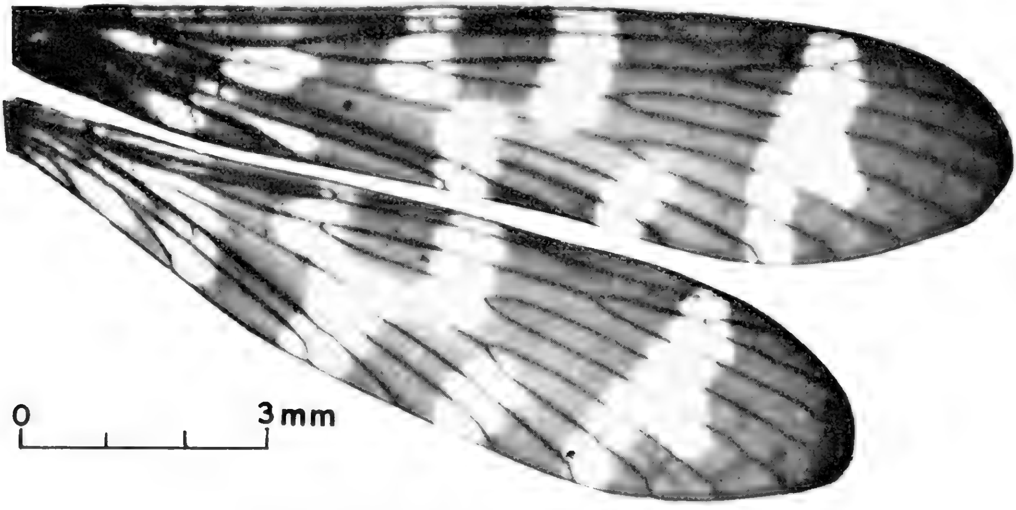
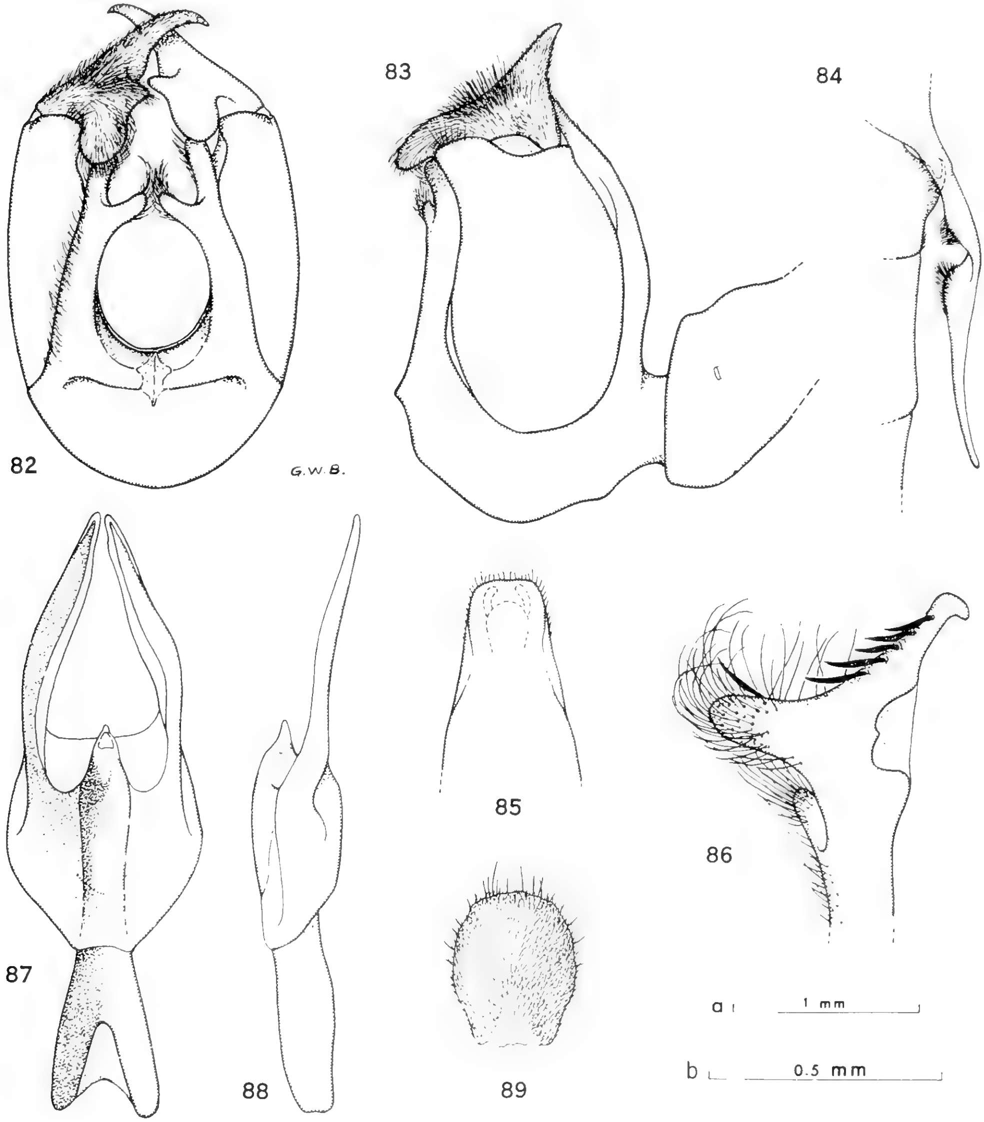


FIG. 81. *Neopanorpa salai* Navás, male, right wings (fore wing length 12.0 mm.).

bands of the wing pattern, this species somewhat resembles *N. ornata* Byers from Vietnam and superficially *N. harmandi* Navás from Vietnam and Thailand (see Byers, 1965). But *ornata* differs from *ocellaris* in having a distinctly bi-colored thorax and brownish abdominal terga. The notched apical band and the unbranched pterostigmal band of *harmandi* differ from those of *ocellaris*.

In *ocellaris,* the gential plate resembles those of some Indo-Chinese species in hav-



FIGS. 82-89. *Neopanorpa salai* Navás. 82, genital bulb, male holotype, ventral aspect; 83, genital bulb, male holotype, right lateral aspect; 84, third and fourth terga, male, left lateral aspect; 85, ninth tergum, male, dorsal aspect (cerci, shown by dashed lines, do not extend beyond margin of ninth tergum); 86, tip of right hypovalve, male, right lateral aspect; 87, genital plate, female, ventral aspect; 88, genital plate, female, right lateral aspect; 89, subgenital plate, female, ventral aspect. Scale a— figs. 82-85, 89; b—figs. 86-88.

ing long spatulate arms and rounded lateral lobes, and in lacking basal (anterior) apodemes. In several Chinese species of *Neopanorpa,* the anterior apodemes are absent, but the shape and size of the basal plate differ from those of *ocellaris.*

Neopanorpa salai Navás

Neopanorpa salai Navás, 1929: 196.

Navás described *salai* from the male holotype only. This species very closely resembles *N. appendiculata* and *N. indica* in general appearance. Until another male and a female of *salai* were discovered among specimens identified as *N. appendiculata,* few characters were known that separated them. There are noticeable differences in the shape of the basal lobes of the dististyles, hypovalves, and posterior process of the third tergum between males of *salai* and *appendiculata.*

This composite redescription is based on notes and drawings of the holotype, one other male, and two females:

Head: Vertex, frons, genae, and rostrum dark yellowish brown. Antennal scape and pedicel dark brown, flagellum blackish brown with 37-38 segments (holotype, 38).

Thorax: Dorsum dark sordid brown. Pleural areas and legs sordid yellowish brown. Wing (fig. 81) membrane hyaline; longitudinal veins brownish, except in distal hyaline spot pale; cross-veins brownish; markings dark brown. Apical band complete, notched in proximal margin or margin straight and hyaline spot included (holotype). Pterostigmal band wide, forked posteriorly with branches sub-equal in width. Marginal spot large, extending from costal margin to first fork of media, fused to pterostigmal and basal bands. Basal band wide, complete. Basal spot large.

Abdomen of Male: Terga 2-9 and corresponding sterna blackish brown. Posterior process of third tergum (fig. 84) long, extending one-third distance across sixth tergum; basal one-third wide, dorsoventrally flattened with ventral tuft of hairs; abruptly becoming cylindrical and tapering to a point. A low sharp ridge across base of hypovalves (figs. 82, 83) with distinct notch at midpoint. Hypovalves somewhat rounded with two long projections (of length sub-equal to width of hypovalves at base) in distal one-half; both proximal, mesal projection and distal ventromesal projection covered with black hairs longest at apex; tips of hypovalves flattened, tapered, directed posterodorsad (into interior of genital bulb), with row of flattened black spines along outer (posteroventral) margin (fig. 86). Entire dististyle covered with blackish hairs longest on basal lobe; basal lobe broad, its bluntly rounded apex directed ventrad.

Abdomen of Female: Terga and sterna 2-6 blackish brown, 7-9 dark sordid reddish brown. Subgenital plate (fig. 89) broad, about three-fourths as wide as long, with long hairs along margin. Genital plate (figs. 87, 88) about 1.25 mm. long; arms of genital plate twisted near base, about one-half total length; anterior apodemal process short, about one-fourth of total length.

Length of Fore Wing: Male, 11.3-13.0 mm. (holotype, 13.0 mm.); female, 12.8 mm.

Holotype: Male, Khandala, India, date unknown; in the Museum National d'Histoire Naturelle, Paris. In addition, the following specimens were examined: 1 male, Bombay, India, and 1 female, India, place and date unknown, both in the British Museum (Natural History), London; 1 female, Coimbatore, Madras, South India, October 1951, in the Naturhistorisches Museum, Basel.

Neopanorpa sordida (Needham)

Panorpa sordida Needham, 1909: 196, figs. 16, 17.

Neopanorpa sordida; Esben-Petersen, 1915: 230.

This species is still known only from one male and two female syntypes from Assam. The original description is somewhat vague, and unfortunately the syntypes could not be obtained from the Indian Museum for further study. According to Needham, the male and one of the female syntypes have unmarked wings. The other female has diffuse bands near the middle of the wing, posterior to the stigma, and distal to the stigma. It seems likely that the more darkly marked female represents a second species.

The following is based entirely on the original description:

HEAD: Dorsum pale brown. Antennae about 10 mm. long (female), their bases tawny yellow.

THORAX: Pronotum pale brown. Meso- and metanotum reddish yellow. Femora, tibiae, and tarsi tawny yellow with brownish apices. Wing membrane smoky-tinged, hyaline, unmarked (1 male and 1 female), longitudinal veins brown; or diffuse pterostigmal band forked posteriorly, oblique apical spot beyond stigma (1 female).

ABDOMEN OF MALE: Basal segments pale brown, terminal segments tawny. Posterior process of third tergum extends half length of fourth tergum. Hypovalves extend to bases of dististyles (apices broken off).

LENGTH OF BODY: Male, 11 mm.; female, 10 mm. Expanse of wings 22 mm.

SYNTYPES: 1 male and 2 females, Khasi Hills, Assam, 5000 feet, May (year unknown); in the Indian Museum, Calcutta.

Neopanorpa zebrata ESBEN-PETERSEN

Neopanorpa zebrata Esben-Petersen, 1915: 228.

This species was originally described from a single female from Travancore, India. A photograph of the wings of the holotype appears in Esben-Petersen's world monograph (1921). With permission of Mr. D. E. Kimmins of the British Museum, the terminal abdominal segments of the holotype were dissected. Several male specimens in the British Museum, tentatively determined to be *zebrata,* are from Periyar Dam, Travancore State, India.

The distal wing markings of the male examined are somewhat smaller and paler but clearly correspond in position to those of the female. In addition, the body coloration of this male is nearly identical to that of the female holotype. This male was collected together with several females of *zebrata.* The following redescription is based on the original description, notes on the female holotype, and one male:

HEAD: Dorsum, frons, and rostrum sordid light yellowish brown. Antennal scape and pedicel sordid yellowish brown; flagellum (broken in holotype) blackish brown, with 38 flagellomeres (male).

THORAX: Short pilosity and four long, black setae on anterior margin of pronotum. Dorsum, pleural areas, and coxae sordid yellowish brown. Femora, tibiae, and tarsi yellowish, with apices of tarsi brown. Wing membrane with light yellowish tinge; markings light brown (male) to smoky brown (holotype); crossveins pale in distal portion of wing, brown in proximal portion. Apical band complete, with a large clear spot extending from R_1 to M_1 in female, absent in male; large notch on proximal posterior margin (holotype), absent in male. Pterostigmal band complete, forked posteriorly, with basal fork constricted at base of M_1 and M_2 (holotype), or incomplete, with posterior branches reduced to two spots (male). Marginal spot large, fused with pterostigmal band in holotype, but not so fused and extending to vein M in male. Basal band complete, constricted at vein

M (holotype). Basal spot large (holotype), absent in male.

Abdomen of Male: Terga 2-4 blackish brown, 5-6 brown, 7-9 sordid yellowish brown. Sterna 2-9 sordid yellowish brown. Posterior process of third tergum (figs. 93, 94) approximately half length of fourth tergum, subquadrate in dorsal aspect, somewhat bulbous at apex; base blackish brown fading to yellowish brown posteriorly. Lateral margins of hypovalves (figs. 90, 96) convex in distal one-fourth; distal half of inner margin with two mesal protuberances, one near mid-length with two setae at apex and one more distal with minute nodules on surface, both with long hairs on mesal surface (fig. 96). Tergum 9 (fig. 92) abruptly narrower in distal portion, apex truncate. Dististyles slightly concave on outer surface near mid-length; basal lobe directed ventromesad, its outer surface with long hairs; prominence at inner base of dististyle (dorsal aspect, fig. 95) with tuft of stout, black setae. Aedeagus (fig. 95) with mesally concave blades extending caudad from lateral processes; blades broad basally, tapering to bluntly rounded apex. Ventral parameres extend between lateral processes and ventral valves, apex of ventral paramere truncate. Dorsal parameres compressed oval blades, narrowly connected at base to lateral processes, posterior edges divergent (fig. 95).

Abdomen of Female: Terga blackish brown, except apical segments brown. Sterna brown. Subgenital plate (fig. 97) strongly keeled ventrally and notched at apex. Arms of genital plate (figs. 98, 99) short, tips bluntly rounded; basal plate somewhat depressed. Apodemes long, nearly straight, slightly divergent near anterior apex.

Length of Fore Wing: Female holotype, 13 mm.; male, 11.6 mm.

Length of Hind Wing: Female, 12 mm.

Holotype: Female, Travancore, date unknown, Hampson; in the British Museum (Natural History), London.

In addition to the holotype, the following specimens are in the British Museum: 3 males, 7 females, Thekkadi, Periyar Dam, Travancore, India, 6-10 May 1937; 1 male, 1 female, Naraikadu, Tinnevelly District, South India, 2500-3000 feet, 3-8 May 1938; 1 male, 1 female, Pirmed, Travancore, 3400 feet, 4-6 May 1937. The illustrations of the male were made from one of the series from Thekkadi, Periyar Dam, now in the Snow Entomological Museum, by exchange.

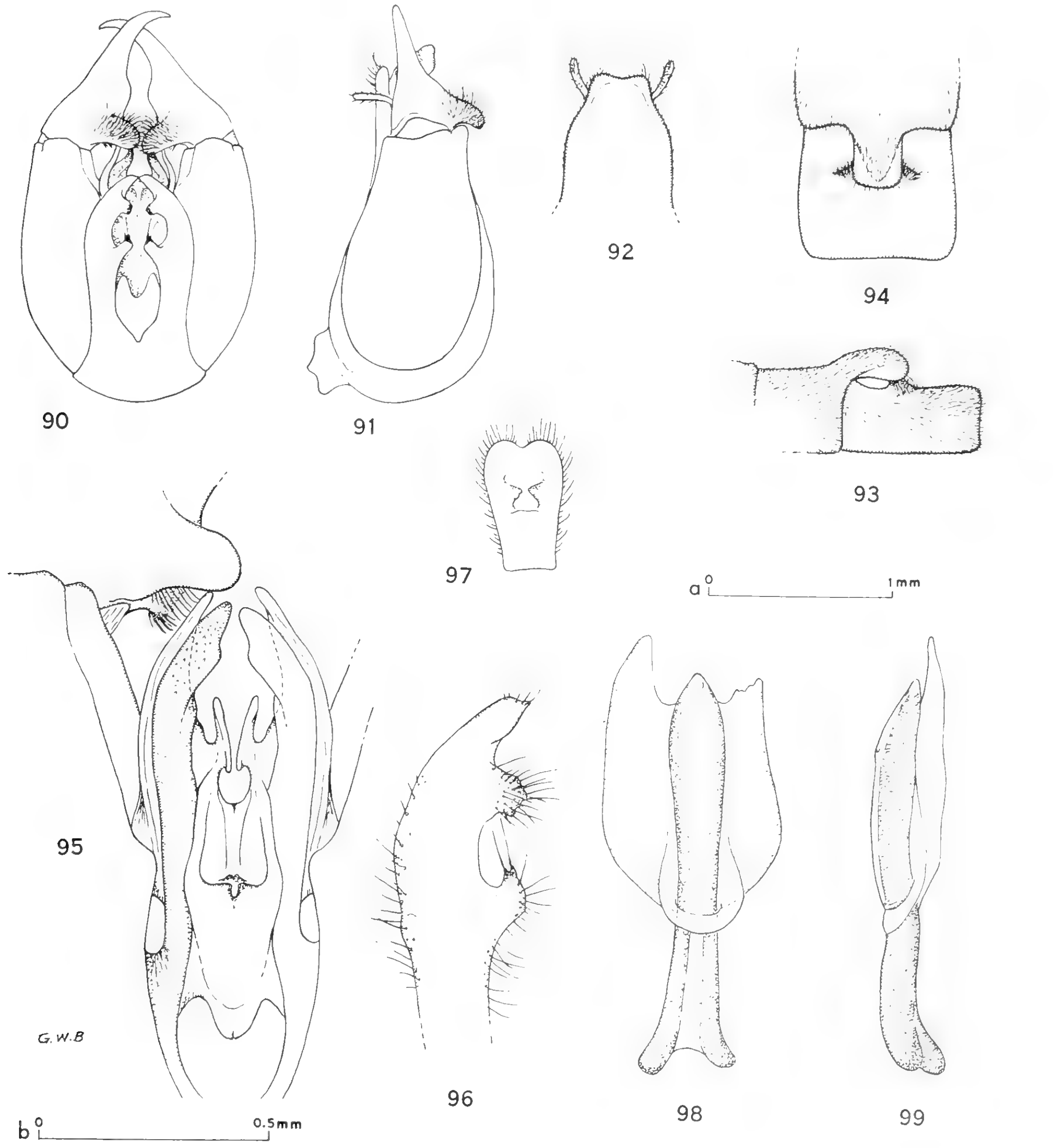
This species can easily be recognized by the large, clear spot in the apical band, especially evident in the female, and by the mesal projections of the inner margins of the hypovalves in the male. The distal wing markings of two Chinese species, *N. chelata* Carpenter (1938) and *N. pielina* Navás (1936), superficially resemble those of *zebrata* in having a large, clear spot in the apical band, but the spot is not nearly as large or centrally situated as in *zebrata*. In addition, these Chinese species lack the extensive basal spots that are present in the holotype of *zebrata*.

On the basis of male and female genitalia, *zebrata* closely resembles the other southern Indian species, especially *N. denticulata* n. sp. In both of these species, the aedeagus bears long, blade-like ventral parameres and fused lateral processes and dorsal parameres. Aside from the southern Indian species, *N. burmana* Byers (1965) from southern Burma is the only known species in which the lateral processes and dorsal parameres have fused, but the ventral parameres of *burmana* (Byers, 1965) are not evident, while they are large in the southern Indian species.

Usually the basal lobes of the dististyles are directed mesad, in *Neopanorpa,* but in *zebrata, appendiculata,* and *indica,* they are directed ventrad; but those of *appen-*

diculata and *indica* are nearly as broad as long, not slender and bluntly rounded as in *zebrata*.

In *zebrata,* the female genital plate superficially resembles that of *denticulata,* but differs in having shorter distal arms and in being more dorsoventrally flattened. The apodemal processes of *zebrata* are not as long or divergent as those of *appendiculata* and *N. hirsuta*.



FIGS. 90-99. *Neopanorpa zebrata* Esben-Petersen. 90, genital bulb, male, ventral aspect; 91, genital bulb, left lateral aspect; 92, ninth tergum, dorsal aspect; 93, third and fourth terga, left lateral aspect; 94, third and fourth terga, dorsal aspect; 95, aedeagus and basal lobe of left diststyle, ventral aspect; 96, tip of left hypovalve, ventral aspect; 97, subgenital plate, female holotype, dorsal aspect; 98, genital plate, holotype, ventral aspect; 99, genital plate, right lateral aspect. Scale a— figs. 90-94, 97; b— figs. 95, 96, 98, 99.

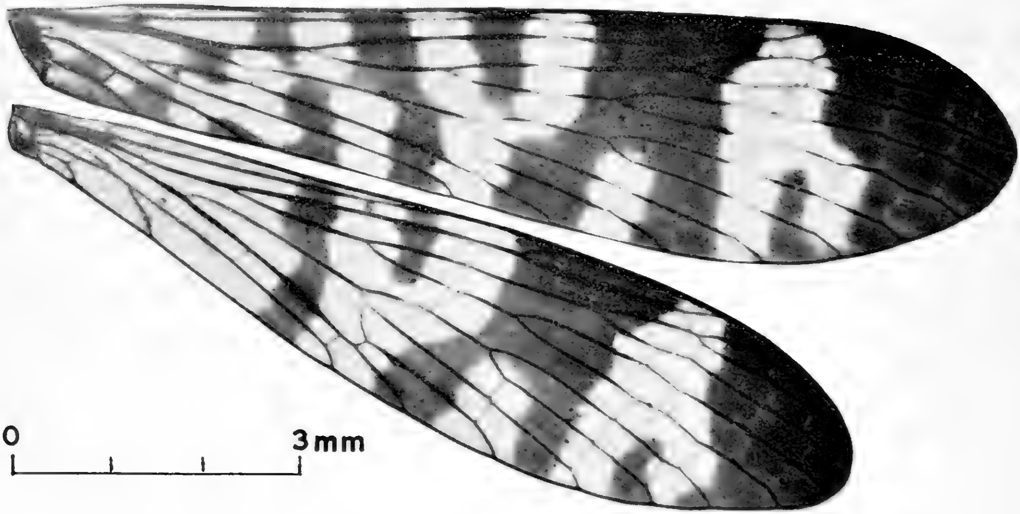


Fig. 100. *Neopanorpa denticulata* n. sp., male paratype, right wings (fore wing length 10.8 mm.).

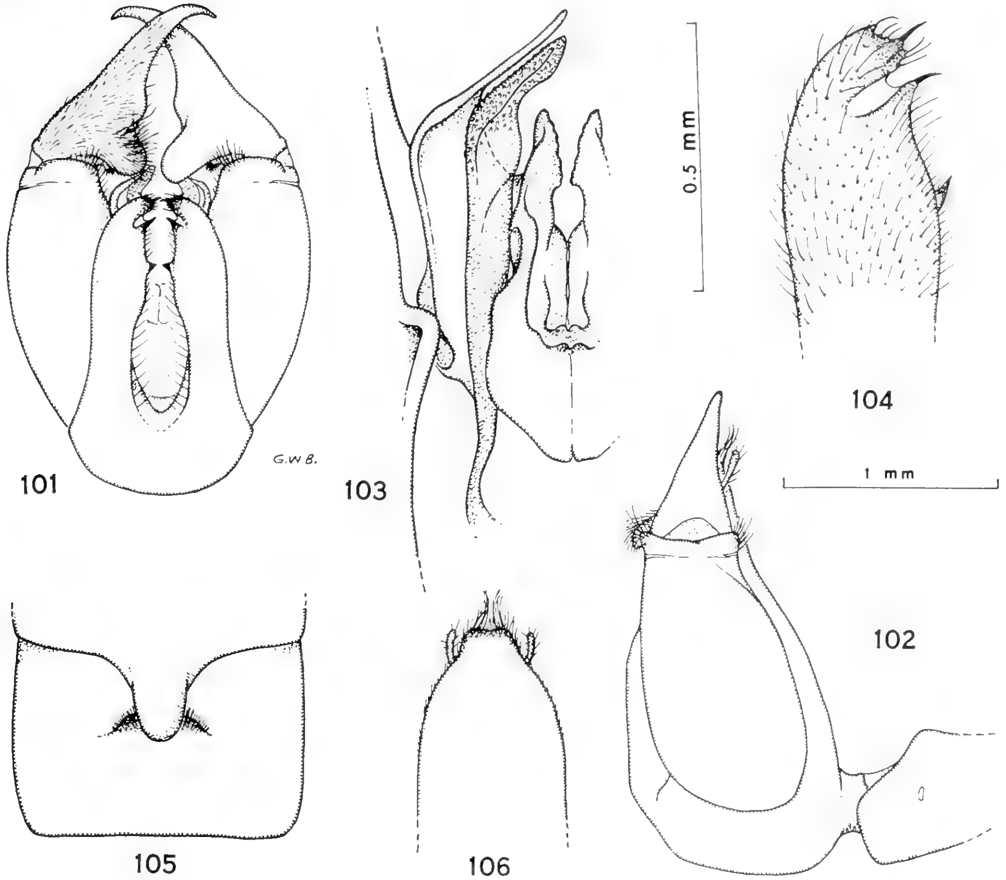
Neopanorpa denticulata New Species

Description based on 150 males and 121 females pinned, 1 male and 13 females in alcohol.

Head: Dorsum, rostrum, frons, and genae sordid yellowish brown (holotype) to dark yellowish brown. Antennal scape yellowish brown; pedicel yellowish brown to dark yellowish brown (holotype); basal portion of first flagellomere dark yellowish brown, remaining flagellum black, with 39-42 flagellomeres (holotype, 42).

Thorax: Short pilosity but no setae on anterior edge of pronotum. Dorsum sordid yellowish brown (holotype) to sordid dark brown; pleural region and coxae yellowish brown (holotype) to dark yellowish brown. Femora and tibiae sordid yellowish brown; tarsi sordid yellowish brown grading to black on segments 4-5. Wing (fig. 100) membrane hyaline, markings brown (holotype) to dark smoky brown. Apical band complete with clear spot or notch at M_1 and M_2 on proximal hind margin (holotype). Pterostigmal band complete, forked posteriorly. Marginal spot variable, sometimes fused with pterostigmal band or with basal band. Basal band variable, partially or completely divided (holotype) into two transverse bands in fore wing (figs. 13, 100). Basal spot present.

Abdomen of Male: Terga 2-5 black; anterior one-third of sixth tergum black, fading posteriorly to dark yellowish brown; terga 7-9 sordid yellowish brown. Sterna 2-8 sordid yellowish brown. Posterior process of third tergum (fig. 105) somewhat triangular, rounded apically, extending half length of fourth tergum. Hypovalves (figs. 101, 104) slightly widened in apical half, then narrowed and abruptly thickened at apex; a mesal thick brown spine on apical enlargement, another on mesal margin just before apex, and a third on dorsomesal margin just beyond mid-length of hypovalves; hypovalves with uniform brown pilosity. Ninth tergum (fig. 106) abruptly narrowed in distal one-fourth, terminating in shallowly emarginate apex with numerous long, brownish hairs. Basal lobes of diststyles directed ventrad (fig. 102), shallowly cupped on dorsomesal surface, with bluntly rounded apices; ventral posterior surface with long blackish hairs; tuft of stout black setae at the dorsal base of lobe. Aedeagus complex (fig. 103), with blade-



FIGS. 101-106. *Neopanorpa denticulata* n. sp. 101, genital bulb, male paratype, ventral aspect; 102, genital bulb, right lateral aspect; 103, aedeagus, ventral aspect (vertical scale); 104, tip of left hypovalve, ventral aspect (vertical scale); 105, third and fourth terga, dorsal aspect; 106, ninth tergum, dorsal aspect.

like ventral parameres and fused lateral processes and dorsal parameres extending between bases of dististyles. Dorsal parameres enlarged, blade-like, directed dorsad.

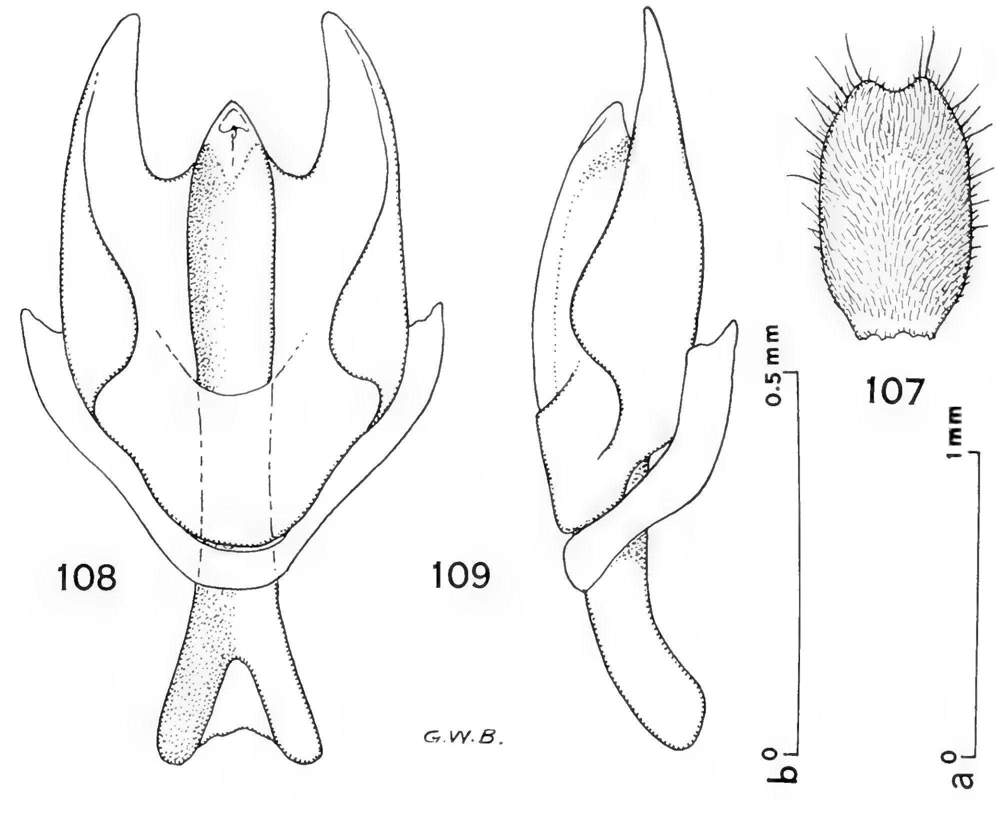
ABDOMEN OF FEMALE: Terga 2-6 black, 7-9 dark yellowish brown. Sterna 2-8 yellowish brown. Subgenital plate (fig. 107) notched apically, with elongate hairs along margins and at apex. Arms of genital plate (figs. 108, 109) short, about one-fifth of total length, slightly curved inward. Apodemes about .3 total length of plate, fused for about half their length, diverging anteriorly. Basal and distal plates broad, with lateral margins of distal plate folded ventrad.

LENGTH OF FORE WING: Male, 10.0-12.0 mm. (holotype, 11.0 mm.); female, 10.3-12.6 mm. (allotype, 12.4 mm.).

LENGTH OF HIND WING: Male, 9.3-10.6 mm (holotype, 10.0 mm.); female, 10.0-11.0 mm.

HOLOTYPE: Male and allotype, female, Devala, Nilgiri Hills, India, 3200 feet, May 1961, P. S. Nathan. Paratypes, 150 males, 133 females: at type locality, May 1961 (120 males, 63 females); type locality, October 1960 (5 males, 6 females); Walayar Forest, Kerala, India, 700 feet, P. S. Nathan, September 1959 (2 males, 9 females), 15 September 1959 (1 male), October 1959 (4 males, 13 females), August 1960 (2 males), September 1965 (1 female); at Chembra Peak area, India, 3500 feet, T. R. S. Nathan, May 1970 (5 males, 6 females), October 1970 (1 female); all in the Snow Entomological Museum; Walayar Forest, S. Malabar, India, 1000 feet, P. S. Nathan, August 1957 (1 male, 9 females), November 1957 (4 females), in the Illinois Natural History Survey collection, Urbana, Illinois; Muthikolam, Coimbatore Dist., India, 3000 feet, 23-26 September 1938 (1 male, 1 female); Siruvani, 1700 feet, 23-26 September 1938 (1 male), in the British Museum (Natural History), London; Cherangoda, Nilgiri Hills, 1200 m., November 1954 (7 males, 14 females), October 1954 (1 male, 3 females), October 1950 (1 male), no date (1 male); Coimbatore, Madras, South India, October 1951 (1 male), in the Naturhistorisches Museum, Basel, Switzerland.

This species superficially resembles in general appearance two regional species, *N. zebrata* and *hirsuta;* and the aedeagus resembles those of *hirsuta, echinata* n. sp., and especially *zebrata,* in having long, blade-like ventral parameres and fused dorsal parameres and lateral processes. The lateral processes and dorsal parameres are also fused in *N. burmana* Byers (1965) from Indo-China, but *burmana* differs from these Indian species in lacking the long, blade-like ventral parameres. In *denticulata,* the dorsal parameres are large, slightly divergent, vertical plates similar



FIGS. 107-109. *Neopanorpa denticulata* n. sp. 107, subgenital plate, female paratype, ventral aspect; 108, genital plate, ventral aspect; 109, genital plate, right lateral aspect. Scale a— fig. 107; b— figs. 108, 109.

to those of *zebrata,* but these plates have a broader connection to the body of the aedeagus than in *zebrata.* The structure of the aedeagus is the primary character used in grouping *hirsuta, echinata* n. sp., *denticulata,* and *zebrata* into the *denticulata* group. It is called the *denticulata* group after the commonest included species.

The basal markings of the wing, the solidly-colored, complete apical band, and the three tooth-like projections on the inner margin of the hypovalves permit easy recognition of *denticulata.* The specific name refers to the three projections of the hypovalves (Latin *denticulus*=small tooth). Some variation in wing pattern, especially the fusion of the two basal bands, was observed in the paratypes from the Walayar Forest.

On the basis of female genitalia, *denticulata* superficially resembles *N. zebrata* in having large, broad basal and distal plates and apodemes subequal in length to the basal and distal plates; but it differs from *zebrata* in having longer arms of the distal plate and a somewhat flattened subgenital plate, not strongly keeled as in *zebrata.*

Neopanorpa echinata New Species

Description based on 2 males, pinned.

Head: Dorsum sordid yellowish brown; frons sordid yellowish brown, with dark brown medial spot; rostrum sordid yellowish brown, edges becoming translucent yellowish brown. Antennal scape sordid yellowish brown; pedicel dark yellowish brown; flagellum blackish brown, with 41-42 flagellomeres (holotype, 42).

Thorax: Short pilosity but no setae on anterior margin of pronotum. Pronotum blackish brown. Medial portion of mesoscutum sordid grayish brown, color extending along midline to scutellum; lateral margins of scutum dark brown. Metanotum similar to mesonotum. Pleural areas and coxae light grayish brown. Femora and tibiae sordid light brown. Basitarsi sordid brown grading to dark brown on segments 4-5. Wings hyaline, except light yellowish brown stigmal spot. Longitudinal veins brownish; cross-veins brown in proximal portion of wing, pale in distal portion.

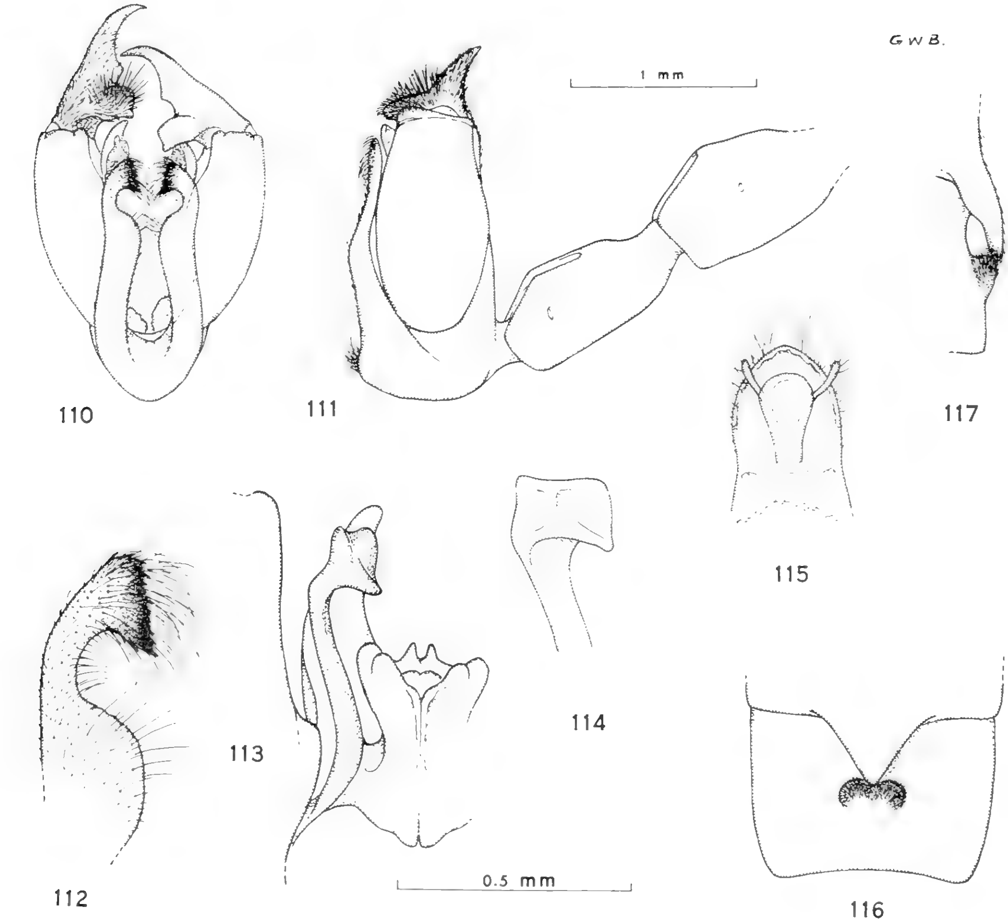
Abdomen of Male: Terga 2-5 blackish brown, 6 dark yellowish brown, 7-9 sordid grayish brown. Sterna 2-9 sordid grayish brown. Posterior process of third tergum (figs. 116, 117), triangular, extending across one-third to one-half length of fourth tergum. Notal process of tergum 4 with short black hairs on anterior two-thirds. Segments 7 and 8 short (fig. 111), each with a dorso-medial trough in its posterior one-half to one-third. Base of hypovalves broad, forming a U-shaped ridge, bearing blackish hairs; hypovalves sinuous (figs. 110, 112), apices with numerous small black spines and long black hairs. Basal lobe of dististyles with concave dorsal surface and long hairs on ventral, posterior surface. Ventral parameres (fig. 113) slender, wedge-shaped apices directed ventrad. Dorsal parameres short, rounded protuberances. Lateral processes of aedeagus long, concave, blade-shaped.

Female: Unknown.

Length of Fore Wing: Male, 11.0 mm. (holotype); hind wings, 9.7-10.0 mm. (holotype, 10.0 mm.).

Holotype: Male, Naduvatam, Nilgiri Hills, India, 6000 feet, May 1958, P. S. Nathan. Holotype and 1 male paratopotype are in the Snow Entomological Museum.

This species can be easily recognized from other regional species by the absence of wing markings, except for a faint stigmal spot, and the narrow, sinuous hypovalves with spiny apices. The specific name (Latin *echinatus*=spiny, prickly)



FIGS. 110-117. *Neopanorpa echinata* n. sp. 110, genital bulb, male holotype, ventral aspect; 111, terminal abdominal segments, right lateral aspect; 112, tip of left hypovalve, ventral aspect (lower scale); 113, aedeagus, ventral aspect, part of right side omitted (lower scale); 114, tip of left ventral paramere, lateral aspect (lower scale); 115, ninth tergum, ventral aspect; 116, third and fourth terga, dorsal aspect; 117, third and fourth terga, left lateral aspect.

refers to the spiny apices of the hypovalves.

On the basis of the aedeagus, this species was placed in the *denticulata* species group. The lateral processes are elongated as in all the other species in this group, but the dorsal parameres of *echinata* are not fused with the lateral processes as in *denticulata* and *zebrata*. The dorsal parameres are not distinguishable in *hirsuta*. The posterior process of the third tergum of *echinata* is triangular, not narrow with subparallel sides as in the other species of the group. The broad, thick base of the hypovalves and the ventral parameres of *echinata* are similar in appearance to those found in several species of the *appendiculata* group.

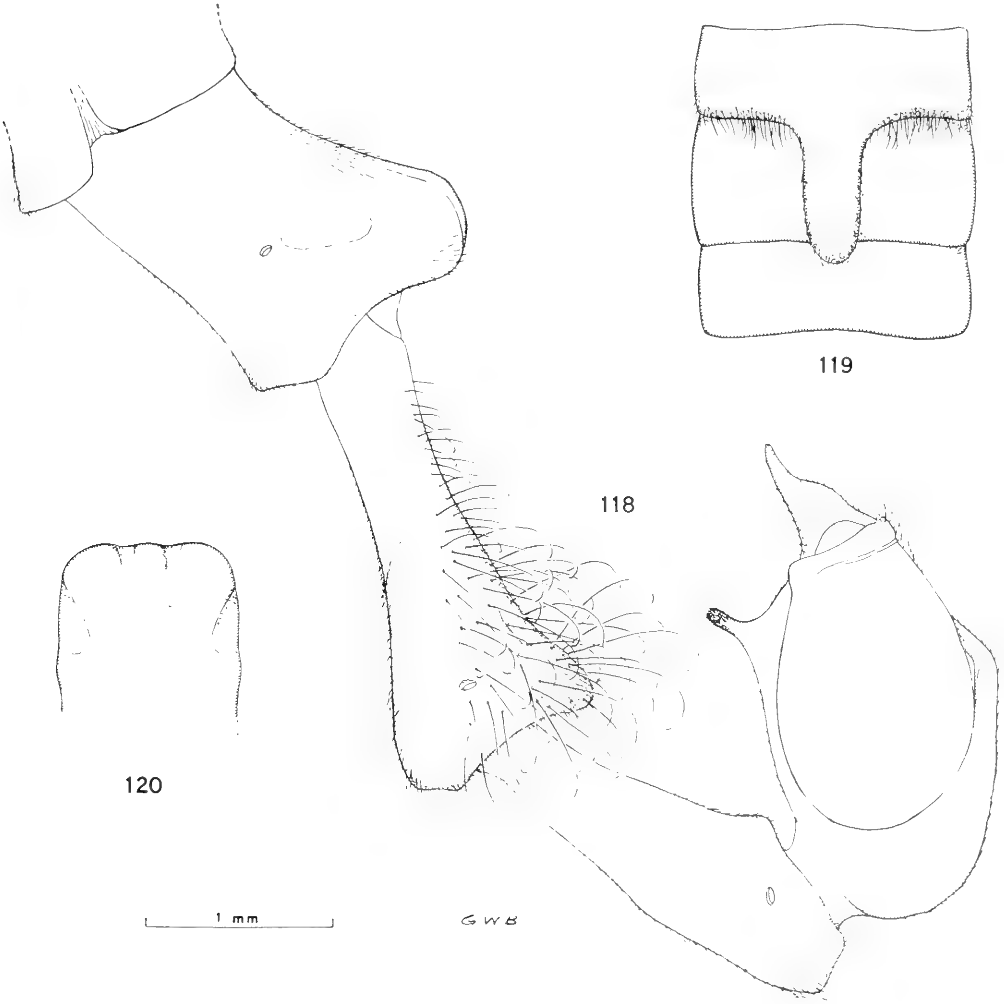
Neopanorpa gibbosa NEW SPECIES

Description is based on one male, pinned.

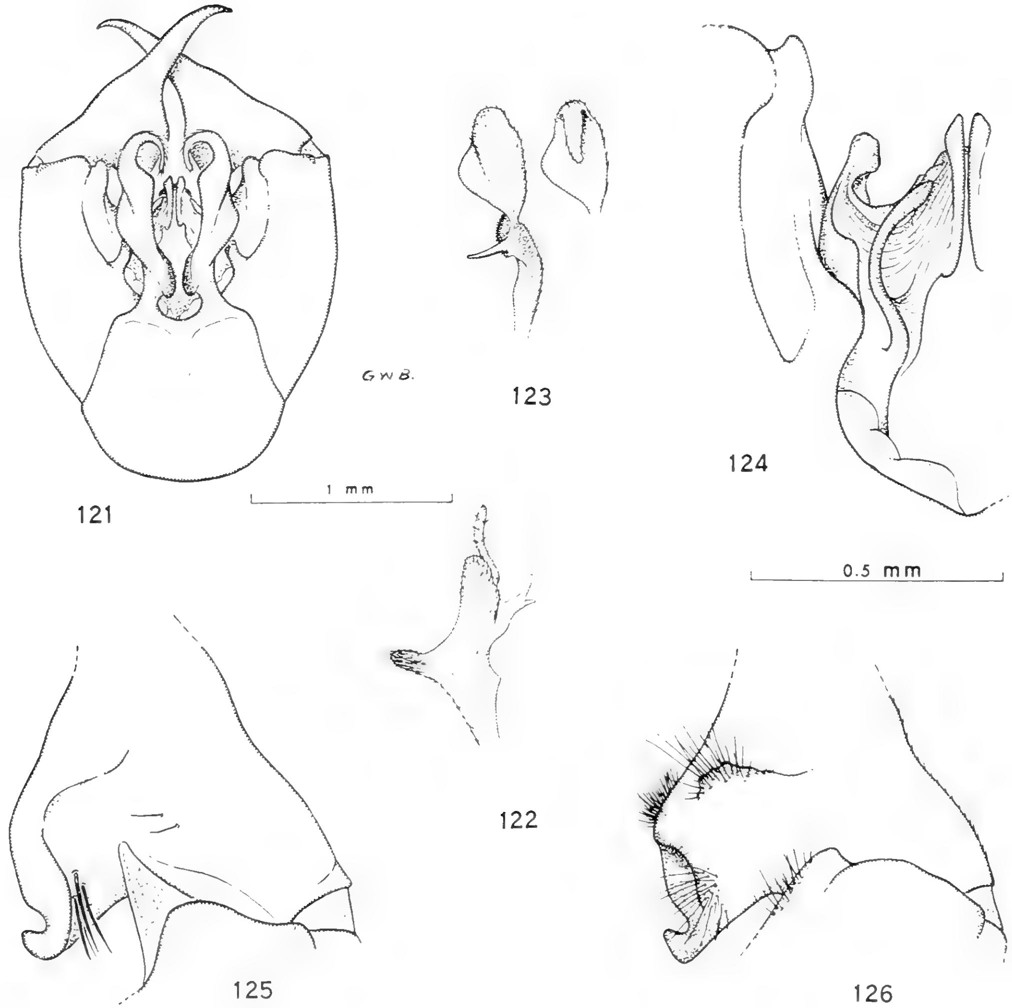
HEAD: Vertex black, rostrum dark sordid yellowish brown, frons and antennal scape and pedicel sordid yellowish brown; antennal flagellum blackish brown, with

43 flagellomeres (left flagellum missing). THORAX: Pronotum blackish brown. Meso- and metanotum blackish brown (metanotum partly obscured by pin), pleural areas grayish brown. Wing membrane hyaline; longitudinal veins brownish, cross-veins brown in proximal half and pale in distal half of wing; markings light brown. Apical band complete. Pterostigmal band constricted near mid-length, forked posteriorly. Marginal spot a narrow band extending from costal margin to basal branch of pterostigmal band. Basal band a small spot near the base of R_s. Basal spot absent.

ABDOMEN OF MALE: Terga 2-3 blackish brown, posterior margin of third tergum and base of posterior process of third tergum with long yellowish hairs, 4-9 yellowish brown. Sterna 2-9 yellowish brown. Posterior process of third tergum (fig. 119) blackish brown, curved downward on fourth tergum, extending across entire length of fourth tergum. Posterior



FIGS. 118-120. *Neopanorpa gibbosa* n. sp. 118, terminal abdominal segments, male holotype, left lateral aspect; 119, terga 3-5, dorsal aspect; 120, posterior portion of sixth abdominal segment, dorsal aspect.



FIGS. 121-126. *Neopanorpa gibbosa* n. sp. 121, genital bulb, male holotype, ventral aspect; 122, distal portion of ninth tergum, left lateral aspect; 123, left hypovalve, left lateral aspect, and apical portion (mesal aspect); 124, aedeagus, left half, ventral aspect (right scale); 125, base of left dististyle, dorsal aspect (right scale); 126, base of right dististyle, ventral aspect.

half of sixth tergum enlarged, curved dorsad into large, broad hump (figs. 118, 120). Posterior half of seventh segment somewhat enlarged with long hairs near posterior margin. Ninth tergum with a median projection extending dorsad near mid-length, with short black pilosity; apex bluntly truncate (figs. 118, 122). Basal petiole of each hypovalve with heavily sclerotized, rounded mesal projection and narrowly triangular dorsal projection; hypovalves broad, thin, laterally flattened lobes. Inner ventral margin of basistyle forms a distinct ridge with a branch leading into interior of bulb. Basal lobe of dististyles cupped mesally, with hair-covered protuberance on posteroventral surface (fig. 126) and 3-4 thick black, dorsal spines (fig. 125). Ventral parameres of aedeagus short, slender, sinuate, convergent at apices. Ventral valves large, thin blades. Dorsal parameres, long, narrow, bluntly pointed blades.

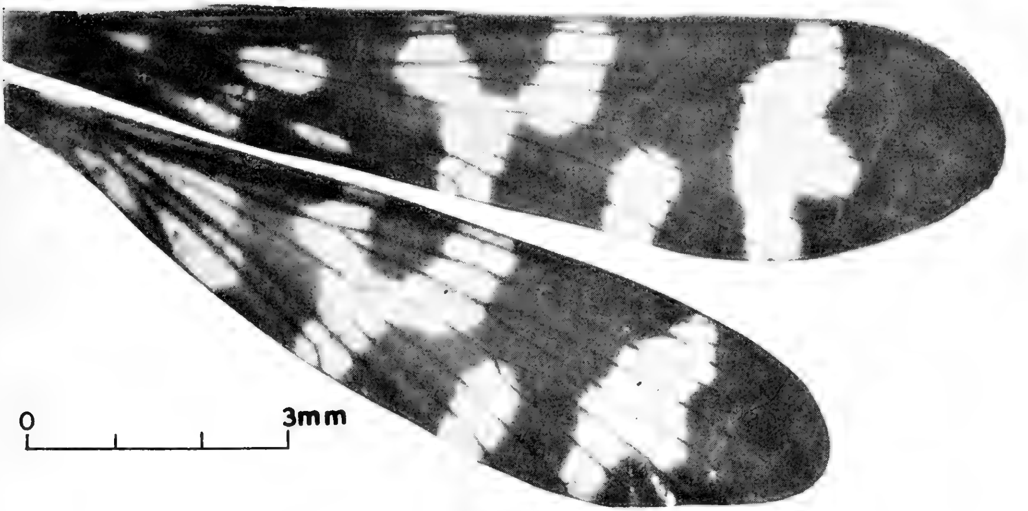


FIG. 127. *Neopanorpa indica* n. sp., male paratype, right wings (fore wing length 11.3 mm.).

LENGTH OF FORE WING: Male holotype, 12.3 mm.; hind wing, 11.0 mm.

HOLOTYPE: Male, Simla, India, from the McLachlan collection in the British Museum (Natural History), London.

On the basis of wing pattern and body coloration, the female should be recognized when discovered. The modification of the sixth tergum and the dorsal projection of the ninth tergum of the male are diagnostic of this species. The specific name (Latin *gibber,* humped, humpbacked, protuberant) refers to this modification. The projection on the ninth tergum is unique among known species of Panorpidae. *N. cornuta* and *N. furcata* have a modified sixth tergum, but in both species it is extremely different from that of *gibbosa.* The aedeagus of *gibbosa,* especially the ventral valves, is similar to that of other northern Indian and Indo-Chinese species.

Neopanorpa indica NEW SPECIES

Description is based on 14 males and 2 females, pinned.

HEAD: Vertex, rostrum, genae, and frons sordid yellowish brown. Dorsum of antennal scape yellowish brown, venter brown; pedicel blackish brown; flagellum black with 39 flagellomeres.

THORAX: Short pilosity, no setae on anterior margin of pronotum. Dorsum sordid dark brown. Pleural areas black. Coxae and femora blackish brown, tibiae pale yellowish brown, tarsi yellowish brown grading to black on segments 3-5. Wing (fig. 127) membrane hyaline; markings smoky brown. Apical band complete with small notch on proximal margin. Pterostigmal band complete, forked posteriorly. Marginal spot large, extending from costal margin to behind R_{4+5}. Basal band complex and variable. Basal spot large.

ABDOMEN OF MALE: Terga 2-9 and corresponding sterna black. Posterior process of third tergum narrow (figs. 130, 131), extending half to three-fourths length of fourth tergum, sordid yellowish brown to dark brown, with bluntly rounded apex. Notal process of fourth tergum (fig. 130) with a tuft of short black hairs. Sternum 9 broad at base (fig. 129), forming interrupted transverse ridge. Hypovalves (fig. 129) stout, rounded basally becoming compressed laterally in distal one-third; small protuberance on mesal margin sparsely covered with long black hairs; posteroventral edge of apex with a row of flattened black setae. Dististyles (fig. 129) about .3 of total length of genital bulb, with large basal lobes directed ventrad; apices of basal lobes bluntly rounded, dorsal surface strongly convex, covered with long, dense black hairs. Ventral parameres of aedeagus narrow, darkly sclerotized, diverging and becoming somewhat compressed laterally in distal one-fourth; apices with short white pilosity. Posterior margin of lateral process forming a thin, finger-like process. Dorsal parameres stout, apices curved mesad. Cerci short, extending to posterior margin of ninth tergum.

ABDOMEN OF FEMALE: Terga 2-9 and corresponding sterna black. Subgenital plate (fig. 134) broad, nearly as wide as long, with shallowly notched apex, ventral keel, and long hairs along periphery. Genital plate (figs. 132, 133) long, about 1.3 mm.; arms of distal plate twisted, slightly narrowed basally; apodemes about one-third total length of plate, diverging anteriorly, with thick interconnecting lamella.

LENGTH OF FORE WING: Male, 12.2-13.4 mm. (holotype, 13.4); female, 13.7-14.9 mm. (allotype, 13.7).

HOLOTYPE: Male, Gudalur, Nilgiri Hills, 3500 feet, September 1960, P. S. Nathan. Allotype, 3 male and 1 female paratypes. Bombay, India, date and collector unknown; in the British Museum (Natural History), London. Eight male paratypes: Nilgiri Hills, May 1954 (5 males), October 1950 (1 male), Cherangoda, 1200 m., no date (2 males), also 26 females not paratypes (same dates), in Naturhistorisches Museum, Basel. Holotype and 3 male paratopotypes in the Snow Entomological Museum.

In wing pattern, this species closely resembles *N. appendiculata* and *N. salai*, but it differs from those species in the shape of the hypovalves and the posterior process of the third tergum. The mesal projection of the hypovalves is short in *indica*, not long as in *appendiculata* and *salai*. The posterior process of the third tergum in *indica* extends midway or a little more across the fourth tergum, not beyond the posterior margin of the fifth tergum as in *appendiculata* and *salai*. The position and shape of the dorsal parameres of *indica* and *appendiculata* are very similar to those of *N. burmana* Byers (1965) from Burma, especially in dorsal aspect.

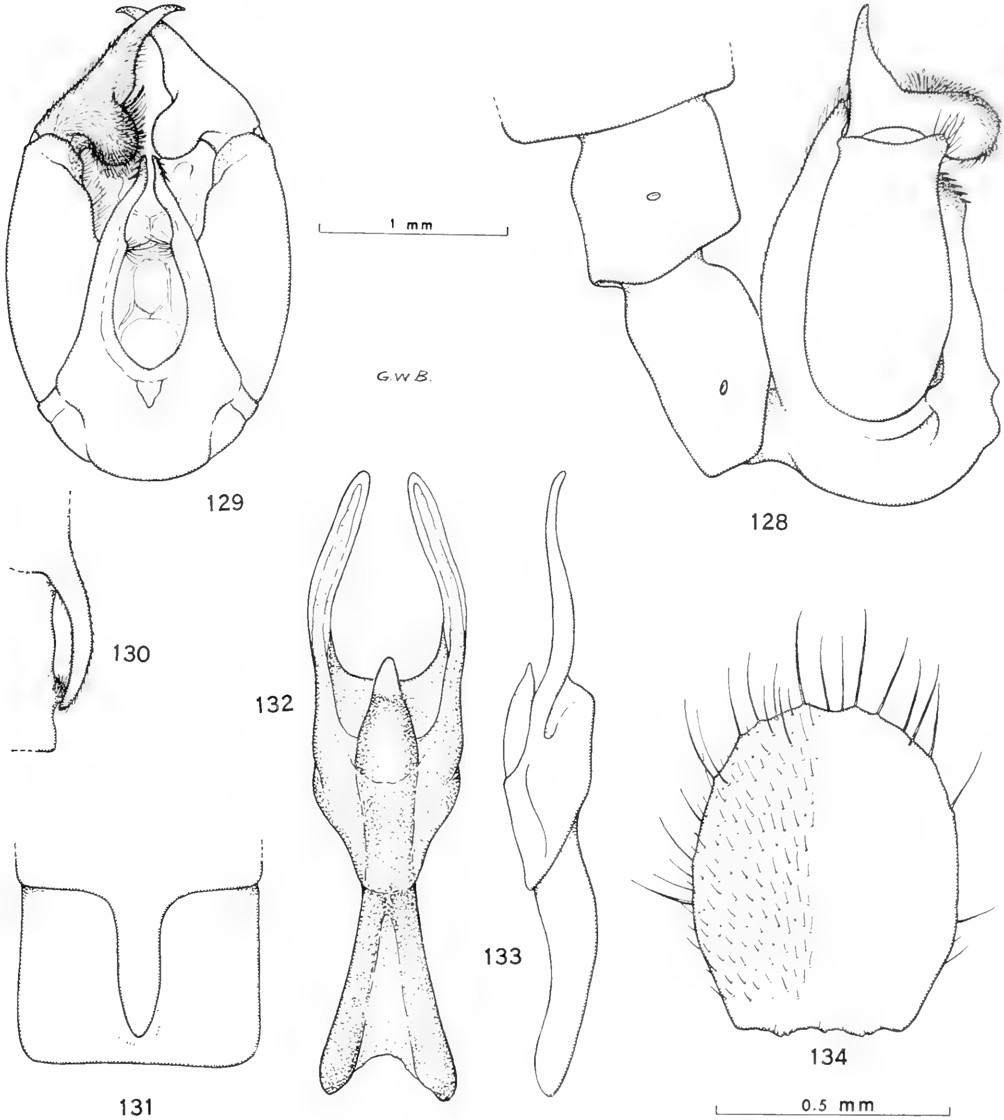
The genital plates of the females of *appendiculata*, *indica*, and *salai* are similar, and these females have been identified in most cases by their association in collections with males. The heavily pigmented wing of *salai* distinguishes that species from *appendiculata* and *indica*. The relative length of the apodemes to the total genital plate length in *indica* is longer than in *appendiculata* and *salai* and may be used to separate the species.

Neopanorpa ochrura NEW SPECIES

Description based on 1 male and 1 female, pinned.

HEAD: Vertex black; frons black medially, sordid yellowish brown beneath antennal sockets; rostrum blackish brown with lateral margins brown (holotype) to dark sordid yellowish brown (allotype). Antennal scape and pedicel brownish black (flagella missing from both types).

THORAX: Pronotum black. Anterior half of mesoscutum and wide median streak, including mesoscutellum, black; posterolateral areas of mesoscutum brown. Metanotum similar to mesonotum. Pleural areas grayish brown to blackish brown. Femora, tibiae, and tarsi brownish with apices dark brown. Wing (fig. 135) membrane hyaline, markings light brown (holotype) to brown (allotype), stigma slightly darker; longitudinal veins brown, cross-veins brown in basal portion of



Figs. 128-134. *Neopanorpa indica* n. sp. 128, terminal abdominal segments, male holotype, left lateral aspect; 129, genital bulb, holotype, ventral aspect; 130, third and fourth terga, left lateral aspect; 131, third and fourth terga, dorsal aspect; 132, genital plate, female allotype, ventral aspect (lower scale); 133, genital plate, right lateral aspect; 134, subgenital plate, ventral aspect (lower scale).

wing, pale in distal portion. Apical band complete, witth several hyaline spots surrounding cross-veins, broadly joined to distal branch of pterostigmal band along hind margin. Pterostigmal band wide, forked posteriorly. Marginal spot not attaining costal margin. Basal band nearly complete.

Abdomen of Male: Terga 2-6 blackish brown, 7-9 yellow ocher. Sterna 2-5 brown, 6 blackish brown, 7-9 yellow ocher. Posterior process of third tergum (fig. 141) short, extending across one-third length of fourth tergum; pale area on fourth tergum beneath process of third. Basistyles not deeply divided. Hypovalves

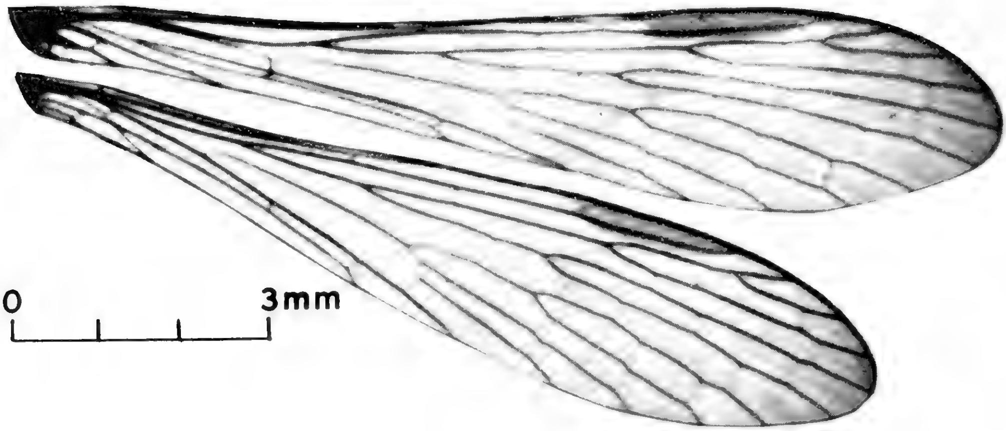


FIG. 135. *Neopanorpa ochrura* n. sp., male holotype, right wings (fore wing length 11.3 mm.).

(figs. 136, 139) narrow at base, broadest near mid-length, apices narrowed and arched ventrad. Basal lobe of diststyles (fig. 138), strongly convex on dorsomesal surface, covered with long hairs ventrally. Basal one-half of ventral parameres (fig. 138) concealed under basistyles, tips bent mesad and converging, apical one-fourth contiguous. Ventral aedeagal valves small, projected ventrad. Lateral processes short. Dorsal parameres absent.

ABDOMEN OF FEMALE: Terga 2-7 blackish brown, 8-10 yellow ocher, cerci black. Sterna 2-6 grayish brown, 7-8 light ocher. Apex of subgenital plate (fig. 142) deeply notched, with many long yellowish hairs along margin and at apex. Axial portion of genital plate (figs. 143, 144) about .4 of total length of genital plate, stout, about .5 width of genital plate. Distal arms of genital plate broad, spatulate, twisted at base.

LENGTH OF FORE WING: Male holotype, 11.3 mm.; female allotype, 11.6 mm.

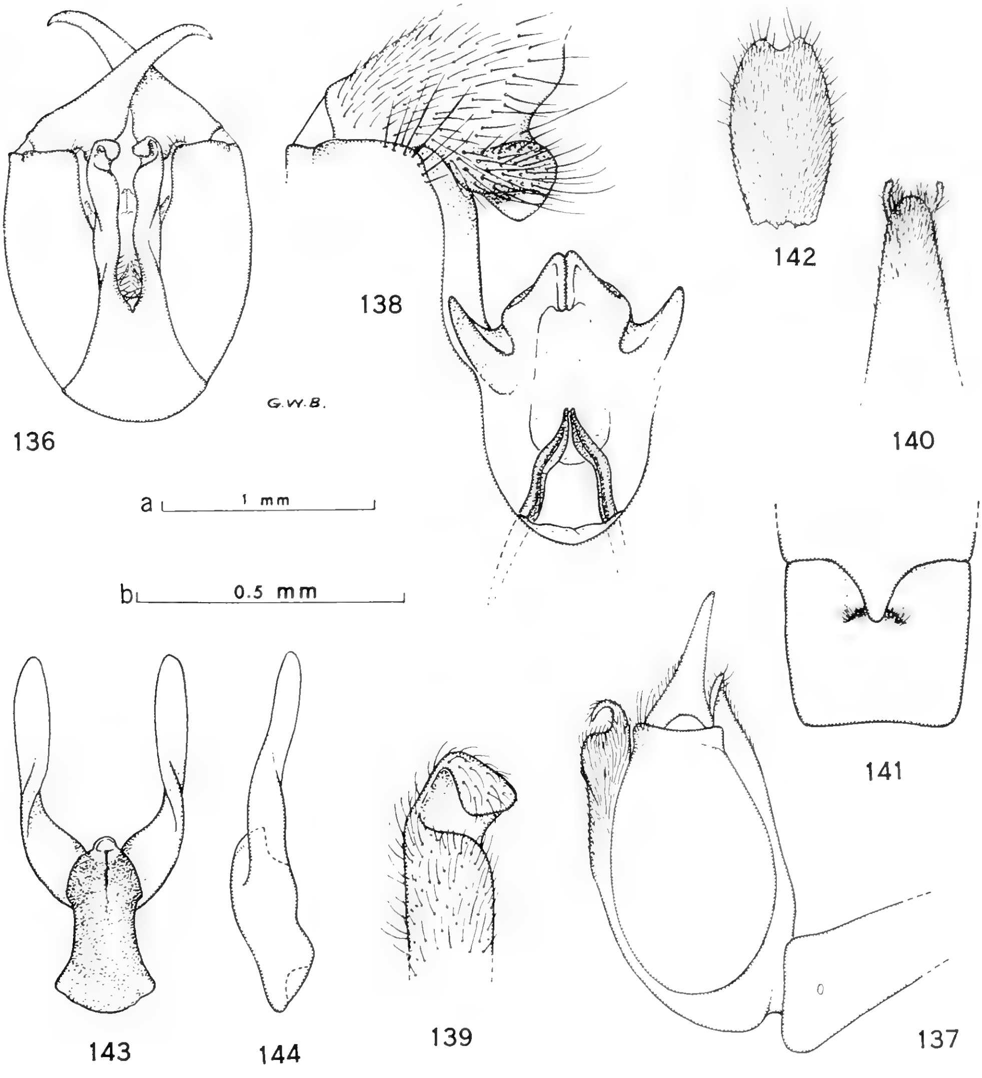
LENGTH OF HIND WING: Male holotype, 10.0 mm.; female allotype, 10.6 mm.

HOLOTYPE: Male, Simla, India, date and collector unknown. Allotype, female, same data as for holotype; both types in the British Museum (Natural History), London.

The wing pattern of this species closely resembles that of *N. cornuta,* but *ochrura* has a different color pattern on the nota and no modification of the sixth tergum in the males. The nota are especially useful in distinguishing the females of these two species. The anterior half of the mesonotum of *cornuta* is dark brown and the posterior half is yellowish, without a median blackish stripe as in *ochrura.* In *cornuta,* there is a small blackish semicircular spot along the anterior margin of the metanotum and no median stripe as in *ochrura.*

In *ochrura,* the female genitalia, especially the genital plate, resemble those of several Indo-Chinese and northern Indian species in having large spatulate distal arms and lacking elongate apodemes. The genital plate of *ochrura* resembles that of *cornuta* but differs in being larger (about 0.7 mm.) and having a proportionately longer axial portion.

The aedeagus of *ochrura* is similar to that of many Indo-Chinese species, but the ventral parameres are much longer. The specific name (from Greek *ochra,* a yellowish brown or ochre color + *oura,* tail) refers to the color of the posterior abdominal segments in both the female and male.



Figs. 136-144. *Neopanorna ochrura* n. sp. 136, genital bulb, male holotype, ventral aspect; 137, genital bulb, right lateral aspect; 138, aedeagus and base of left dististyle, ventral aspect; 139, tip of left hypovalve, ventral aspect; 140, ninth tergum, dorsal aspect; 141, third and fourth terga, dorsal aspect; 142, subgenital plate, female, ventral aspect; 143, genital plate, ventral aspect; 144, genital plate, right lateral aspect. Scale a— figs. 136, 137, 140-142; b— figs. 138, 139, 143, 144.

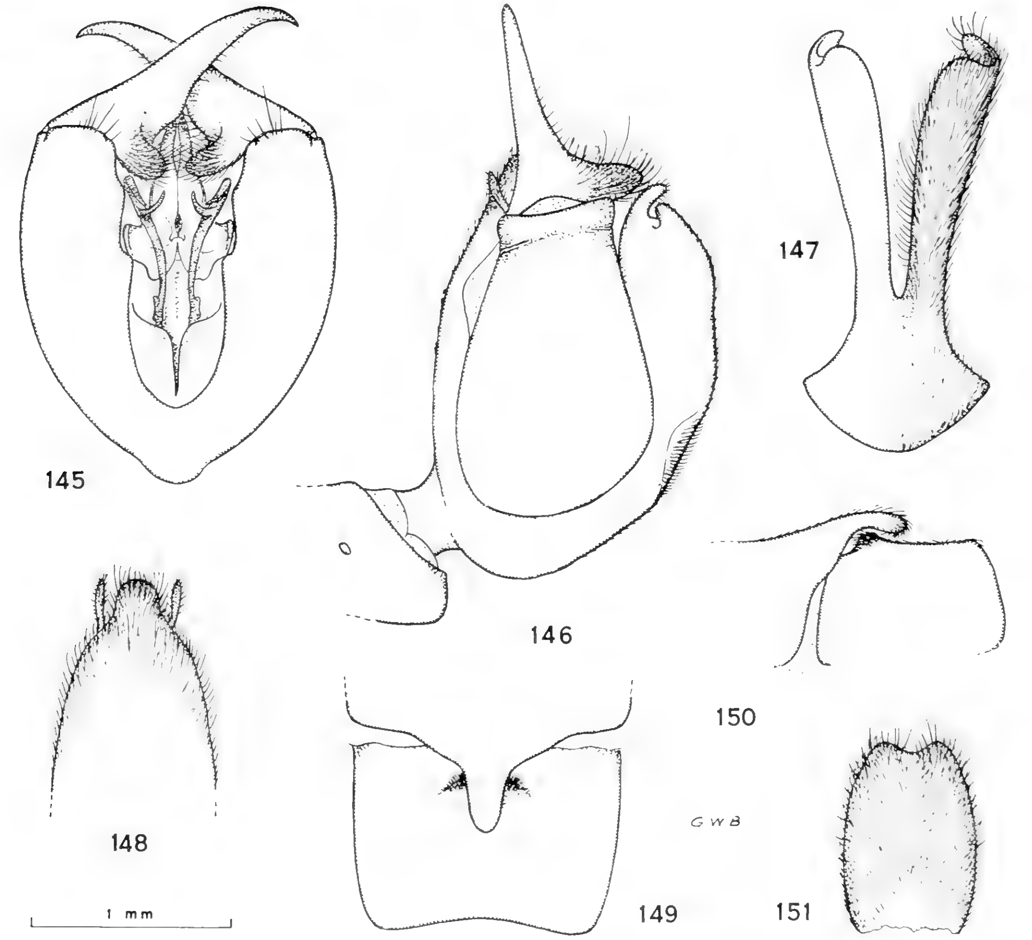
Neopanorpa ramulata Byers

Neopanorpa ramulata Byers, 1975: 87-91, figs. 1-11.

Since this species from Bhutan was recently described, only its more important and diagnostic characteristics are redescribed here, to permit comparison with other regional species. The following paragraphs are based upon the original description:

Head: Dorsum shiny black, rostrum pale brown with two diffuse longitudinal stripes. Antennae about 14 mm. long in male, 12 mm. in female, with 47-48 flagellomeres.

Thorax: Pronotum dark brownish black throughout, with only very short hairs

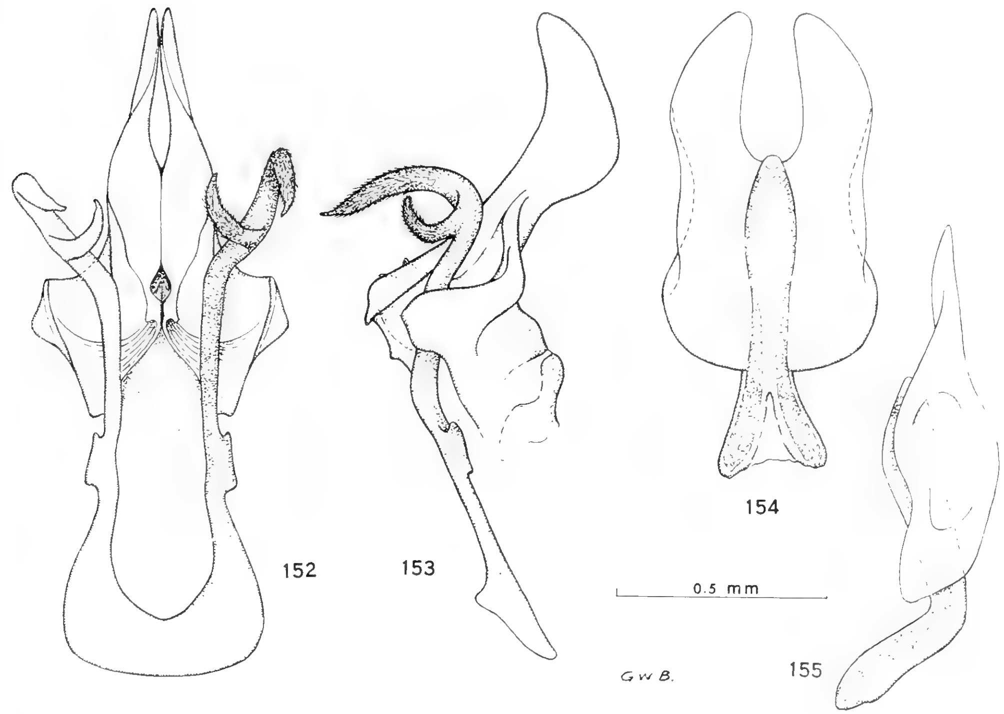


FIGS. 145-151. *Neopanorpa ramulata* Byers. 145, genital bulb, male paratype, ventral aspect, hypovalves removed; 146, genital bulb, male holotype, left lateral aspect; 147, hypovalves, male paratype, ventral aspect; 148, apex of ninth tergum, paratype, dorsal aspect; 149, third and fourth terga, dorsal aspect; 150, third and fourth terga, left lateral aspect; 151, subgenital plate, female allotype, ventral aspect.

on anterior margin. Mesonotum and metanotum dark brownish black on anterior half, along mid-line and on scutellum; dark yellowish brown spot adjacent to each wing base.

WINGS: Lightly tinged with brown; bands and spots light to dark smoky brown. Apical band darkest anteriorly, fading or absent behind vein R_5. Pterostigmal band nearly black over stigma, entire and forked, the branches fading toward posterior edge of wing. Marginal spot from near C to slightly behind R_{4+5}. Basal band absent, or rarely faintly indicated by diffuse spots.

ABDOMEN OF MALE: Terga 1-5 black, segment 6 dark brown anteriorly, yellowish brown on posterior one-third, segments 6-9 yellowish brown except dististyles dark brown. Posterior process of third tergum (figs. 149, 150) broad at base, slender and curved downward apically. Hypovalves (figs. 146, 147) somewhat rolled, convex ventrolaterally, concave



Figs. 152-155. *Neopanorpa ramulata* Byers. 152, aedeagus, male paratype, ventral aspect; 153, aedeagus, right lateral aspect; 154, genital plate, female allotype, ventral aspect; 155, genital plate, right lateral aspect.

mesally, pale at tips, with lateral apical corner slightly extended and curled over ventral apex (fig. 146). Tergum 9 (fig. 148) narrowed and rounded at apex. Outer margins of diststyles slightly concave near mid-length (fig. 145); basal lobe of each diststyle prolonged ventrad, rounded and somewhat flattened, bearing numerous long hairs. Ventral parameres elongate, slender, darkly sclerotized, forked near apex, one branch curving ventrad, the other caudad, both covered with fine, short hairs (figs. 152, 153). Dorsal parameres greatly enlarged, expanded dorsad and caudad as subparallel pale blades.

Abdomen of Female: Terga 1-5 black, 6 dark brown, 7-9 yellowish brown, cerci black. Subgenital plate (fig. 151) slightly narrowed toward apex, broadly and shallowly notched at tip. Genital plate (figs. 154, 155) weakly sclerotized, with elongate anterior apodemes strongly deflected ventrad.

Length of Fore Wing: Male, 15.2-15.8 mm., female 14.2-15.0 mm.

Holotype: Male, Tongsa (Tongsa Dzong, 27°33′N, 90°30′E), Bhutan, 2150 m., 24 June 1972, Naturhistorisches Museum Basel Bhutan Expedition. Allotype and 1 female paratype, same data as for holotype. One male, 1 female paratypes, Changra, 18 km. south of Tongsa, 1900 m., 22 June 1972. Holotype, allotype and 1 female paratype in Naturhistorisches Museum, Basel; 1 male, 1 female paratypes in Snow Entomological Museum, University of Kansas.

Neopanorpa ramulata resembles *N. chillcotti* Byers and *N. nipalica* (Navás) in having slender ventral parameres and conspicuously developed dorsal parameres, in the male, and in the female a large genital plate, the axial portion of which is strongly sclerotized and bears divergent anterior apodemes. From these species, males of *ramulata* may be differentiated by the peculiar, antler-like branched ventral parameres, by the shape of the hypovalves, and shape of the basal lobe of the dististyles. In aedeagal structure of males and genital plate of females, *ramulata* approaches some species of *Panorpa.*

SPECIES OF NEOPANORPA NOT DESCRIBED

Since most of the reliable taxonomic characters in females are on the subgenital and genital plates, dissections are usually necessary to identify species, especially to differentiate those having similar wing patterns. On the other hand, males have several excellent external taxonomic structures. Association of males and females of a species has been based mainly on body coloration, wing pattern, body size, and date and place of collection.

Six female specimens, probably representing four new species, were not described because of lack of associated males. Two males, probably representing two additional new species, were not described because they were so badly damaged. Following is a summary of information concerning these specimens:

Two large-winged female specimens from Nepal externally resemble *N. furcata,* but the genital plates and color pattern of the thorax differ from those of *furcata.* These two females are in the collection of Canada Department of Agriculture.

One badly damaged male specimen (missing genital bulb) from Darjeeling, India, generally resembles *N. nipalica.* Another male from Darjeeling (missing hypovalves) has distinctly shaped dististyles. Both males are in the Illinois Natural History Survey collection.

One female from India (no more detailed locality) resembles *N. effusa* but is smaller than *effusa* (wings about 14 mm.). It is in the British Museum (Natural History).

One female specimen from Chinchona, Anaimalai Hills, southern India, resembles *N. appendiculata,* but the basal half of the wing is much paler. This specimen is in Snow Entomological Museum.

Two additional females from Changra, Bhutan, somewhat resemble *N. ramulata* but have yellow-tinged wings with more extensive markings and reduced genital plate more typical of other Neopanorpas of the Himalayan region. For further details, see Byers (1975).

DESCRIPTIONS OF SPECIES: GENUS *Panorpa*

Panorpa davidi NAVÁS

Panorpa davidi Navás, 1908: 415.

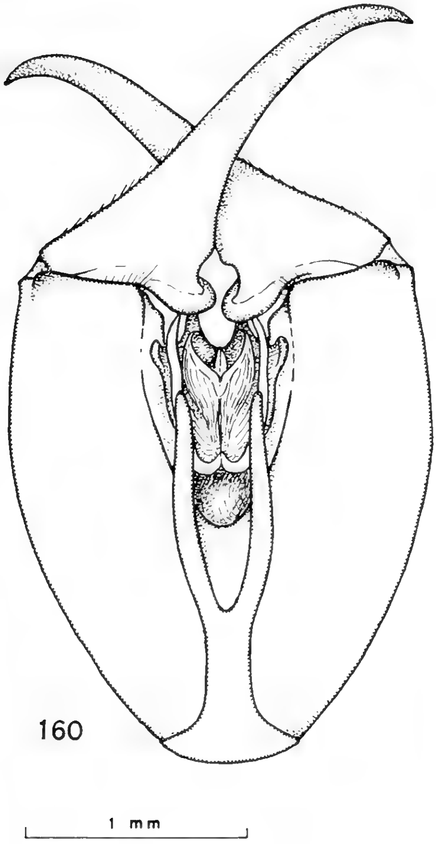
Originally *P. davidi* was described from one male and one female. The female syntype is now the holotype of *P. guttata.* The distinctive apical, pterostigmal, and incomplete basal bands may allow recognition of the female when discovered. Rarely is body coloration helpful in the recognition of a species, but the blackish head with reddish brown rostrum in *davidi,* and the blackish thorax with a reddish brown median streak, may be diagnostic.

The original label on the holotype reads "David, Moupin, Thibet," and a later one "Museum Paris, Mou-Pin, A. David 1870." Since 1908, the borders of Tibet have shifted westward from about 102° E to their present position, about 95° E. No such locality as Mou-Pin appears in detailed gazetteers of Tibet proper, today, but in southwestern Szechwan, at 28° 48′ N, 103° 39′ E, about 50 kilometers east of the 1908 Tibetan border, there is the town of Mapien, whose pronunciation would resemble that of "Mou-Pin" in French. At an elevation of 2000 feet, it is in a more likely habitat for *Panorpa* than the higher, colder regions in modern Tibet.

Esben-Petersen (1921), illustrated in the ventral aspect of the genital bulb, two separate appendages between the ventral parameres. These, however, are merely basal thickenings of the ventral parameres. The following redescription is based in part on drawings of the holotype:

HEAD: Dorsum black, rostrum reddish brown. Antennal scape and pedicel reddish brown; both flagella missing.

THORAX: Dorsum black, with longitudinal median reddish streak; pleural areas black. Legs testaceous. Wing membrane with a faint yellowish tinge; longitudinal veins brownish; cross-veins in apical portion pale. Apical band incomplete, ending at margin between R_5 and M_1; large spot extending from hind margin to cell R_5 (fore wing only). Pterostigmal band con-



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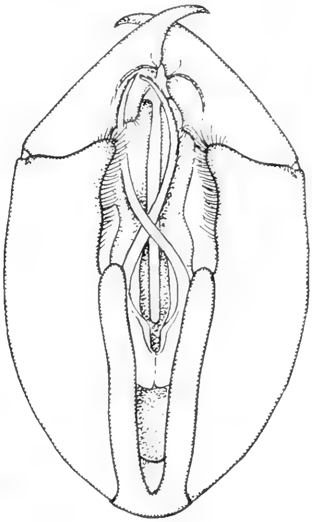

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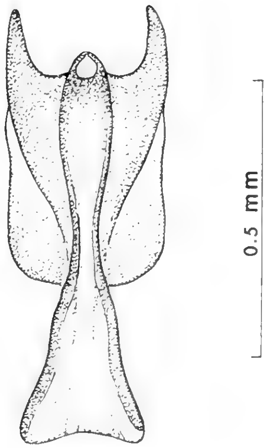

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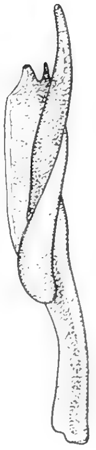

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FIG. 156. *Panorpa davidi* Navás, male holotype, genital bulb, ventral aspect. FIGS. 157-159. *Panorpa guttata* Navás. 157, subgenital plate, female holotype, ventral aspect; 158, genital plate, ventral aspect (vertical scale); 159, genital plate, right lateral aspect. FIG. 160. *Panorpa stigmalis* Navás, male holotype, genital bulb, ventral aspect.

tinuous, diagonal, not forked; distal branch not present. Marginal spot absent. Basal band incomplete, comprising three spots.

Abdomen of Male: Terga and sterna 2-6 black, 7-9 testaceous. Virtually no modification of terga 3-4 (i.e., notal organ poorly developed). No anal horn on sixth tergum. Basistyles (fig. 156) deeply separated ventrally; distal mesal margin of each with dense fringe of hairs. Dististyles slightly more than half length of basistyles; basal "lobe" shallowly cup-shaped, one-half length of inner margin of dististyle. Hypovalves narrow, strap-like, with rounded apices; extending to about two-thirds length of basistyles. Ventral parameres long, thick at base but tapering to sharp tips, setose on outer margins, extending to distal ridge of basal concavity of dististyle, sinuate, crossing near mid-length. Dorsal parameres thin, flattened dorsoventrally, strap-like, extending beyond bases of dististyles.

Female: Unknown.

Length of Fore Wing: Male holotype, 13 mm.; hind wing 11.5 mm.

Holotype: Male, Mou-Pin, Thibet (Tibet), 1870, A. David; in the Museum National d'Histoire Naturelle, Paris.

Cheng (1957) based the *davidi* group, in which there is no anal horn on the sixth abdominal segment, on this species. The structure of the genital bulb, however, is not similar to that of any other species assigned to this group. According to Cheng (1957), the wing markings resemble those of *P. cheni* Cheng from Chekiang, China; but the genital bulbs of these two species are quite different. Several Chinese species have extremely elongate dorsal parameres, especially *P. waongkehzengi* Cheng from Kiangsi, China. The dorsal parameres in that species are somewhat similar to those of *davidi*, but the ventral parameres and hypovalves are much shorter in *waongkehzengi*.

Unfortunately, 12 Chinese species are known only from their female holotypes. Eight of these can be eliminated from consideration as the possible female of *davidi* because they have forked pterostigmal bands, and several of them also have basal spots. The pattern of the wings of *P. leei* Cheng and *P. semifasciata* Cheng is similar to that of *davidi* but differs in having the apical band somewhat reduced and the basal band absent. From the original description (Cheng, 1957), it seems that *P. grahamana* Cheng and *P. carpenteri* Cheng have wing patterns nearly identical to that of *davidi*. The wing membrane in these two females is hyaline, not with a faint yellowish tinge as in *davidi*. Due to a somewhat vague description of overall body coloration of these two females, it is impossible to compare them accurately with the male type of *davidi*.

Cheng (1957) states that the only differences between *grahamana* and *carpenteri* are the coloration of the rostrum and the bent apices of the two distinct apodemes of the genital plate of *carpenteri*. Future investigation may indicate that these two nominal species, both collected in Szechwan, are synonymous. And we think there is some likelihood that both are synonyms of *davidi*.

Panorpa guttata Navás

Panorpa guttata Navás, 1908: 416.
Panorpa davidi Navás, 1908: 415 (in part).

Navás originally described the holotype of *guttata* as the female of *P. davidi* (1908). In his closing statements, he suggested that the female be called *guttata* if the differences in the wing markings were significant; therefore, Esben-Petersen (1915) recognized the female as the holotype of *guttata*. The indistinct apical and pterostigmal bands of *guttata* differ from those of *davidi* in being paler in color and much smaller. In *guttata*, the thorax and abdomen are grayish brown, not reddish brown and black as in *davidi*.

The locality data on the original label are the same as for *P. davidi*: Mou-Pin, Tibet (see *P. davidi* for discussion). The following redescription is based on previous descriptions and on notes and drawings of the holotype:

HEAD: Dorsum and rostrum grayish brown, except ocelli on blackened prominence. Antennal scape grayish brown, pedicel brownish black: flagellum pale grayish brown grading to dark brown towards apex.

THORAX: Dorsum pale brown, pleural regions pale grayish yellow. Legs brownish yellow, except apices of tibiae and tarsomeres brown. Wing membrane hyaline with a faint yellowish tinge, longitudinal veins brownish. Apical band incomplete, reduced to several spots in front wings. Pterostigma yellowish; pterostigmal band incomplete.

ABDOMEN OF FEMALE: Terga and sterna pale yellowish brown. Blackish pigmented spot on each side of basal part of eighth sternum. Subgenital plate evenly rounded at apex, with numerous long hairs on margin (fig. 157). Arms of genital plate (figs. 158, 159) short, slightly longer than one-sixth of total length; basal plate large; apodemes long, projecting cephalad about two-fifths of total length of plate, divergent from anterior edge of basal plate but connected by pale, sclerotized lamella.

MALE: Unknown.

LENGTH OF FORE WING: Female holotype, 12 mm.; hind wing 11 mm.

HOLOTYPE: Female, Mou-Pin, Thibet, 1870, A. David; in the Museum National d'Histoire Naturelle, Paris.

Nine species of Chinese *Panorpa* are known only from male holotypes. They differ from *guttata* in having darkly colored thoracic and abdominal sclerites and more extensive markings on the wings, except for *P. obtusa* Cheng. The color pattern of the wings of *obtusa* resembles that of *guttata*, but the stigma is grayish brown, not with a yellowish tinge as in *guttata*.

Cheng (1957) was unable to assign *guttata* to any one of his groups of Chinese *Panorpa*. He noted similarities in the pterostigmal band and differences in the apical band between *guttata* and *P. tjederi* Carpenter from Yunnan. Comparison of the subgenital and genital plates of these two species indicates no particular relationship of *guttata* with the *diceras* group to which *tjederi* belongs. The genitalia of *guttata* resemble those of the *centralis* group, especially *P. leei* Cheng and *P. emarginata* Cheng. But the genital plate of *guttata* also resembles that of some eastern North American species in having a sclerotized lamella between the apodemes and the basal and distal plates broad.

Panorpa stigmalis NAVÁS

Panorpa stigmalis Navás, 1908: 416, fig. 20.

When Byers examined the probable male holotype in 1964, it did not have a type label. The labels read "Museum Paris, Mou-Pin, A. David 1870," "*Panorpa stigmalis* Navás," and "*Panorpa stigmalis* Navás, Longin Navás det. 1907." Since there was no mention of any other specimen in the original description, this male may be regarded as the holotype, and a label reading "probably holotype. G. W. Byers '64" was added. Cheng (1957) stated the type locality of *stigmalis* to be Mou-Pin, Sikang. The collecting labels are the same as those of *P. davidi* and *P. guttata*, except in the latter two species the type locality is Mou-Pin, Tibet (see *P. davidi* for complete discussion).

Esben-Petersen's redescription (1921) is adequate; however, he did not present any additional information concerning the genitalial characters. The following redescription is based in part on notes and a drawing of the holotype:

HEAD: Dorsum and rostrum brown, ocelli enclosed by blackish spot. Antennal scape and pedicel brown; flagellum brown grading to dark brown at apex, with 42 flagellomeres.

Thorax: Dorsum, pleural areas, and coxae black. Femora, tibiae, and tarsi brown; apices of tarsi blackish. Wings long and narrow, membrane with sordid yellowish tinge; bands and spot smoky brown, stigma red. Longitudinal veins yellowish brown. Apical band complete but ending on outer margin at M_1. Pterostigmal band narrowly connected to apical band along costal margin. Marginal spot absent. Faint spot extending from M_3 to hind margin (fore wings only). A narrow band extending from Cu_1 to hind margin (fore wings only).

Abdomen of Male: Terga 2-3 black, 4-9 reddish brown. Sternum 2 black, sterna 3-9 reddish brown. Posterior process of third tergum two-thirds length of fourth tergum. Hairs on dorsal and ventral posterior margins of sixth segment twice as long as other pilosity. Apex of tergum 9 bearing a pair of lobes. Basistyles (fig. 160) separated only to about mid-length, with sharp ridge along ventral mesal margins of each. Hypovalves short, narrow, strap-like, borne on slender pedicel. Basal lobes of diststyles (fig. 160) rounded, with thickened edge, not noticeably cupped on inner surfaces. Ventral parameres slender, slightly curved mesad at apices. Dorsal parameres elongate, extending between diststyles; lateral processes short, fully exposed in ventral aspect.

Female: Unknown.

Length of Fore Wing: Male holotype, 17.4 mm.; hind wing 16.0 mm.

Holotype: Male, Mou-Pin, 1870, A. David; in the Museum National d'Histoire Naturelle, Paris.

The sordid yellowish wing membrane and distinctly red stigmal spot should allow recognition of the female when discovered. In addition, such body coloration as the solidly black thorax and the black and reddish brown abdomen may prove helpful. The absence of the anal horn from the sixth abdominal segment of the male places *stigmalis* in the *davidi* group as defined by Cheng (1957). The narrow hypovalves, simple aedeagus, and the hairs on the sixth segment separate *stigmalis* from the other members of this group.

Cheng (1957) noted the similarity of the genital bulb (hypovalves) of *stigmalis* to those of the *kongosana* group of Korea but also the differences in the wing markings. The illustrations of *P. kongosana* by Okamoto (1925) are not usefully detailed; the hypovalves of *kongosana* are similar to those of *stigmalis* but somewhat longer.

Localities and Habitats of Mecoptera in the Indian Subcontinent

Previously published distributional information has usually consisted of locality name, date and occasionally elevation. To aid in the location of collection localities, we have included the name of the state, district, and geographic coordinates. Since we found no detailed gazetteers of India, it was necessary to estimate the coordinates of several localities. Names of localities are in alphabetical order, and other data appear in the following sequence:

1. Name of locality from pin label.
2. Synonyms or variant spellings of name, in parentheses.
3. State, district, and country if all pertain to locality.
4. Geographic coordinates of locality. There may be a slight difference between the site used for identification and actual collecting site.
5. Elevation, if known. Elevation derived from maps are stated as ranges.
6. Reference for locality data, if previously published.

Anaimalai Hills (Anamalai Hills), Kerala and Madras, India; about 10°15′ N, 77°00′ E; 1950-5750 feet (600-1750 m.).

Bombay, Maharashtra, India; about 18°56′ N, 72°51′ E; 0-330 feet (0-100 m.).

Changra (village 18 km. S of Tongsa), Bhutan; 1900 m.; (Byers, 1975).

Chembra Peak, Kerala State, India; summit 3500 feet (1070 m.).

Chinchona, Kerala, Anaimalai Hills, India; 10°22′ N, 77°55′ E; 3500 feet (1070 m.).

Coimbatore, Madras, India; 11°00′ N, 76°58′ E; 1400 feet (430 m.).

Darjeeling, West Bengal, India; 27°05′ N, 88°16′ E; 6500 feet (1980 m.); (Cheng, 1953).

Deesa, Gujarat, India; 24°14′ N, 72°13′ E; 330-660 feet (100-200 m.).

Devala, Madras, India; 11°29′ N, 76° 22′ E; 3500 feet (1070 m.).

Godavari (a village 10 mi. SE of Katmandu), Nepal; about 27°45′ N, 85°19′ E; 5000 feet (1530 m.); (Byers, 1971).

Gudalur (in Nilgiri Hills), Madras, India; 11°30′ N, 76°30′ E; 3200 feet (975 m.).

Hambantota, Hambantota Dist., Ceylon; 6°15′ N, 81°16′ E; 100-150 feet (30-45 m.), numerous forests in surrounding area.

Igatpuri, Maharashtra, India; 19°41′ N, 73°38′ E; about 1640-3280 feet (500-1000 m.).

Karachi, Pakistan; 24°52′ N, 67°03′ E; 0-330 feet (0-100 m.).

Katmandu, Nepal; 27°45′ N, 85°19′ E; 5000-6000 feet (1520-1830 m.).

Khandala, Maharashtra, India; 18°45′ N, 73°25′ E; 660-3280 feet (200-1000 m.); (Navás, 1928).

Khasi Hills (N. Khasia), Assam, India; about 25°30′ N, 93°00′ E; 5000 feet (1520 m.); (Needham, 1909).

Kurseong, Bihar, India; 26°52′ N, 88° 17′ E; 4860 feet (1480 m.).

Ma-pien (Mou-Pin), Szechwan, China; 28°48′ N, 103°39′ E; 3280-4920 feet (1000-1500 m.); there are a river and a town by the same name; (Navás, 1908).

Muthikolam, Coimbatore Dist., India; no additional data.

Naduvatam (in Nilgiri Hills), Madras, India; 11°30′ N, 76°34′ E; 6000 feet (1830 m).

Naga Hills, Assam, India; about 26° 00′ N, 94°30′ E; 3000-12000 feet (910-3660 m.).

Nagarkot, Nepal; 27°42′ N, 85°31′ E; 7000 feet (2130 m.).

Nainital, Uttar Pradesh, India; 29°23′ N. 79°30′ E; 4920-6560 feet (2000-3000 m.); (Penny, 1969).

Naraikadu, Tinnevelly Dist., India; 2500-3000 feet (760-910 m.).

Nilgiri Hills, Madras, India; 11°30′ N, 76°30′ E; summits up to 8650 feet (2640 m.).

Peermade (Pirmed), Kerala, India; 9°31′ N, 77°02′ E; 3400 feet (1040 m.).

Periyar Dam, Kerala, India; 9°30′ N, 72°20′ E; approximately 1075 m.

Pondicherry, Madras, India; 11°59′ N, 79°50′ E; 0-330 feet (0-100 m.).

Shillong, Assam, India; 25°34′ N, 91° 53′ E; 5000 feet (1520 m.).

Simla, Himachal Pradesh, India; 31° 07′ N, 77°09′ E; 6560-9840 feet (2000-3000 m.).

Simra, Nepal; 27°37′ N, 84°16′ E; 330-660 feet (100-200 m.).

Thanikudi, Kerala, India; 9°30′ N, 77°16′ E; town in valley, surrounding hills 4000 feet.

Tongsa (Tongsa Dzong), Bhutan; 27°33′ N, 90°30′ E; 2150 m.; (Byers, 1975).

Vavuniya, Vavuniya Dist., Ceylon; 8° 45′ N, 80°30′ E; 200-600 feet (60-180 m.).

Walayar Forest, Kerala, India; about 10°48′ N, 76°48′ E; about 700 feet (215 m.).

Wattegama, Monaragala Dist., Ceylon; 6°48′ N, 81°30′ E; 0-330 feet (0-100 m.).

Yala, Yala Dist., Ceylon; 6°22′ N, 81°31′ E; town is on coast, many small forest reserves nearby inland.

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THE UNIVERSITY OF KANSAS
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FIELD OBSERVATIONS ON RARE OR LITTLE KNOWN MAINLAND ANOLES

By

HENRY S. FITCH, ALICE F. ECHELLE AND
ANTHONY A. ECHELLE

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Field Observations on Rare or Little Known Mainland Anoles

Henry S. Fitch,* Alice F. Echelle and Anthony A. Echelle**

TABLE OF CONTENTS

ABSTRACT

Species of mainland anoles that have remained little known because of rarity, restriction to remarkably small geographic areas, inaccessibility of range or habitat, or similarity to a commoner species, include *Anolis anisolepis, A. cuprinus, A. dunni, A. gadovii, A. megapholidotus, A. microlepidotus, A. parvicirculata, A. subocularis* and *A. taylori* in Mexico; *A. aquaticus, A. attenuatus, A. biscutiger, A. carpenteri, A. dollfusianus, A. haguei, A. insignis,* and *A. rodriguezi* in Central America, and *A. aequatorialis, A. chloris, A. gemmosus, A. maculiventris, A. nigrolineatus, A. peraccae* and *A. princeps* in Ecuador. Field observations on each of these species are presented. Morphological traits (mean adult size and sexual dimorphism, weight, size and color of dewlap, relative lengths of tails and limbs) and behavioral and ecological traits (temperature preferenda, height and diameter of perch, season of egg-laying, display-activity patterns) are listed and discussed. In the past, several of the species have been considered subspecies of other species. In each instance status is discussed and evidence for full specific status is presented. Lack of close ecological counterparts between Mexico, Central America and Ecuador is demonstrated. The Ecuadorian series of species tends to arboreal habits, large size, and relatively long tails. The Mexican species tend to terrestrial habits, small size, and marked sexual dimorphism, with males usually larger than females.

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INTRODUCTION

Field studies of anoles have been carried on by us intermittently over an eight-year period in Mexico, Central America and northwestern South America with most concentrated efforts devoted to demographic investigations of several abundant species: *Anolis cupreus, A. limifrons, A. humilis, A. tropidolepis,* and *A. sericeus* (Echelle, Echelle and Fitch, 1971a; Fitch, 1972, 1973a,b,c, 1975; Henderson and Fitch, 1975). Also, considerable attention has been devoted to poorly known species of this genus of iguanid lizards, and these are the subjects of the present report. The objective has been to obtain information that will help to clarify the ecological and phylogenetic relationships of these species with the commoner and better known kinds, and will lead to a better understanding of anoline lizard biology.

Data were obtained on a series of field trips (Costa Rica, February-March, 1965, November 1967 to July 1968, August-September 1968, February-March 1969, August-September 1969, January-March 1970, February-March 1973, June-July 1973, February-March 1974; Guatemala, February-March 1971; Mexico, Guerrero, June-July 1971 and March 1972, Chiapas and Oaxaca, February-March 1972; Ecuador, February-March 1975). A. A. and A. F. Echelle participated in some of the field trips, but their main contribution to the present report has been photographing and analyzing the display-activity patterns of many of the species. Fitch is solely responsible for the display diagrams of *Anolis attenuatus, A. insignis,* and *A. maculiventris,* all of which are based on relatively few filmed sequences.

Some of the species were found only once, or on a few occasions. Others that are still little known, were found to be abundant at certain times and places. This report includes 25 species that have been mentioned few times in published literature. New information is presented about each, especially with regard to habits, habitats, and characters that can be seen or determined only in the living animal, such as color of eye, color and size of dewlap, body weight, and sexual dimorphism.

Relationships within the genus are exceedingly complex, and *Anolis,* with its plethora of species, has provided excellent material for study of evolutionary processes, illustrating adaptive radiation, parallel and convergent specializations, and character displacement. Also this group of lizards has provided exceptional material for ecological and ethological studies. The sympatric and syntopic co-occurrence of species in various combinations and various habitats has created excellent opportunities for investigating competitive relationships and partitioning of resources (Fitch, 1975).

This genus of iguanid lizards was originally described in 1803 by Daudin, who named several species. Additional species were named in the 1830's, and in every decade thereafter the list has continued to grow, until now approximately 150 species are recognized from the North, Central and South American mainlands, while at least 90 species and many subspecies are recognized from the West Indian Islands. Naming of the mainland species accelerated to its maximum rate in the 1860's and 1870's, then dwindled to a low point in the 1920's. However, more recently, the discovery and naming of new species has again increased, and has continued up to the present, with the prospect that many still remain to be discovered and described.

The insular West Indian species often occur in spectacularly high population densities, in situations where they are readily accessible for field studies. Mainland species generally occur in much lower densities, sometimes in remote and relatively inaccessible areas. Many of the species currently recognized are known from

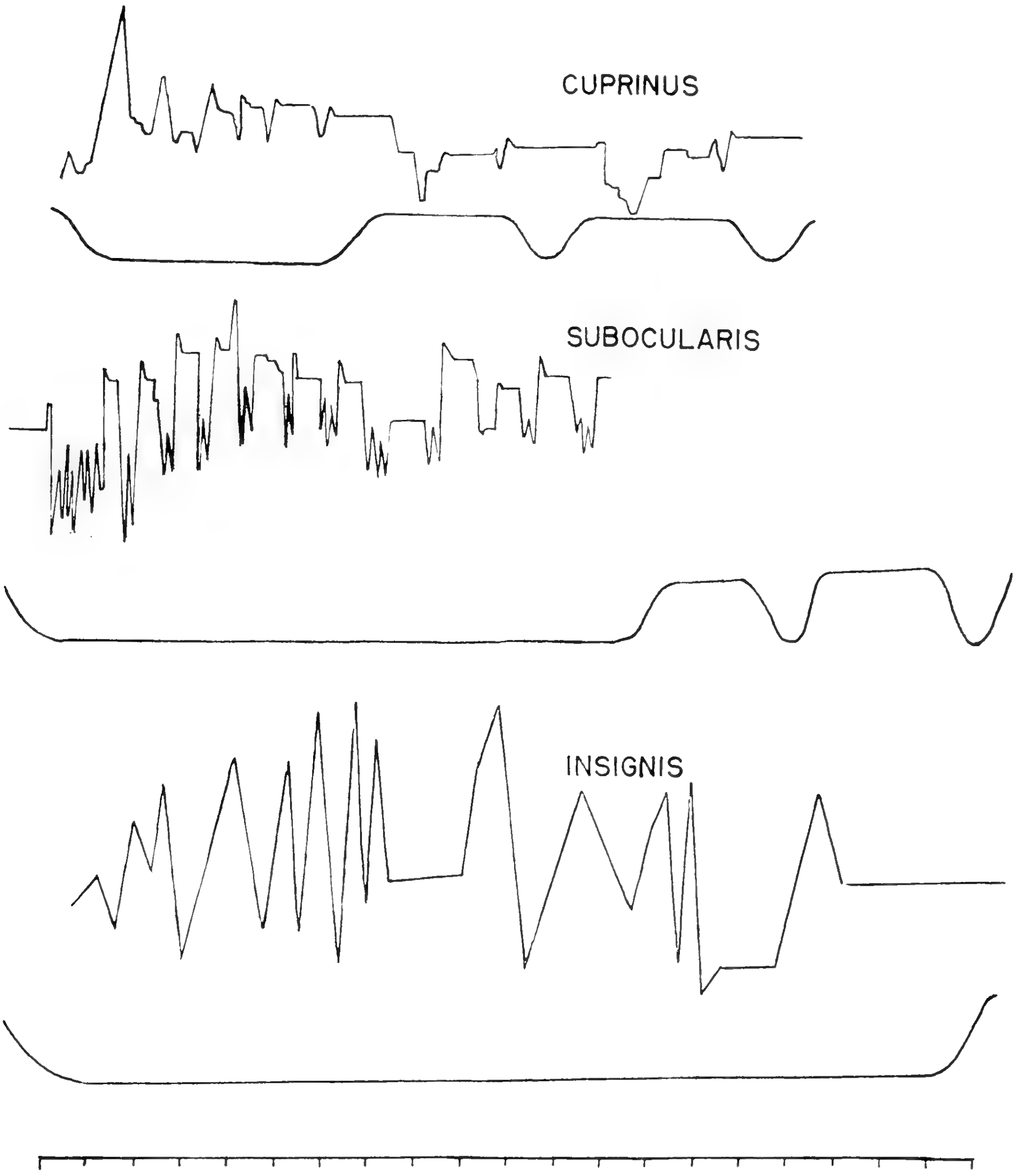

Fig. 1. Diagrams of Display-movements of Anoles. Upper line of each diagram shows vertical movements of head and lower line shows movements of dewlap. The metered line at bottom shows 1-second intervals. Upper: *Anolis cuprinus,* Zanatepec, Oaxaca Province, Mexico. Middle: *Anolis subocularis,* Marquelia, Guerrero Province, Mexico ("terminal" portion of display, which is sometimes given without initial portion). Lower: *Anolis insignis,* Monteverde, Puntarenas Province, Costa Rica.

only one locality or from few localities all within a small area. Many are known only from the original description, and some of these were described more than 100 years ago. Hence, in some instances, there is serious doubt whether a name represents a valid, but rare and elusive species, or was based upon an atypical or aberrant individual of a species already named.

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Robert W. Henderson, Richard K. LaVal, Virginia R. Fitch and Chester W. Fitch helped at various times with the field work. Charles C. Carpenter loaned us equipment for study of displays, and read the manuscript. William E. Duellman gave advice and made available for study specimens in the University of Kansas Museum of Natural History. Stephen R. Edwards, John D. Lynch and James R. Dixon provided information essential to our field work in Mexico and Ecuador. Thanks are due to all these persons. Some of the material on displays included here was part of an M.S. dissertation submitted by A. F. Echelle to the Department of Zoology, University of Oklahoma. Funding for some of the field work was provided by the University of Kansas (General Research Grant # 3344-5038) and the National Science Foundation (GB 6724).

METHODS AND MATERIALS

Tables 1-5 summarize ecological traits of the species studied insofar as these traits could be determined and also summarize characters of color and external morphology that are best observed on freshly collected or living anoles, but may be obscure or indiscernible on those that have been long preserved. Table 1 is concerned with color, size and proportions: Color of dewlap and iris, mean tail-length as a percentage of snout-vent length, point reached by forwardly extended hind limb, mean snout-vent lengths and weights in adult males and females, and dewlap areas. Dewlap patterns are sometimes complex and when necessary are described in more detail in the species accounts. For the ratio of tail-length to snout-vent length, only individuals which seemed to have their original tails intact were included in calculating the means. The point reached by forwardly extended hind limb has provided a character much used in anoline systematics, but this character is much influenced by state of preservation and also is subject to individual variation. The limbs of hardened specimens are stiff and cannot be fully extended without breaking the bones and do not reach as far forward as in more flexible specimens. For this reason in the live anoles used for Table 1 the hind limb reached a little farther forward in some cases than indicated in published accounts based on preserved material. The adult snout-vent measurements and weights are intended to show typical sizes, which are poorly known even for most common species, and also to indicate trends of sexual dimorphism in size. In instances where few individuals were available, the size ratios of the sexes may be misleading and are subject to revision (*anisolepis, parvicirculata, chloris*) but in others represented by adequate series it is evident that males are larger (*cuprinus, gadovii, subocularis, taylori, dollfusianus, gemmosus*), that females are larger (*biscutiger, carpenteri, rodriguezi*), or that the sexes are very nearly the same size

Fig. 2. Diagrams of Display-movements of Anoles. Explanation as in Figure 1. Upper: *Anolis anisolepis,* San Cristóbal de Las Casas, Chiapas Province, Mexico. Second from top: *Anolis crassulus,* Panajachel, Guatemala, for comparison with the closely related *A. anisolepis* and *A. haguei.* Third from top: *Anolis haguei,* Quezaltenango, Guatemala. Bottom: *Anolis dollfusianus,* two populations; on left Tapachula, Chiapas Province, Mexico; on right Retalhuleu, Guatemala.

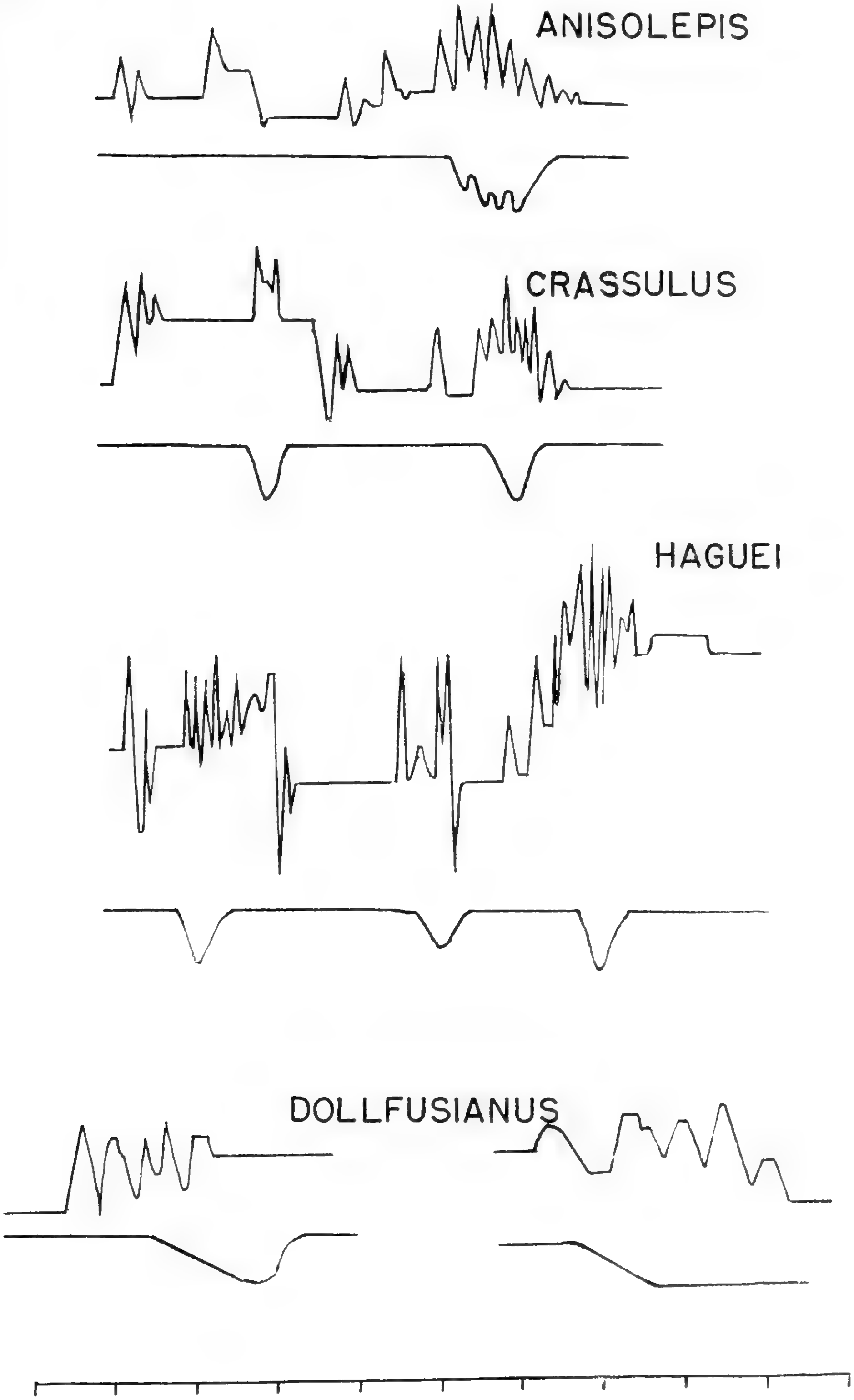

ANISOLEPIS
CRASSULUS
HAGUEI
DOLLFUSIANUS

TABLE 1

MORPHOLOGICAL CHARACTERISTICS OF *Anolis* SPP.

SPECIES	*Color of dewlap*	*Color of iris*	*Adult snout-vent length* (mm)		*% Tail-lengths to S-V*	*Point reached by forward extended hind limb*	*Dewlap area* (mm²)		*Weight* (grams)	
			♂	♀			♂	♀	♂	♀
anisolepis	red; yellow edge	dark	53.0(2)	56.0(1)	186(2)	ear or beyond	....	....	3.5 (2)	3.9 (1)
cuprinus	rose; tan edge	dark	63.3(22)	46.5(15)	176(14)	eye	606(22)	51(11)	4.6 (14)	2.4 (7)
dunni	red	dark	53.4(3)	44.7(6)	192(1)	eye	330(1)	....	3.2 (1)	....
gadovii	purplish pink; 8 dark purplish streaks	dark	70.6(10)	62.6(12)	173(10)	nearly to eye	650(5)	124(5)	5.0 (10)	4.2 (12)
megapholidotus	reddish orange; 2 rose bands	dark	44.2(7)	43.4(14)	173(13)	ear	141(6)	23(14)	....	....
microlepidotus	purplish red; pale edge	dark	41.0(1)	48.0(2)	175(2)	neck	....	....	1.9	2.2 (2)
parvicirculata	orange; central reddish spot	dark	46.0(1)	50.0(1)	178(1)	eye to nostril	....	40(1)	....	2.5 (1)
subocularis	red; pale edge	yellowish	51.0(49)	38.8(19)	175(42)	eye to nostril	312(31)	100(6)	2.8 (45)	1.9 (7)
taylori	purplish red; pale bands	dark	71.8(45)	57.0(21)	190(15)	eye	670(16)	53(12)	6.4 (24)	3.7 (20)
aquaticus	yellowish-orange; 4 red bands	blue	62.3(12)	59.7(10)	165(8)	eye	567(18)	....	7.8 (5)	....
attenuatus	dark olive brown	blue	84.5(24)	80.6(18)	219(31)	eye to nostril	788(2)	87(1)	10.7 (19)	10.9 (12)
biscutiger	cream; dark yellow center	dark	37.3(42)	39.4(33)	197(43)	eye to nostril	....	....	0.89 (15)	0.93 (8)
carpenteri	orange	dark	38.5(6)	40.4(14)	161	ear	150	....	0.70	1.00
dollfusianus	yellow; pale edge	dark	39.0(54)	36.7(42)	187(56)	eye or beyond	116(33)	....	1.28 (41)	1.14 (29)
haguei	reddish orange; yellow edge	dark	45.0(2)	....	185(1)	eye to ear	....	....	2.6 (2)	....
insignis	dull white; orange red streaks	dark	....	151.0(1)	192(5)	neck	....	....	....	....

rodriguezi	orange yellow	dark	43.3(15)	43.7(23)	190(13)	nostril	133(7)	....	....	....
aequatorialis	checkered light and dark brown	blue	82.2(7)	80.0(3)	258(3)	beyond snout	797(3)	....	10.5 (3)	....
chloris	dull yellowish white; pale blue anteriorly; dark scales	blue	53.3(3)	58.0(1)	188(3)	ear to eye	402(2)	....	1.72 (3)	....
gemmosus	yellow; streaked w/blue, white, green	blue	62.5(38)	58.5(28)	268	eye to nostril	433(27)	....	4.1 (27)	3.7 (31)
maculiventris	rusty red	pale golden yellow	46.0(1)	....	194(1)	ear to eye	187(1)	....	1.48 (1)	....
nigrolineatus	dull white w/black lines	yellow	50.9(14)	48.0(15)	201(16)	neck	127(14)	....	1.97 (15)	1.96 (15)
peraccae	dull white; gray streaks	dark; blue inner rim	49.9(21)	46.3(9)	221(12)	ear to eye	182(16)	....	1.78 (15)	1.48 (7)
princeps	white anteriorly; greenish posteriorly	golden brown	117.0(2)	....	211(2)	beyond snout	1485(2)	....	22.9 (2)	....
sp.	pale red; black spot	dark	70.0(1)	73.0(1)	214(2)	eye to snout	400(1)	94(1)	6.2 (1)	9.0 (1)

(*megapholidotus*). The area of the dewlap was determined by tracing the outline on paper while the organ was held fully extended and then measuring it with a planimeter.

Table 2 summarizes information about body temperature (first three columns) and reproduction (last two columns). It shows mean body temperature, range of body temperature, and adjacent air temperature for several species. The fourth column indicates observed occurrence, by month, of individuals indicating reproductive activity: Females with enlarged follices or oviducal eggs; and juveniles, or large young. Although most populations were not sampled throughout the year, breeding seasons are inferred (Table 2) from the observed occurrence of eggs and young, from the observed incubation periods and growth-rates of several species (Fitch 1973a), and from observations that, in general, dry weather inhibits reproduction of anoles and wet weather induces it.

Table 3 shows preferred resting places for each of the 25 species, whether at ground level (leaf litter, rock surface) or above ground (height, and kind of perch such as tree trunk, rocks, foliage or stem). Perch-diameter is shown for those that used stems. Table 4 is also concerned with perches, but limited to the nine species for which most data were available, with intraspecific comparisons of adult males, females and immatures.

Table 5 summarizes interspecific co-occurrences. The alphabetical series at the top of the page includes 16 of this study and eight other commoner species that co-occur and interact with them. Although interactions are still poorly known in most instances, relative size, abundance, and extent of distribution are indicated, because these are factors that might influence the outcomes of interactions. Ordinarily, larger species would tend to dominate or displace smaller ones. Interactions between a common and/or widespread species and a rare and/or geographically limited species would be relatively important and perhaps critical for the latter, but relatively inconsequential for the former.

The displays were filmed with a Super-8 motion picture camera (Bolex 155 Macrozoom) at a speed of 18 frames per second. A Bell and Howell Super-8 projector adapted for single-frame advancement was used in the analysis of the displays. Some of the displays filmed were induced in unconfined anoles by presenting them with a mirror or a tethered rival, others were filmed in Plexiglas enclosures when several individuals of the same species or different species were confined together. The aggressive displays of iguanid lizards are complex, stereotyped, and species-specific (Carpenter, 1961a, 1961b). These displays may reflect both genetic relationships and environmental factors (Echelle *et al.* 1971a). The displays have been filmed and analyzed in few kinds of mainland anoles, notably in *Anolis nebulosus* (Jenssen, 1971). It has been demonstrated by Jenssen that interpopulational differences in displays may exist, and T. A. Jenssen (pers. comm.) has indicated that certain species show a variety of displays that differ in basic form. However, in such instances, one display type is much more frequent than the others and may be considered *the* display. Various display modifiers may cause differences in detail, reflecting the motivational state of the lizard.

TABLE 2
DATA ON BODY TEMPERATURE AND REPRODUCTION OF *Anolis* SPP.

SPECIES	Body temperatures when active	N	Air temperature when active	Observed occurrences of ovarian follicles (OF) oviducal eggs (OE) juveniles (J) and large young (LY)	Inferred breeding season
anisolepis				OE: Feb.	July-Sept.
cuprinus	30.7(34.3-26.2)	24	30.5	J: Sept.-Dec.	July-Sept.
dunni				OE: June-July	July-Sept.?
gadovii	30.5	1	30.9	OF, OE: July J: Feb.	July-Sept.
megapholidotus			17.5	OF, OE: June-July	June-Sept.
microlepidotus			21-17	OF, OE: July	July-Sept.
parvicirculata				OF, OE: Feb.	year round?
subocularis	31.4(34.6-28.0)	13	30.0	OF, OE: July	June-Oct.
taylori	29.1(32.8-26.2)	28	27.9	OF, OE: July LY: Feb., Mar.	July-Oct.
aquaticus				OF, OE: Mar.	year round?
attenuatus	21.5	1	18.0	OF: Mar., July, Aug., J: Sept., Oct.	year round?
biscutiger	31.0(32.5-28.5)	36	32.6-27.3	OE: Dec., Jan., Feb., Mar., May, Aug.	year round?
carpenteri	27.3	1	27.0	J: Nov. LY: Feb.	year round?
dollfusianus	28.4(31.9-26.0)	31	27.6	OF, OE: Feb. J, LY: Feb.	?
insignis			20.0	J: Mar.	?
aequatorialis	22.3(24.5-20.1)	2	22.0	J: Feb.	?
gemmosus	21.0(29.3-18.2)	34	20.4		year round
nigrolineatus	29.9(30.5-29.4)	5	30.5	OF, OE: Mar.	Feb.-July?
peraccae				OF, OE, J, LY: Feb., Mar.	year round? low Oct.-Dec.
princeps	27.4	1	27.2		?
sp.	26.0(26.4-25.6)	2	26.0	OF, OE: Feb. J: Feb.	year round?

TABLE 3

RESTING PERCHES OF *Anolis* SPP.

		Ground level			Above ground						
SPECIES	N	%	Leaf litter	Rock surface	%	Height (m)	Trunk of large tree	Rock	Foliage	Stem	diameter (m) Perch
anisolepis	5	80	++	......	20	.45	......	......	......	+	
cuprinus	30	17.8	+	......	82.2	1.01	......	++	......	+++	.171
dunni	2	......	++	......	......	......	+++	......	......	......	
gadovii	..	......	......	......	......	......	......	+++	......	......	
megapholidotus	11	45	+++	......	55	.25	......	......	......	......	
microlepidotus	6	100	+++	++	......	......	......	......	......	......	
parvicirculata	1	100	+	+	......	......	......	......	......	......	
subocularis	63	6.4	+++	......	93.6	1.14	+	......	......	+++	.102
taylori	34	5.9	......	......	94.1	1.46	......	+++	......	+	
aquaticus	.	...	++	+++	.	...	......	......	......	......	
attenuatus	52	7.7	++	......	92.3	2.00	+++	......	......	......	
biscutiger	6	33.3	+++	......	66.6	1.07	......	......	......	......	
carpenteri	11	36.3	+	......	63.7	.90	+++	......	......	++	
dollfusianus	39	23.6	......	......	76.4	.70	......	......	......	+++	
haguei	....	......	......	......	100	......	......	......	......	+++	
insignis	1	......	......	......	100	2.50	+++	......	......	......	
rodriguezi	7	15.3	+	..	84.7	.83	+++	......	......	++	.357
aequatorialis	2	......	......	......	100	1.25	......	......	++	++	.012
chloris	..	......	......	......	100	....	+	......	......	+++	
gemmosus	67	......	......	......	100	1.74	+	......	++	......	
maculiventris	1	..	......		100	1.20	+++	......	......	......	
nigrolineatus	24	......	......	......	100	.96	......	......	......	+++	.143
peraccae	18	5.5	......	......	94.5	1.90	......	......	......	(cacao) +++ (banana)	
princeps	2	......	......	......	100	.80	++	......	......	++	.050
sp.	2	......	......	......	100	2.01	......	+	+++	......	

TABLE 4

Comparison of Resting Perches of Nine *Anolis* spp.

Species	Male % ground level	Male % above ground	Male mean height (meters)	Female % ground level	Female % above ground	Female mean height (meters)	Immature % ground level	Immature % above ground	Immature mean height (meters)	Total % ground level	Total % above ground	Total mean height (meters)	N
attenuatus	3.6	96.4	2.2	15.8	84.2	1.8	0	100	0.5	7.7	92.3	2.0	52
carpenteri	0	100	1.4	33.3	66.6	0.9	50	50	.08	36.3	63.7	0.9	11
cuprinus	5.3	94.7	1.1	33.3	66.6	0.9	......	......	...	17.8	82.2	1.0	27
dollfusianus	11.5	88.5	0.7	39.0	61.0	0.7	28.6	71.4	0.6	23.6	76.4	0.7	39
gemmosus	0	100	2.2	0	100	1.5	0	100	1.5	0	100	1.7	67
nigrolineatus	0	100	1.2	0	100	0.8	......	......	...	0	100	.96	24
peraccae	9	91	2.5	0	100	0.7	0	100	2.0	5.5	94.5	1.9	18
subocularis	0	100	1.1	40	60	0.8	......	......	...	6.4	93.6	1.1	63
taylori	0	100	1.6	25	75	4.7	0	100	1.4	5.9	94.1	1.5	34

ACCOUNTS OF SPECIES

The Mexican Species

Anolis anisolepis

This species was described by Smith, Burley and Fritts (1968) from 23 specimens collected at San Cristóbal de las Casas and several nearby localities in western Chiapas. In describing it the authors stated that its specific distinctness from the closely related and similar *Anolis haguei* was demonstrated by sympatry; both were found together between San Cristóbal de las Casas and Tenaja. The authors distinguished *A. anisolepis* from its near relatives *A. crassulus* and *A. haguei* by the following diagnostic characters.

A. anisolepis: Dorsal crest prominent (with scapular and sacral gaps); dorsal scales enlarged, with largest, at mid-back, about half the size of ventrals, gradually becoming smaller laterally and grading into granular scales of sides; dorsal stripe lacking; size relatively small (S-V up to 47 mm).

A. crassulus: Dorsal crest lacking; dorsal scales abruptly larger than small lateral scales, the largest about equal to ventrals, with lateral dorsals larger than median dorsals; dorsal stripe lacking; size relatively small.

A. haguei: Dorsal crest prominent (with scapular and sacral gaps); dorsal scales enlarged, with largest at mid-back about half the size of ventrals, gradually becoming smaller laterally and grading into granular scales of sides; dorsal stripe present; size relatively large (S-V up to 53 mm). As do all other Mexican species here discussed, *Anolis anisolepis* and its near relatives belong to the *Chrysolepis* species series of *Beta* anoles.

On 14 February 1971, we captured five *A. anisolepis* 4.5 km S of San Cristóbal de las Casas beside Highway 190. There had been frost on the preceding night (elevation approximately 2150 m), general ter-

TABLE 5

INTERSPECIFIC CO-OCCURRENCES OF *Anolis* SPP.

Some rare or little known mainland anoles (left) and associated species (upper). For each co-occurrence the three symbols show whether associated species is: larger (+) or smaller (—), more abundant (+) or less abundant (—), encompasses range (+) or merely overlaps it (—).

	anisolepis	*dunni*	*gadovii*	*megapholidotus*	*nebulosus*	*sericeus*	*subocularis*	*taylori*	*tropidonotus*	*attenuatus*	*biscutiger*	*capito*
MEXICAN												
anisolepis												
cuprinus						—+—						
dunni				—+—	—+—		++—					
gadovii					——+		——+					
megapholidotus		+——			—+—							
microlepidotus					—+—							
parvicirculata									+++			
subocularis		———	++—		———			++—				
taylori					——+		——+					
CENTRAL AMERICAN												
aquaticus											——+	
attenuatus												
biscutiger												+——
carpenteri												++—
dollfusianus						+++						
haguei	—+—											
insignis											—+—	
rodriguezi						+++						
SOUTH AMERICAN												
aequatorialis												
chloris												
gemmosus												
maculiventris												
nigrolineatus												
peraccae												
princeps												
sp.												

TABLE 5—(*continued*)

	cupreus	*haguei*	*humilus*	*intermedius*	*limifrons*	*polylepis*	*aequatorialis*	*chloris*	*gemmosus*	*maculiventris*	*peraccae*	*princeps*	*sp.*
MEXICAN													
anisolepis		+ — —											
cuprinus													
dunni													
gadovii													
megapholidotus													
microlepidotus													
parvicirculata													
subocularis													
taylori													
CENTRAL AMERICAN													
aquaticus						— — +							
attenuatus			— + —	— + +									
biscutiger	+ + —		— — —			+ — —							
carpenteri			+ + +		+ + +								
dollfusianus													
haguei													
insignis			— + +	— + +									
rodriguezi													
SOUTH AMERICAN													
aequatorialis									— + —				
chloris										— — —	— + —	+ — +	+ — —
gemmosus							+ — ?						
maculiventris								+ + +			+ + +		+ + ?
nigrolineatus													
peraccae								+ — +		— — —		+ — —	+ — —
princeps								— + +		— — —	— + +		— + —
sp.								— + +		— — +	— + +	+ — +	

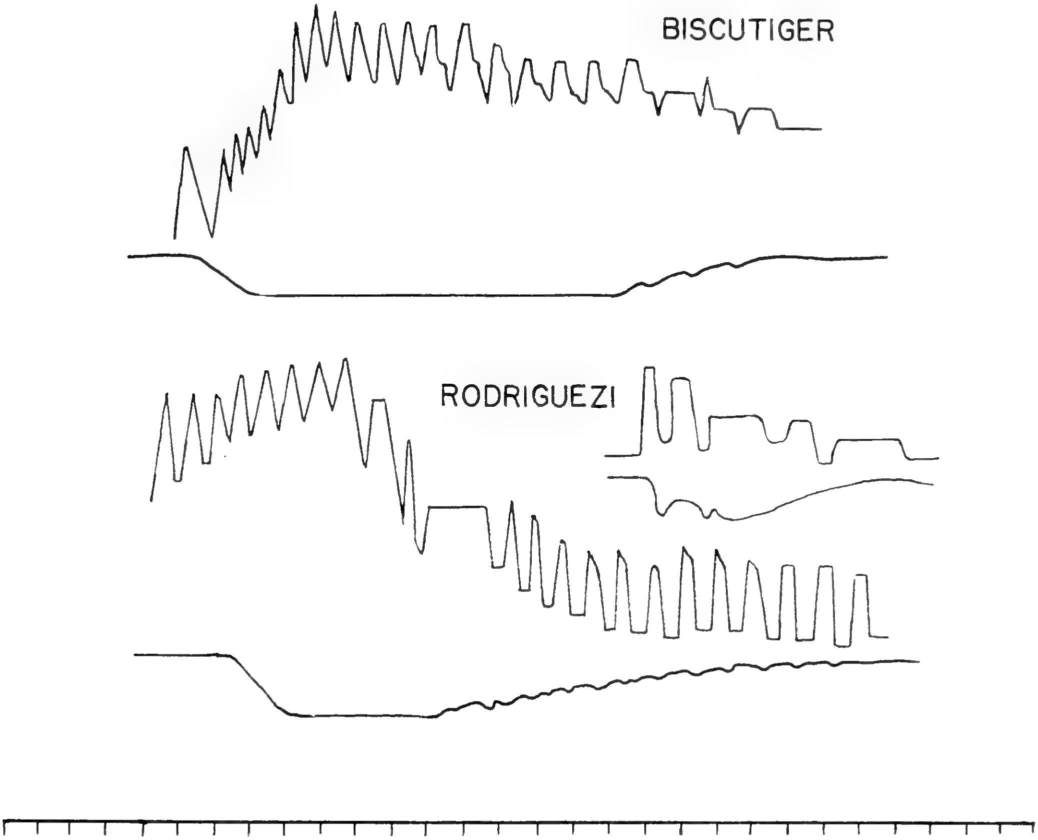


FIG. 3. Diagrams of Display-movements of Anoles. Explanation as in Figure 1. Upper: *Anolis biscutiger,* San Isidro del General, San José Province, Costa Rica. Lower: *Anolis rodriguezi,* Puerto Barrios, Izabal Province, Guatemala (typical display, and on right atypical short display).

rain was flat, open and xeric, but there was a roadside spring flowing into a marsh with vegetation including *Scirpus, Typha* and *Equisetum*. There was a dense thicket of *Crataegus,* with *Cornus, Sambucus, Smilax, Ribes, Salix* and other woody plants bordering the marsh along the road bank. The anoles were found, all within a 30 m radius, in this brush patch. One was on a horizontal stick .5 m over the spring, two were in dense grass at the edge of the marsh and two were in leaf litter beneath the bushes. They were relatively slow and clumsy and were easily caught.

The three adults each weighed between 3 and 4 grams and their lengths (S-V) were: 53 (♂), 53 (♂), and 56 (♀). All thus equalled or exceeded the maximum size indicated for *Anolis anisolepis* by Smith, Burley and Fritts (1968).

The only adult female among the five lacked oviducal eggs, but had somewhat enlarged ovarian follicles (diameter 5.6 left, 2.6 right). Absence of fully developed eggs and of young less than half-grown suggested a cessation of breeding for several months and from analogy with other species it may be inferred that reproduction of *A. anisolepis* is limited to the wettest part of the year (July-September).

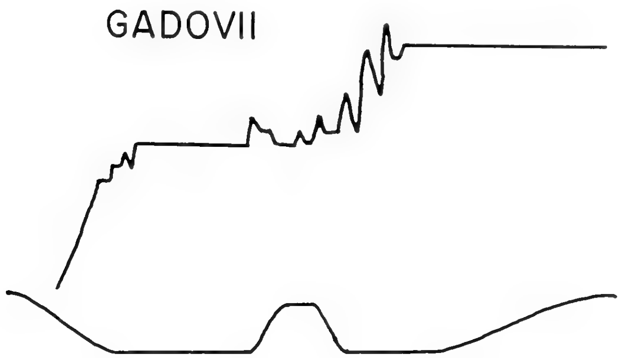
The typical full display-activity pattern began with 1 (20.9%) to 4 (12.5%) preliminary sets of bobs—most commonly with 2 (41.6%) or 3 (25%) performed with the dewlap retracted. Duration of bobs of these preliminary sets was as follows: Set I, .52 ± .075 sec (n = 9); Set II, .26 ± .063 sec (n = 8); Set III, .70 ± .042 sec (n = 5). A bobbing series followed (mean duration, 1.53 ± .121 sec, n = 23) during which the dewlap was pulsed in and out one to five times (usually three or four times). Duration of the entire display was 5.2 ± .39 sec (n = 16). Six of the 22 filmed sequences included no preliminary series of bobs and the figures for total time do not include these. The number of bobs per unit were noted for eight additional filmed sequences, although these were not analyzed frame by frame. In Figure 2 a display of *A. anisolepis* is compared with those of *A. crassulus* and *A. haguei*.

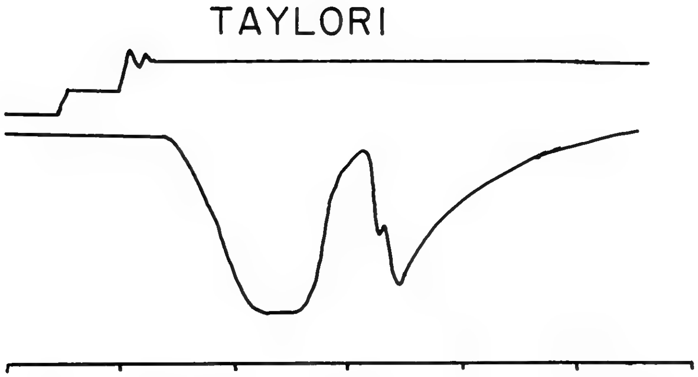
Anolis cuprinus

The original description (Smith, 1964) was based on a single adult male from near Zanatepec, Oaxaca, stated to be a member of the "*cupreus* group" closely related to *Anolis cupreus* of the west coast of Central America, but larger (53 mm S-V), with a distinct frontal concavity, having interparietal smaller than ear opening, having a "bright, blood-red dewlap," not bicolored as in *A. cupreus* and differing in a few details of lepidosis. Lynch and Smith (1966) reported a series of 26 from the same area as the type, and agreeing with it in most characters. Henderson and Fitch (1975) compared the structural niche of *Anolis cuprinus* with that of the smaller, syntopic *A. sericeus*.

Collections were made on 10 and 22 February 1972, at Rancho Las Vigas, 8 km E Zanatepec, Oaxaca, Mexico. This locality is a relatively humid wooded canyon between 270 and 340 m elevation. Although the type locality was stated to be Zanatepec in the original description, intensive search by us near the town failed to reveal *Anolis cuprinus* there and the locality is in open, arid terrain of the coastal plain at an elevation of 240 m. In the original description Smith stated that

FIG. 4. Diagrams of Display-movements of Anoles. Explanation as in Figure 1. The diagrams for *Anolis taylori* and *A. dunni* shown here indicate relative amplitudes of dewlap and head movements (unlike other diagrams in Figs. 1-3 and *A. gadovii* in Fig. 4). Upper: *Anolis gadovii,* Tierra Colorada, Guerrero Province, Mexico. Middle: *Anolis taylori,* Puerto Marqués, Guerrero Province, Mexico. Lower: *Anolis dunni,* Palo Blanco, Guerrero Province, Mexico.


GADOVII


TAYLORI


DUNNI

the holotype was from 5,000 feet (about 1575 m) elevation, which suggests that the locality must have been several kilometers removed from Zanatepec, in the Sierra Madre to the north. Our specimens agree well with the description of the holotype in most respects, but in Smith's photograph the holotype has much more prominent transverse dark bands on the body and more dark pigment on the ventral surface.

The population found by us was limited to a few hectares at the head of a small canyon. Doubtless there are other localized populations in the same general region, but adjacent canyons were drier, with much evidence of fire, and none of the lizards could be found in them. Many *A. cuprinus* were found on the ground in leaf litter. Others were found on vertical tree trunks and stems, usually suspended head downward within 2 m of the ground. A few were on the vertical rock-faces of cliffs or outcrops.

All *A. cuprinus* were found within a few meters of the ravine bottom where there were large boulders and a trickle of water even at the height of the dry season. Even here there were signs of fire; trees, including large ones, had been partly burned. Some of the anoles found were on charred wood. Burning evidently had occurred within the previous year. Perhaps the lizards were able to escape incineration only in unusually protected situations such as were provided by the ravine bottom, but anoles that wandered onto the adajacent exposed slopes probably would have been killed off whenever burning occurred.

Most of the 37 *A. cuprinus* collected in February 1972, were adult, as were others seen that escaped, but a few were subadults. Evidently there had been no reproduction for many months—since the rainy season. The females had neither enlarged follicles nor oviducal eggs at this time, at the height of the dry season. Lynch and Smith (1966) noted that their series of 26 collected between 6 September and 10 December consisted of adults and juveniles. Probably egg-laying begins soon after the onset of the rainy season (July?) and continues into September or even October, but ends in time for all but the latest eggs to develop into adults by February. If so, the annual cycle is like that of the more southerly *Anolis cupreus,* but with the breeding season even more concentrated by the constraints of the long and severe dry season.

Several males that were confined together displayed, and three sequences of different individuals were analyzed (Fig. 1). The displaying lizard tilted its head far back to allow ample space for extension of the relatively large dewlap, which was sometimes tipped or wobbled to make it more conspicuous to a nearby adversary. There was a series of 7-10 bobs (3.9-7.6 sec), a pause (.7-1.2 sec) and then three head drops with intervening pauses. Extension of the dewlap began with the first bob and lasted 5.3-9.6 sec, with retraction in the pause before the first head drop or immediately after it, lasting 2.7-3.2 sec. The dewlap was spread again between or after the head drops, for 1.0-1.9 sec, but not maximally. Following the second retraction by 2.1-3.4 sec was a third extension, .8-1.4 sec, after the last head drop. The bobbing sequence and head drops lasted 10.4-13.8 sec.

Anolis dunni

The original specimen, from Agua de Obispo "between Rincón and Cajones," Guerrero, was first reported by Smith (1933) as *Anolis gadovii.* Later the same author (Smith 1936) after having examined *gadovii* material, named the present species and distinguished it from *A. gadovii* by its widely separated, narrow and ill defined frontal ridges, vertically compressed nares, supraorbital semicircles broadly in contact, separated from inter-

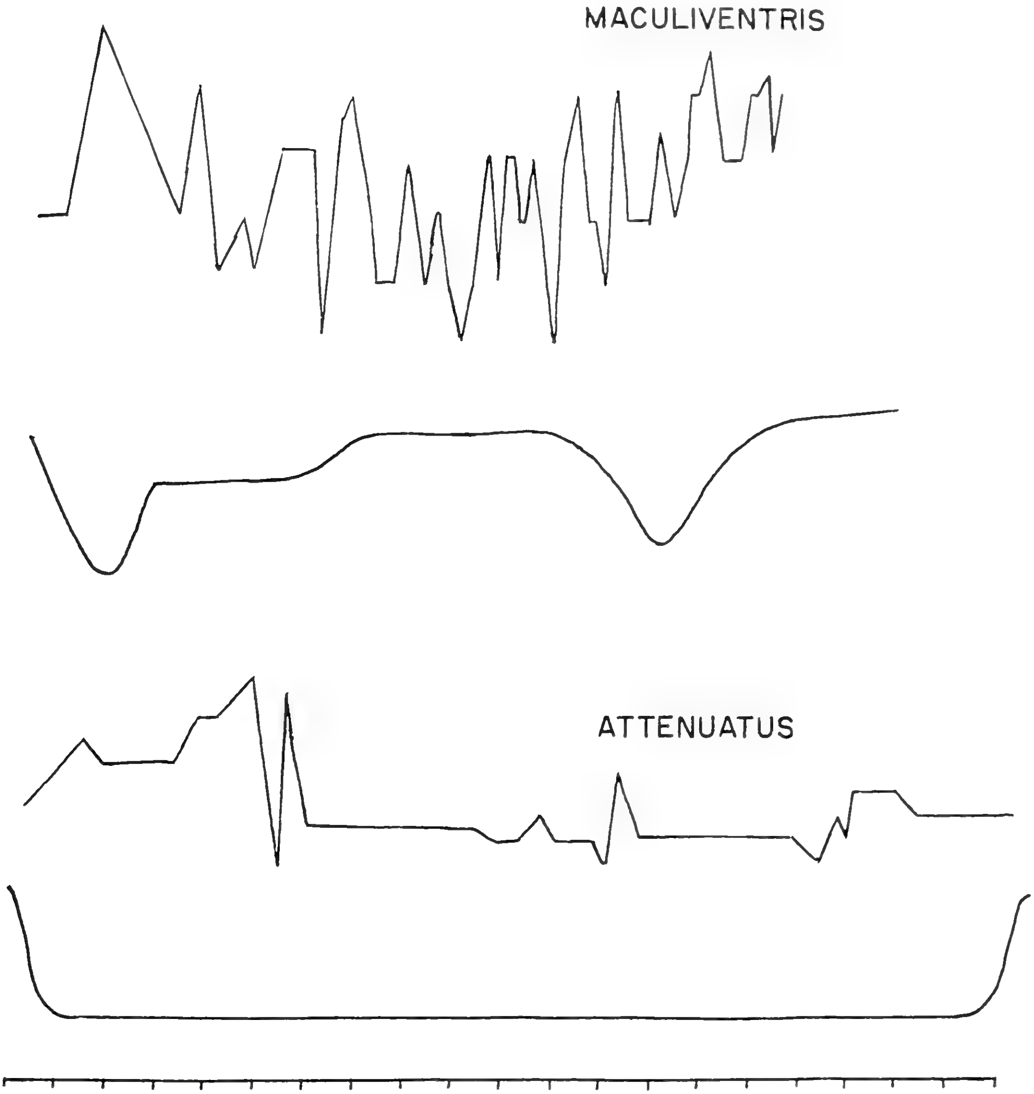


Fig. 5. Diagrams of Display-movements of Anoles. Explanation as in Figure 1. Upper: *Anolis maculiventris,* Tinalandia, Imbabura Province, Ecuador. Lower: *Anolis attenuatus,* Monteverde, Puntarenas Province, Costa Rica.

parietal by a single series of scales, and reddish dewlap. Davis (1954) mentioned additional characters. Davis and Dixon (1961) reported *A. dunni* from the same part of southern Guerrero, at elevations between 2,800 and 3,300 feet, in tropical deciduous forest and pine-oak forest adjacent to it at higher elevations. Duellman (1961) reported it 300 km farther west in Michoacán.

On 24 July 1971 an adult male was found in the lichen-covered crotch of a tree 2.13 m above ground in a humid canyon near a stream 7.5 km S Palo Blanco, Guerrero. A gravid female was found on the same day about .5 km down the same ravine on the ground in herbaceous vegetation at the edge of the water. No others could be found in a week of field work in the general area. Davis and Dixon (1961) found fully developed eggs in several females taken in June and July. Evidently the breeding season begins after the onset of summer rains.

In life the male was olive brown with a lateral white stripe on each side beginning behind and below the eye on the supralabials and ending above the thigh insertion. There were four pairs of lateral white spots on the body, each about the size of the ear opening, the first, on the shoulder, twice as high as long, and the others successively more rounded. The ventral surface was dusky, with small and obscure white dots. Dewlap coloration consisted of four or five dark red bands on a lighter red background; the bands ran parallel with the free edge of the dewlap.

The single male that we collected in July 1971 was kept alive for several months, and he displayed vigorously whenever other anoles were placed with him. The display (Fig. 4) was almost identical to that of *Anolis taylori,* having the same three dewlap movements, preceded by several shallow head jerks. In three of the four displays analyzed there was a preliminary extension of the dewlap preceding the final three dewlap movements by 3.9 to 4.6 secs.

Anolis gadovii

This species was named by Boulenger (1905) from a specimen collected by H. Gadow at Tierra Colorada, 300 m in the mountains of southern Guerrero. It was not mentioned again in the literature until Mosauer (1936) rediscovered it and published a brief account of the habitat and saxicolous habits. Davis (1954) in describing *Anolis omiltemanus, A. subocularis* and *A. microlepidotus* from Guerrero, compared each with *A. gadovii* and included the latter in his key to Guerreran anoles. He characterized *A. gadovii* as large (up to 80 mm S-V), with long hind limb (reaching nearly to eye), having upper parts gray with dark markings, dewlap reddish, ventrals smooth, and with four gulars between the anterior chin shields.

Our observations on *A. gadovii* were made at Tierra Colorada, especially on a rocky hillside 1 km N Palo Gordo (an outlying village southeast of Tierra Colorada) in July 1971. The lizards were on steep rocky hillsides where there were loose boulders 1.5 to 4 m in diameter, sometimes in several layers with luxurious vegetation (including gnarled trees) growing among the rocks and vines screening some of the rock-faces. The anoles were extremely abundant. All were adults, usually associated in pairs, with intervals of usually 5 to 8 m between pairs. Most often the anoles were on vertical rock surfaces. They were shy and elusive, hiding beneath concealing vines and relying on their cryptic pattern, or moving downward out of sight and out of reach beneath the rocks. "An estimated 25 per cent of those seen used tree trunks or stems ranging from 2 to 50 cm in diameter" (Fitch and Henderson, 1976).

All the females seen appeared to be gravid. Ten that were dissected had both oviducal eggs and enlarged follicles. Seven had an oviducal egg (10.5 to 14.6 mm) in each oviduct, and one enlarged follicle. The remaining three each had an oviducal egg on one side only and had a single follicle on the side opposite to the egg.

We revisited Tierra Colorada and Palo Gordo in the dry season, in February 1972. Trees were bare and leafless then and herbaceous vegetation was withered and dry. In prolonged search only three juveniles were seen. Evidently activity is much reduced, the anoles tending to stay in relatively cool and humid situations deep beneath the rocks. The breeding season of *A. gadovii* is believed to resemble that of *A. taylori* (July through October?) but to be even more restricted by the more xeric conditions where it occurs.

Five displays of two individuals were analyzed. The displays were characterized by one or two dewlap extensions each associated with a short series of ascending head bobs (Fig. 4).

Anolis megapholidotus

This species was described by Smith (1933) from four males and two females, all from Agua de Obispo about 45 km S Chilpancingo, Guerrero, Mexico. The species was diagnosed as having ventral and dorsal scales strongly keeled, scales of supraorbital semicircles enlarged, strongly keeled and in contact or separated by a single row of scales, occipital about equal in size to ear opening, dorsal scales larger than ventrals; dewlap red, extending to mid-belly in male, small in female.

Davis (1954) included *Anolis megapholidotus* in his key to Guerreran anoles and compared it with other species. Davis and Dixon (1961) found *A. megapholidotus* at additional localities near Agua de Obispo, in tropical deciduous forest and pine-oak forest, from 850 to 1350 m.

Females they collected in June were all gravid. Eight adult females we collected at Agua de Obispo 10-12 July, 1971, also were all gravid. Four had one oviducal egg, each in the left and right oviducts and four others each had an egg in only one oviduct. Also, each female had either one (in 3) or two (in 5) enlarged ovarian follicles. Only adults were seen, suggesting that there had been no reproduction for several months during the dry season. Meanwhile, young of the previous year had grown to adult size.

Displays were easily elicited when males were confined together, but also were readily interrupted by movements of other lizards, and no fully complete sequences were filmed. Displaying males spread their small, brightly colored dewlaps to the fullest extent and, with head elevated, strained upward in several slow, irregular, bobbing movements. The dewlap movements were the most conspicuous part of the display. The dewlap was gradually and fully extended during the first 1.2 seconds, then collapsed, and finally gave three double pulses, each shorter and more rapid than the previous one, in the final three seconds. The entire display lasted approximately five seconds.

Anolis microlepidotus

This species was described by Davis (1954) from three specimens collected in the mountains of southern Guerrero near Chilpancingo, and was characterized as small and slender, with short legs, small ear opening, keeled ventrals, small keeled dorsals, grayish coloration, and ruby red dewlap. Davis and Dixon (1961) reported it from additional localities in the same general area. They found it in pine-oak and tropical deciduous forest types, in both xeric and swampy habitats.

We found *Anolis microlepidotus* at several localities in southern Guerrero and Oaxaca, at medium altitudes in rocky open woodland of scrub oak (*Quercus* sp.). The lizards were always associated with leaf litter and were at or near ground level.

An adult female found 4 km S Almolonga, Guerrero, June 1971, was perched on a small flat boulder in a clearing; another was on a horizontal stick 75 mm above the ground. In the mountains of northern Oaxaca, 3.2 km E Ixtepeji at about 1830 m, an adult male was found in a ravine bottom and ran into the cavity at the base of a large oak tree before capture. Two immatures were captured along the same ravine the following morning. One was in a small brush pile of oak cuttings and one flushed in a thicket ran up onto the stem of an oak bush. On 8 February in the mountains south of Oaxaca .8 km N Portillo San Andrés, 2,220 m, a juvenile female flushed from leaf litter climbed 75 mm on an oak stem 13 mm in diameter. The sky was overcast and the lizard was active at air temperature of about 17° C.

In life, these lizards were dull-brown dorsally, reddish brown head contrasting with body, and dewlap bright purplish red. Their habitats were among the most xeric in which we have found anoles of any kind.

One of the females collected near Almolonga in early July contained in each oviduct an egg nearly ready to be laid (11.0 x 5.6 mm left, and 11.2 x 6.5 mm right) and also contained large ovarian follicles (6.0 mm left, and 2.7 mm right). The other had an egg only in the right oviduct (10.1 x 6.2), but had large ovarian follicles on each side (7.2 left, 4.5 right). Both females show concentrated egg production after the onset of summer rains. The presence of juveniles in February seems to show that egg-laying may continue into November, and perhaps incubation and early growth are much slower at the altitudes where *A. microlepidotus* occurs than they are in species of the neighboring lowlands and foothills.

When an adult male and two immatures were confined together they displayed several times. One sequence, filmed from the adult male, may be complete. As in other species of Guerreran anoles the display was relatively simple and was notable for the dewlap movements. The displaying lizard did not greatly elevate its head as do some other kinds, and there was conspicuous antero-posterior rocking movement accompanying the display bobs. The display consisted of three slow and high bobs with intervening deep bows and with a pause preceding the last bob. Each bob was accompanied by an extension of the dewlap, about halfway on the first one, fully on the second and about three-fourths on the third. This main part of the display lasted for 9 sec. In the following 7 sec after the bobs there were two small dewlap pulses, the second barely perceptible.

Anolis parvicirculata

This species has been reported only in the original description (Alvarez del Toro and Smith, 1956) from two specimens collected at Suspiro (between Ocozocuautla and Quechula) in west-central Chiapas, Mexico. The authors characterized the species as a member of the "heteropholidotus group," thus associating it with *Anolis heteropholidotus,* a slender, long-tailed, high-montane species of El Salvador. *Anolis parvicirculata* has smooth ventrals, and has small scales in the supraorbital semicircles.

An adult female, captured near the type locality (3 km NW Suspiro) 15 February, 1972, was in life olive drab dorsally with a narrow pale tan, middorsal line; ventral surface pale grayish brown with coarse faint speckling laterally; legs were of the same color as body with no discernible markings, but the fingers and toes had faint dark bands; the dewlap was small and uncolored.

This is an unusually slender species, most readily recognizable by the extremely large eye with dark iris. The female's length of 50 mm (S-V) equalled the length of the paratype and exceeded that of the male holotype (46 mm). As in most other rain-forest species the male probably is little, if at all, larger than the female and may average smaller.

The female contained a full-sized oviducal egg and a large ovarian follicle, although females of several other species collected in the same month in Chiapas and Oaxaca in more xeric habitats were all nonreproductive.

Anolis subocularis

In the original description, Davis (1954) listed 100 specimens from Tierra Colorada and nearby localities in southern Guerrero. He stated that some of the specimens had previously been reported as *Anolis nebuloides,* but they were different from that species in having dorsal scales noticeably smaller than ventrals. Other diagnostic characters mentioned were: Row of small intercalated scales between suboculars and supralabials; ventral scales keeled; long hind leg, reaching forward beyond eye; dewlap orange or reddish (p. 4, but also stated to be ruby red, p. 6); males considerably larger than females. Davis stated that *Anolis subocularis* was the commonest anole in Guerrero below 1500 m elevation.

An adult male we collected at Puerto Marqués had the following appearance in life: Dorsal color yellowish olive, with narrow, jagged-edged lateral brown line from above axilla to above thigh on each side and a second lower line, from behind axilla to thigh; several whitish spots with dark borders on each side; two longitudinal ventrolateral rows of black dots; ventral surface dull white; five pairs of dorsolateral light spots with dark edges; broad, faint, dark bars on limbs, more distinct on toes; top of head spotted with black, largest spots in supraocular region; tail faintly banded; dewlap red, extending posteriorly to level of elbows.

We found *Anolis subocularis* at many localities in southeastern Guerrero and southwestern Oaxaca, sometimes in great abundance, in a variety of habitats, as indicated by the following field notes in July 1971, and February 1972.

25 February, 12 km ESE Río Grande, Oaxaca, in oceanside coconut grove. Many anoles were found mostly among dried palm fronds on ground.

26 February, .8 km N Guachupin, Oaxaca. East-facing hillside with open type of scrub forest (trees leafless then in dry season) interspersed with gigantic boulders, some in groups. Anoles were found on bare rock-faces and on tree trunks, within 1 m of ground.

26 February, 9.0 km E Jamiltepec, Oaxaca. One juvenile found in thicket beside swift, rocky stream.

27 February, 7.2 km W La Estancia, Oaxaca. Low, rolling grassland, recently burned off. Along a gully, which then, in the dry season, had a mere trickle of water, there was a band of green vegetation, with trees, brush and some herbaceous growth. Anoles were abundant in ground litter and on stems and tree trunks near the ground.

27 February, Ometepec, Guerrero. One found at dusk beside swift, rocky, mountain stream.

28 February and 21 and 22 July, 12 km W Marquelia, Guerrero. Anoles were found in moderate numbers on coconut palms in an open grove. Most often they were between 1 and 2 m on the trunk, clinging head downward and were conspicuous from a distance. They were somewhat wary and upon approach of a person would ascend the trunk far out of reach.

29 February, Puerto Marqués, Guerrero. Several were seen on the steep mountainside (strewn with gigantic boulders, interspersed with gnarled trees and thickets). Here they were associated with the much more numerous *Anolis taylori* and the relatively scarce *A. nebulosus. A. tay-*

lori was most often on rock surfaces, whereas *A. subocularis* was here seen only on tree trunks.

21 July, 7.2 km ESE San Marcos, Guerrero. Three adults were taken and others seen on the trunk of an isolated large thorny tree at the edge of a cultivated field.

21 July, 14.3 km N Cruz Grande, Guerrero. Eight were captured and others seen on tree trunks in a riparian grove.

All those collected or seen in late February and late July were adults. The February specimens were sexually inactive, with neither oviducal eggs nor enlarged follicles and with fat bodies minute. All seven July females were sexually active with a total of 9 oviducal eggs and 13 enlarged follicles. All but one had an enlarged follicle in each ovary; three each had 2 oviducal eggs, three each had 1, and one had none. Evidently, breeding had begun within the previous month, after the onset of the summer rains. Breeding must be limited to late summer and early autumn, probably ending in October or even earlier, because young had all attained adult size by late February.

Sexual difference in size is much greater in *Anolis subocularis* than in most other mainland anoles. Mean female-to-male length ratio was 76.1%. Mean female-to-male weight ratio was 49.1% in February, but had increased a 83.5% in July when all females were gravid.

Six displays of four individuals were analyzed. Initial and terminal portions of the display were often given separately. The initial portion, less stereotyped than the terminal portion, consisted of three or four bobs, a pause (2.5-5 sec) and another bobbing sequence, sometimes followed by a third. The terminal portion (Fig. 1) consisted of 11-17 bobs. Between the first two major bobs of the terminal series there were 3-6 short, rapid bobs. Each major bob consisted of a rapid upward movement from which the head was lowered about one-third of the downward distance and paused .2-.6 sec before it lowered the remaining distance. The dewlap was spread and retracted three times during the initial portion of the display and four times during the following pause, and was maximally extended during the long series of terminal bobs. It was retracted after the last bob but subsequently might be pulsed two or more times.

Anolis taylori

This species was described by Smith and Spieler (1945) from eight specimens collected in the vicinity of Acapulco, Guerrero. It was stated to be a "rock anole" closely related to *A. gadovii* and *A. dunni*, separable from the former by having only 2 (rather than 3 or 4) gulars in contact with mental, and separable from the latter by having smaller ventrals and having 7 or 8 (rather than 6) scales between nasals. Smith and Taylor (1950) included *A. taylori* in their checklist of reptiles of Mexico, but the species seemingly has not been investigated further in the last 25 years. Fitch and Henderson (1976) described the structural niche and field behavior of a population of *A. taylori* at Puerto Marqués 7 km SE Acapulco. These lizards are extremely abundant in their chosen habitat of enormous boulders on steep, wooded mountainsides.

In late July (early in the rainy season) only adults and adolescents could be found. All of the 13 adult females dissected were gravid. Five had an oviducal egg on each side and also an enlarged follicle in each ovary; 2 had an egg on each side, but had an enlarged follicle in only one ovary; 5 had an egg in one oviduct and a large follicle in each ovary; and one had only one egg and (on the opposite side) an enlarged follicle. Reproduction seemed near a peak at that time, with eggs being produced in rapid succession. In late February and early March (late in the dry season) the population sample consisted largely of immatures, mostly more than half-grown, and adult females were nonreproductive.

The incidence of reproductive females and young of various sizes indicated suspension of reproduction in the dry season, perhaps from November through June, and resumption of breeding in July, with hatchlings beginning to appear around August and continuing to appear into October or November. A relatively short and concentrated breeding season, as compared with those in other anole species, is indicated.

Fitch and Henderson (1976) recorded a mean of approximately 29° (26.0 to 32.8) for 30 body temperatures of *A. taylori*. Generally air temperatures were near these levels when the lizards were most active. Activity tended to reach a peak about midmorning and was much reduced at midday with some tendency to increase again in late afternoon.

The display of *A. taylori* was distinctive in having the dewlap fully extended or in motion for the entire sequence and constituting the dominant component, whereas head movement was minimal, generally consisting of 3-5 preliminary twitches. The dewlap was first slowly and fully extended, then gradually retracted (1.90 ± .092 sec, n = 18). The extension and retraction covered approximately equal intervals, with a slight intervening pause (.64 ± .092 sec, n = 18) while the dewlap was held maximally extended. There was another slight pause (.98 ± .056, n = 18) between the retraction and the pulse that followed, during which the dewlap was spread to no more than half its full extent. A third extension, usually to no more than three-fourths of full extent, ended the series (1.58 ± .198 sec, n = 18). The pulse between the two major extensions ranged from a completely separate movement to a momentary pause in the second major extension. The active, pulsing movements rendered the dewlap-display highly conspicuous. The final retraction of the dewlap was often much more prolonged than the retraction occurring after the first dewlap display. In contrast to the first dewlap extension, the final extension immediately graded into retraction with no pause after maximal extension (Fig. 4).

Some variation in the display was noted. The dewlap was occasionally extended once, before (5 displays) or after (3 displays) the sequence described. Usually there was a pause of two or more seconds between these extra dewlap extensions and the main sequence.

THE CENTRAL AMERICAN SPECIES

Anolis aquaticus

This species was described by Taylor (1956), who had one specimen from Palmar and two from Golfito, both in Puntarenas Province, Costa Rica. Diagnostic characters listed in the original description include: Heavy, dark, transverse bars wider than interspaces on body, limbs, and tail; dewlap, large, orange; tail compressed with a middorsal row of enlarged serrate scales; ventrals keeled and much larger than dorsals; scales of middorsal pair of rows on body markedly enlarged; suboculars separated from supralabials by two or three rows of small scales; three or four scale rows between supraorbital semicircles.

In our study many *A. aquaticus* were observed and others were collected and preserved at Finca Las Cruces near San Vito, Puntarenas Province, Costa Rica. All of the lizards were found along swift, flowing, rocky, mountain streams. Usually, they perched on rocks; sometimes they were on logs or sticks. They were wary and when approached they dove into the water, swam for distances up to several meters, and emerged in well concealed places, such as cavities beneath log jams or overhanging rocks, or in accumulations of drift.

Of 9 adult females collected at Finca Las Cruces, 14 March, 1974, two had neither oviducal eggs nor enlarged follicles, but the remaining seven were all reproductive. Four each had an oviducal egg on one side and an enlarged follicle on the opposite side. One had an enlarged follicle on each side (4.5 and 3.4mm), but lacked oviducal eggs. One had an oviducal egg (left), but no follicles. One had an enlarged follicle (5.9 mm, left), but no oviducal eggs.

In other species of anoles, it is most typical for a female to have two oviducal eggs simultaneously—one larger than the other and destined for earlier laying—with ovarian follicles also developing, ready to replace each egg soon after it is laid. The smaller number of such reproductive units in the females of *A. aquaticus* suggests that it has a lower reproductive potential, although rate of development and extent of seasonal change are not known. In both February 1973 and March 1974, young of various sizes were seen (though in small numbers), suggesting year-round reproduction, as might be expected in the consistently warm and humid climate where *A. aquaticus* occurs.

Anolis attenuatus

Taylor (1956) named this anole (as a subspecies of *Anolis woodi*) from three specimens collected at Isla Bonita, altitude 1680 m, on the southeastern slope of Volcán Poás, Heredia Province, Costa Rica. Diagnostic characters that he listed in the original description include: Large size (S-V 78-83 mm); tail 2.4 times body length; ventrals keeled and slightly larger than dorsals; approximately 140 scales about body; postanals enlarged; extended hind leg reaching forward beyond eye; extended foreleg reaching back to groin; body dull-red with black markings; dewlap large, dark olive, with magenta scales.

Anolis woodi was described by Dunn (1940) from El Volcán, Chiriquí, Panama, from a single female specimen, but Taylor (1956) reported it from Cañas Gordas, Puntarenas Province, Costa Rica, and other specimens have been reported from several localities in the southern half of Costa Rica. *A. woodi* and *A. attenuatus* are both large, slender, long-legged and long-tailed anoles with large dewlaps. However, they differ in body size, relative sizes of the sexes, color of body and of dewlap, and relative length of tail and limbs (Table 6). In view of these numerous and trenchant differences and the fact that their known ranges are well separated, so that there seems to be no opportunity for geographic integradation, they are best considered distinct species.

We found *Anolis attenuatus* at Monte-

TABLE 6
COMPARISON OF *Anolis attenuatus* TO *A. woodi*

	A. attenuatus	*A. woodi*
Geographic range	Cordillera de Tilarán and C. Central	Cordillera de Talamanca
Size S-V		
mean for ♂♂	84.5 in 24	80.8 in 4
mean for ♀♀	80.6 in 18	69.9 in 10
♀ to ♂ size ratio	94.4%	86.6%
Dorsal color	Dull red with black markings	Olive with rusty spots
Dewlap color	Dark olive or black	Bluish white at base, bordered with amber yellow; pink orange on outer edge
Approximate number of scales around mid-body	140	125

verde, Puntarenas Province, Costa Rica, 70 km W and 11 km N of the type locality; from March 1973 to March 1974, 49 records were accumulated, many of them by Dr. Richard K. La Val. Most of the lizards were found on tree trunks; a few were on the ground.

These lizards were slow-moving and depended largely on cryptic behavior and coloration to avoid detection. Once seen, they were easily captured. On many occasions those that were captured and released, or merely observed in the field, were seen again after intervals of hours in almost the same location and position.

In their montane habitat, mean air temperature was about 18° C at the times of capture. The seasonal distribution of females that appeared gravid (March, July, August, September, and October) and of immatures suggested year-round reproduction.

Taylor (1956) described the behavior of two of the original specimens from Isla Bonita, before they were collected, as follows: ". . . on the top of a tree fern . . . fighting. The male with dewlap extended would attempt to bite the female. Then the female would retreat to another frond and shortly would return to attack the male . . . who at all times had the throat fan extended. . . ." In our study, presentation of mirrors and of transferred individuals and placing individuals together in confinement did not elicit display, except when a juvenile was placed with a juvenile *A. insignis* and responded to its challenge. The displays were notable for the small amount of movement and the long pauses, with the large, dull-colored dewlap held fully extended (Fig. 5). The single display analyzed lasted 20 sec, with initial, middle and terminal phases separated by pauses of about 3.3 sec. The first phase consisted of a slow elevation of the head and spreading of the dewlap, then a slight dip and pause (1.4 sec) and a high bob interrupted by a half-second pause near the top, a very rapid dip closely followed by another high bob and dip. The middle portion following the first main pause, began with a small dip followed by a small bob, short pause, second dip and medium bob. The terminal portion consisted of a small dip and then a rapid small bob followed by a medium bob with a pause (.7 sec) at the top, a small dip, pause, and final retraction of dewlap.

Anolis biscutiger

Taylor (1956) named *Anolis biscutiger* from 11 specimens collected in Puntarenas Province, Costa Rica (Golfito 1—the holotype, Palmar 8, 24 km WSW San Isidro del General 2). Among the diagnostic characters mentioned were: Small size (length S-V less than 40 mm); tail twice snout-vent length; extended hind limb reaching between eye and nostril; two pairs of much enlarged postanals; supraorbital semicircles separated by one scale row; seven loreal series. Taylor did not specifically discuss the relationships of *A. biscutiger* and *A. limifrons,* but his descriptions of the two differ only in minor details and obviously they are closely related. Savage (1973) in his list of the amphibians and reptiles of Costa Rica did not include *A. biscutiger,* but considered it a synonym of *A. limifrons* (pers. comm.). Williams and Smith (1966) recorded it from Julieta and this locality remains the northwesternmost record.

Accumulated evidence has led to a reconsideration of the relationship of *A. biscutiger* to *A. limifrons.* The differences between them, though small, are numerous and fairly constant. The known range of *A. biscutiger* is in the Pacific lowlands of Costa Rica from Julieta to Golfito, effectively separated from *A. limifrons* in the Caribbean lowlands by the mountain-mass of the Cordillera de Talamanca. The type locality of *Anolis limifrons* is Cucuyas de Veraguas, Panama. Fresh material from there is needed for comparison with other populations, including those of *A. biscutiger* and Costa Rican *A. limifrons*. However, it is known that Panamanian *A. limifrons* differ in size, proportions, dewlap-color and scalation from both these Costa Rican populations.

Some characters of *A. biscutiger* which reflect its relationships are the following: Female-to-male length ratio 105.6%, males 37.3 ± .332 mm, 43-33 in 42, females 39.4 ± .416 mm, 44-36 in 33; tail to snout-vent ratio 1.96%, 1.77 to 2.18 in 43; postanals much enlarged in males; adpressed hind limb reaches between eye and nostril; adpressed forelimb reaches beyond snout.

A total of 33 body temperatures were recorded for *A. biscutiger* at Quepos. All but two were in the range 30-33 and nearly half were in the interval between 31 and 32. In samples collected at Quepos in December, January, February, March, May and August, most females were gravid and juveniles were not prominent in any of these samples. Hence, it seems that in the humid climate where *A. biscutiger* occurs, its breeding is extended throughout the year, or much of it, but probably with changing levels of incidence.

The display begins with a series of 3-18 bobs (duration, 2.5 ± .47 sec, n = 11) as the dewlap is slowly extended. A series of 2-5 inverse head bobs (Echelle *et al.,* 1971a) follows (duration 1.57 ± .183 sec), during which the dewlap is gradually retracted. The pause between the two parts of the display is short (.12 ± .051 sec). The dewlap is pulsed submaximally during each down movement of the inverse head bobs, which are of small amplitude. The display is relatively short, averaging 4.3 ± .46 sec.

Anolis carpenteri

This species was described by Echelle, *et al.* (1971b) from 10 specimens collected at the Río Reventazón, Turrialba, Cartago Province, Costa Rica. Distinctive features indicated were: Small adult size (35 to 45 mm S-V); grayish green color; buffy eye ring; female-to-male ratio 104.9 per cent; relatively short tail (1.61 times body length); hind limb extending to ear or slightly beyond; forelimb extending to midway between eye and nostril; and orange dewlap. Myers (1971) described the species (as *Anolis procellaris*) from a single male (illustrated with a photograph from life) from Veraguas Province, Panama. A fairly extensive range in the Caribbean lowlands of Central America is indicated. There is one specimen in the K.U. Natural History Museum from 10.5 km N and 9 km E Matagalpa, Nicaragua. One was seen, but not captured, at Beverly, Limón Province, Costa Rica, and numerous individuals have been captured or seen at Finca La Selva, Heredia Province, Costa Rica.

At the latter locality, females examined and released in February, April, August, October and November all appeared to be carrying eggs and probably there is some reproduction throughout the year.

In the display, an initial crouch was followed by a series of two to four ascending push-up bobs and these were followed by a series of four to six slower and more uniform bobs, with a distinct pause after each. In three of seven displays, there was a preliminary series of two to four low, short bobs before the ascending push-ups, but in the remaining four displays this preliminary series was absent. The dewlap was fully extended during the entire display, which lasted about 15 seconds. In two displays, the tip of the conspicuous, red tongue protruded from the mouth. A more detailed description of the display was included in the original description of the species (Echelle *et al.,* 1971b).

Anolis dollfusianus

This small Guatemalan species was

named by Bocourt (1873) from San Augustín, Volcán Atitlán, altitude 1200 m. Stuart (1955) made a detailed comparison of *A. dollfusianus* with *A. cupreus,* implying that the two might be closely related and might even intergrade, as their ranges seem to be complementary. He stated that *A. dollfusianus* occurs commonly in the upper part of the tropical zone between altitudes of 600 and 1500 m and is abundant in coffee groves. He erroneously stated that the adult male of *A. dollfusianus* is only 25 mm in snout-vent length. Other diagnostic characters which he mentioned were the yellow dewlap, keeled ventrals, rugose plates of occipital region, and anterior head shields with upturned edges and central keel, making them appear tricarinate.

Field observations indicate that *A. dollfusianus* occurs in high population densities in favorable habitats. However, it has remained little-known because of the small geographic range, extending from the vicinity of Escuintla in Guatemala west to the vicinity of Tapachula, Chiapas, Mexico, a distance of approximately 270 km, in a band of perhaps half that width, at low and medium altitudes on the south slope of the Sierra Madre del Sur.

Our field observations on *A. dollfusianus* were made near Retalhuleu, Guatemala, 16-24 February 1971, and Tapachula, Chiapas, Mexico 17 February 1972. At the Guatemalan locality four of the six adult females each had a single oviducal egg and an enlarged follicle in the opposite ovary. A fifth which lacked the oviducal egg had an enlarged follicle (3.4 mm). The sixth female had a follicle that was only slightly enlarged. Approximately half of the 64 anoles in this sample were immature, but only five were less than half-grown.

In contrast, the series of 53 from southern Chiapas had only six immatures (from half-grown to adolescent size), and only one of 13 adult females had an oviducal egg, while one other individual had an enlarged follicle. Seemingly, the timing of reproduction is influenced by locality and weather. At low altitude in southern Chiapas, there was little reproduction in late fall and winter 1971-72, but at higher altitude in southwestern Guatemala in a somewhat cooler and moister climate in late fall and winter 1970-71, reproduction was maintained at a considerably higher level.

Fifty-five displays were analyzed, 41 from 14 males from near Tapachula, Chiapas, Mexico, and 14 from 9 males from Retalhuleu, Guatemala. The two localities are 75 km apart and average differences were discernible in the displays. The most common display was a series of 3-10 rapid low-amplitude bobs that averaged 2.32 ± 1.77 sec for the Guatemalan lizards and 2.93 ± .222 sec for the Mexican lizards and were accompanied by a single dewlap movement of 1.66 ± .094 sec (Mexican) or 3.2 ± .30 sec (Guatemalan). In the Mexican lizards, dewlap extension began 1.07 ± .061 sec before the end of the last bob and 1.19 ± .140 sec after the beginning of the first bob. For the Guatemalan lizards, corresponding figures were 2.28 ± .198 sec and .66 ± .111 sec. Although dewlap extension was definitely more prolonged in the Guatemalan lizards, the displays in the two populations were essentially similar (Fig. 2).

Anolis haguei

In the original description of *Anolis haguei,* Stuart (1942) distinguished it from the closely related *Anolis crassulus* by its much smaller dorsal scales. Later the same author (Stuart 1948, 1955) relegated *haguei* to subspecific status, indicating that it replaced *Anolis crassulus crassulus* in cloud forests of Alta Verapaz, Guatemala at altitudes above 1300 m. Smith and Kerster (1955) reported a single specimen, allegedly from "Región Soconusco" in the Pacific lowlands of southern Chiapas, Mexico, and suggested that *haguei* was a species distinct from *crassulus.* Smith, Burley and Fritts (1968) described *Anolis anisolepis* from San Cristóbal de las Casas in the mountains of central Chiapas, as a near relative of both *A. crassulus* and *A. haguei,* and recognized an *'anisolepis group'* of species characterized by small size and having scattered small groups of enlarged scales irregularly distributed over the sides where most of the scales are minute granules. Members of the *anisolepis* group also have strongly keeled ventral scales, enlarged dorsals, and knobby, rugose dorsal head scales. The diagnostic characters that distinguish *A. haguei* from *A. crassulus* and *A. anisolepis* are listed under the account of the latter species.

On 16 February 1971, four of these anoles were captured and many others seen in a roadside hedge of agaves 2.4 km west of Quetzaltenango, Guatemala. The lizards were active and shy, responding to approach of a person by running back toward the stalk at the base of the leaf. The long, rigid leaves with recurved spines along their margins provided effective protection. The dorsal pattern of grayish brown with a series of paired dark blotches rendered these lizards remarkably like *Sceloporus* in appearance and the impression was heightened by their behavior and by the xeric aspect of the habitat. Two females had neither oviducal eggs nor enlarged follicles, but they may not have been fully mature.

The display usually consisted of 4 or sometimes 5 series of rapid bobs interrupted by short pauses. The final or main series of bobs had more than the preliminary series. The first consisted of 2 quick bobs with no extension of the dewlap. The second was longer (average 1.24 ± .089 sec, n = 11) with 3 to 6 bobs and a pronounced dip of the head toward the end of the series. A dewlap flash of .42 ± .045 sec, n = 11 accompanied this series. Compared with the display of *A. crassulus* from Panajachel, Guatemala (Fig. 2), the display of *A. haguei* was more variable, with an apparent repetition of the second preliminary bobbing series of *A. crassulus.* Homology with the second series of *A. crassulus* was predicated on the form of the bobs and the fact that they were accompanied by a dewlap movement. The third preliminary series was the shortest (.24 ± .052 sec, n = 11) and usually consisted of a single quick bob occurring within a second before the final bobbing series. The latter involved 4-10 bobs and another dewlap flash (.61 ± .065 sec, n = 11). Twice in displays of high intensity, two deep bobs (adding 2.6 and 4.1 seconds to the duration of the display) preceded the main display as described above. During these bobs, the dewlap was extended, the mouth gaped, and the engorged red tongue was conspicuous.

Anolis insignis

This species was described by Cope (1871) from a specimen purportedly from San José, Costa Rica (collected by a Dr. Van Patten). Diagnostic characters mentioned were: Giant size (total length up to 440 mm, snout-vent 145); ventrals smooth; tail base compressed; extended hind limb short of ear; ear opening half size of eye; body light brown, with four transverse double bands of greenish blue, a large ocellate spot, greenish blue with brown center anterior to axilla.

Taylor (1956) did not find the species in the course of his extensive collecting in Costa Rica, but he cited published records including La Palma between Guapiles and San José, Cariblanco, Ballena, and El Valle, Panama. Peters and Donoso-Barros (1970) stated the range to be "Panama to Costa Rica in mountainous areas."

The single specimen obtained by us, at Monteverde, Puntarenas Province, Costa Rica, constitutes an extension of the known range northwestward into the

Cordillera de Tilarán. It was a hatchling and was on a horizontal branch 2.5 m above ground. Local people reported finding a giant anole, almost certainly *A. insignis,* on the ground in a road, near the same location. When approached it displayed but did not attempt to escape. Probably the rarity of *A. insignis* in collections results partly from highly arboreal habits and preference for large trees in dense primary forest.

In displaying, the juvenile male held his head aligned with the body or only moderately elevated, not tipped far back as in most other species, and the dewlap was not extended to its maximum. The display consisted of a long series of bobs, with either two or three pauses of from 1 to more than 2 sec at low points between successive bobs. In each of two series, duration was 20 sec and there were 13 bobs (Fig. 1).

Anolis rodriguezi

This species was named by Bocourt (1873) from Panzos, Guatemala. Stuart (1948) discussed its similarity to *Anolis limifrons* of southern Central America and relegated *A. rodriguezi* to subspecific status under the former species. The range of *A. rodriguezi* extends from Central America into the Yucatán Peninsula, and various authors have commented on its distribution, habitat and lepidosis in that area.

Whether anoles of the *limifrons* species-complex occur uninterruptedly through the Caribbean lowlands from Costa Rica to Guatemala remains to be demonstrated, but there are extensive gaps in the known range and geographic intergradation between *rodriguezi* and *limifrons* has not been established. Seemingly, there are well-defined habitat differences. *A. limifrons* occurs in primary lowland rain forest and in edge situations. In Yucatán, Duellman (1963) found *A. rodriguezi* in great abundance in xeric areas of scrub, but found it to be rare in rain forest.

Etheridge (1960), in his study of skeletal morphology of the anoles, found *A. rodriguezi* to agree with species of the *Chrysolepis* series, whereas *A. limifrons* and its near relatives were allocated in the *Fuscoauratus* series. In view of this discrepancy and other differences between the two (Table 7) it seems inadvisable to assign *rodriguezi* to the species *A. limifrons* without actual proof of intergradation. Differences in habitat, body size, proportions, sexual dimorphism, dewlap color and aggressive display provide further evidence against conspecificity of the two forms.

Two distinct types of displays were observed in *A. rodriguezi.* The more common display began with 2-5 preliminary bobs of 2.8 ± .39 sec, n = 13. The dewlap was then fully extended during an ascending series of bobs (2-17, most commonly 5, in 5.6 ± 1.7 sec, n = 13) followed by 2-3 descending bobs in 1.44 ± .119 sec, n = 12. Thereupon, the dewlap was partly retracted during a "plateau" bob (1.78 ± .169 sec, n = 11), followed by 1-16 bobs with the head held alternately high and then low for approximately equal intervals, producing a rectangularly shaped bob. Mean duration of this series of bobs was 6.2 ± 1.21 sec, n = 9. During these bobs the dewlap was pulsed—outward as the head lowered and inward as it rose. The rectangularly shaped bobs closely resemble the "inverse head bobs" of *A. biscutiger* and those of *A. limifrons* described by Echelle *et al.* (1971a).

The less common type of display was observed only twice, performed by different individuals. These displays lasted 5.3 and 6.3 sec, and consisted of two rectangularly shaped bobs, a plateau bob, and two final bobs. The dewlap was extended for the entire display in one instance and was pulsed in the other (Fig. 3).

THE SOUTH AMERICAN SPECIES

Anolis aequatorialis

This large species was described by Werner (1894) with no more specific locality than "Ecuador." Peters and Donoso-Barros (1970), described the geographic range as "middle altitudes of western slopes in Ecuador," and they listed various diagnostic characters, including keeled ventrals, long hind leg extending beyond snout with tibia exceeding head length, smooth head scales and keeled supraoculars.

Williams (1974) mentioned that nothing was known of the habits of *A. aequatorialis,* but that, with *A. mirus* and his newly described *A. parilis,* it was a member of the *eulaemus* species subgroup of *Alpha* anoles. In this group, the toe pads are "*Norops*-like"—reduced as in strictly terrestrial kinds and not adhesive, so that the lizards are dependent on their claws for such climbing as they may do.

Five *Anolis aequatorialis* were captured at Tandapi, Pichincha Province, Ecuador on 18, 19 and 23 February, 1975. All were between 2 and 3 m above ground, on outer twigs or foliage of small trees or herbaceous plants. They were not wary or elusive, but seemed to depend on concealment for escape, and were well hidden by screening vegetation. They were found in the same sorts of situations as the smaller and much commoner *Anolis gemmosus.* Partitioning of resources was not evident.

A live, adult male was described as follows: Olive brown dorsally, with seven pairs of dark, dorsal chocolate marks each in the form of an elongate oval, meeting its counterpart middorsally in a chevron-like pattern; second series of oblique dark markings low on sides, partly merged with those of dorsolateral series; midventral area coppery; chin barred and speckled with black; supralabial region from loreals to ear dull white; limbs sharply barred; toes faintly barred; posterior half of tail black; top of head pale green spotted with black; large black patch with white specks on each side of neck; dewlap large, lacking bright colors but with strikingly checkered pattern of light and dark brown. A juvenile of 43 mm (S-V) was much like the adults in color and pattern, but the area between eye and ear, dull white in adults, was malachite green, and the chin was pale blue.

Anolis chloris

This was one of several species described by Boulenger (1898) from Paramba, Imbabura Province, in northwestern Ecuador. Peters and Donoso-Barros (1970) stated the range to be Pacific lowlands of Ecuador and Colombia, and Darién, Panama. They listed diagnostic characters, including keeled ventrals, extended hind limb reaching a point between ear and eye, supraorbital semicircles separated by two rows of scales, five rows of loreals, and six supralabials anterior to

TABLE 7

COMPARISON OF *Anolis rodriguezi* TO *A. limifrons*

	A. rodriguezi	*A. limifrons*
Geographic range	Yucatán Peninsula and northeastern Guatemala	Central America in Caribbean lowlands
Morphological relationships	*Chrysolepis* series of *Beta* anoles	*Fuscoauratus* series of *Beta* anoles
Size S-V		
♂♂	43.4 in 15	37.5
♀♀	43.7 in 23	38.6
♀ to ♂ size ratio	100.9%	102.9%
Dewlap color	Orange yellow	Dull white with faint yellowish central spot

center of eye. *A. chloris* is an *Alpha* anole of the *Latifrons* species series.

In late February and early March, 1975, three of these lizards were captured at Tinalandia, Río Pupusa, Pichincha Province, Ecuador, and several others were seen at the Río Palenque field station. All were adults. Dorsal color was emerald green. The dewlap was medium-sized, pale greenish with a pale blue outer edge. The eyes were blue and the tongue was orange. Those seen at the Río Palenque field station were all on balsa trunks, and only one was captured. Upon approach of a person the lizards would run several meters up the vertical trunks and escape. The sexes were not noticeably different in size.

Anolis gemmosus

This species described by O'Shaughnessy (1875, type locality unknown) was figured and further described by Boulenger (1885). It was included in the list of valid Neotropical anole species by Peters and Donoso-Barros (1970), who stated the range to be "lowlands of Pacific Ecuador" and summarized its scale characters and bodily proportions in their "matrix" for 116 anole species. Williams (1970) stated that its affinities were with other Ecuadorian species, the high-montane *Anolis andianus,* and *A. fasciatus* of the Pacific lowlands. All these are *Alpha* anoles of the *Latifrons* species series.

Despite Peters and Donoso-Barros' (*op. cit.*) statement, it is doubtful whether *A. gemmosus* occurs in the Pacific lowlands, as it seems to be a species of middle altitudes. It has remained poorly known. All published accounts are based upon preserved material, with erroneous statements concerning color and pattern.

In 1967, John D. Lynch and Robert W. Henderson, while carrying on field work on frogs at Tandapi, Pichincha Province, Ecuador, found *A. gemmosus* to be abundant there and they collected a large series. Directed to Tandapi on Lynch's and Henderson's advice, we likewise found *A. gemmosus* to be fairly abundant on 18, 19, 23, 25 and 27 February and 15 March, 1975.

Much variation, individual, sexual and ontogenetic, was evident among the specimens collected, and those seen in the field. In life the general ground-color was deep emerald green. As in many other kinds of anoles, females often had a pale, longitudinal, middorsal band, but its occurrence and development was variable. The band was pale tan to rust color, usually set off by black margins, but these margins varied from broad to narrow. Among 21 adult females, nine had a broad dorsal band, two had a medium band, three had a narrow band, three had a broken or discontinuous band, two had remnants of a band and two were uniform-green. As in other species, the banded female pattern is already present in hatchlings. Though lacking the dorsal band, males were almost as variable as females in their dorsal patterns. Some were almost uniform-green while others were heavily spotted. Small, round or oval, buffy yellow spots were arranged in lateral, slightly oblique series, with as many as eight spots on each side in each series. Irregularly arranged black dots were also present on some, concentrated mainly in the ventrolateral area. Limbs were faintly barred, with black stippling on undersides of limbs and tail. Some white facial markings were present beneath the eye and extending onto the cheek.

In most populations of mainland anoles, male dewlaps are notably homogeneous in color and markings, but *A. gemmosus* is an exception. The highly-variable dewlaps did not seem to comprise well-defined classes but tended to form a continuum between extremes. At one extreme were dewlaps with little contrast, dull yellowish green on the basal area, shading to dull greenish yellow on the outer part. The more contrasting and colorful type of dewlap was similar in having a dull greenish yellow outer part, but the basal part was bluish green with six narrow sharply defined white stripes diverging from a center on the anterior basal portion. The stripes had bright blue edges proximally at their origins, but distally the blue changed to green and the stripes themselves became suffused with the yellow background and finally blended into it and blended with their brighter colored edges.

In our sample of 70, only 13 were immature. Three were judged to be in their first two months (33, 28 and 27 mm) and three others, of 39, 38 and 37 mm were almost surely younger than six months old and more than two months old. The remaining six included four of adolescent size (53 and 52 mm, all females) and two that were more than half-grown (48 mm). A low incidence of reproduction through the fall and early winter months is indicated. However, at the time of sampling, in the rainy season, all females were reproductive. Seventeen each had two oviducal eggs; 11 each had an egg in only one oviduct and an enlarged follicle in the ovary of the opposite side; three each had only one oviducal egg, but no enlarged follicle; and three each had one enlarged follicle but no oviducal eggs. Some reproduction throughout the year is indicated, but with relatively low levels in the fall and early winter.

Anolis maculiventris

This small species was named by Boulenger (1898) from Paramba, northwestern Ecuador, and was stated to have a red dewlap, snout-vent length 45 mm, brownish and metallic purple dorsal color and smooth ventrals. Peters and Donoso-Barros (1970) listed additional characters: Frontal crests present; extended hind limb reaching between ear and eye; 3 or 4 series of scales separating supraorbital semicircles; 8 rows of loreals; 8 supraoculars anterior to center of eye. *A. maculiventris* is a *Beta* anole of the *Fuscoauratus* species series.

A single adult male was found 22 February 1975 at Tinalandia, Río Pupusa, Pichincha Province, Ecuador, low on a tree trunk. In life it was dull grayish brown dorsally, with a pale rusty-red dewlap (having scales paler, yellowish), and with iris golden yellow. When confined with other male anoles, *A. chloris* and *A. peraccae,* this one displayed vigorously, although the others were unresponsive.

The display was complex, consisting of a long series of bobs (16 in 17 seconds) highly variable in amplitude and duration, with occasional short pauses in both the elevated and depressed positions. The first bob was the highest and shortest (2.5 sec) and the dewlap was slowly extended to a maximum corresponding to the peak of the bob. It was then retracted about halfway and held so for 2.5 sec, further retracted and held for 4 sec, and finally was slowly spread (not quite to the maximum) and retracted in the last 6 sec (Fig. 5).

Anolis nigrolineatus

This species was named by Williams (1965) on the basis of two specimens, from Machala and Guayaquil, El Oro Province, Ecuador. Williams (1974) mentioned two additional specimens from Playa de Montalvo, Los Ríos Province, Ecuador, and listed the following characters: Scales across snout 8 or 9; scales between supraorbital semicircles 1 or 2, loreal rows 4 to 7; scales between semicircles and interparietal 2 or 3; 7 to 11 supralabials anterior to center of eye; enlarged postanals in male; one middorsal scale row enlarged. Williams called attention to the swollen rostrum of *Anolis nigrolineatus,* projecting beyond the tip of the chin. He interpreted this development as indicating relationship to other anoles having bizarre nasal appendages—*Anolis proboscis, A. phyllorhinus* and *A. laevis.* These, with *A. caquetae, A. dissimilis, A. nigrolineatus* and *A. punctatus* were considered to be near relatives comprising the *Punctatus* Group of *Alpha* anoles in the *Latifrons* species series.

On 10 and 11 March 1975, many individuals of this recently described species were observed in groves at the highway junction 5 km E Machala, El Oro Province, Ecuador. Males averaged larger than females (S-V 50.9 ± .488, range 55-47, and 48.0 ± .390, range 51-45). In life, the male was greenish with oblique rows of dark spots and fainter white spots on the sides and there was rusty suffusion on the sides and back of the head becoming fainter middorsally on the body. The undersurface was whitish with faint dark spots, with limbs and toes barred; the bars were formed from dark specks in a reticulate pattern; eyelids were buffy tan and iris was yellow. The chin was speckled with dull green. The tail was black for the middle third of its length. The dewlap was relatively small and of unusual shape, more than twice as long as deep when fully extended, dull white with a jet black horizontal line along its base on each side. The female was similar, except in lacking the dewlap, in having a pale tan middorsal stripe with a double dark line along each edge, and in having faint dark spots on the sides.

All the lizards seen were on cacao trees. They were shy and active, and at least half of those seen escaped. Most often they were first seen at heights between 1 and 3 m on the main trunks, but when approached they would dodge to the farther side of the stem and climb out of reach.

All that were seen were adults. Absence of young of any size indicated that there had been cessation of breeding activity for several months, for an interval that must have included fall and early winter. However, 14 females dissected were all reproductive. Nine of them had an egg in each oviduct and the remaining five each had an egg in one oviduct and an enlarged follicle in the ovary of the opposite side. Thus, reproductive activity was near a peak at the height of the rainy season. However, southern Ecuador has a long and severe dry season and probably egg-laying does not occur during that interval.

Anolis peraccae

This species was described from Chimbo, Ecuador, by Boulenger (1898). Peters (1959) synonymized *Anolis irregularis* (Werner, 1901, type locality "Ecuador"), indicating that nearly all characters listed by the describer were identical, and that the details of pattern, arrangement of head scales and numbers of digital lamellae in which the two taxons differed were subject to much individual variation. Characters listed by Peters and Donoso-Barros (1970) for *A. peraccae* include: Smooth ventrals; frontal crests present; supraorbital semicircles contacting supraoculars, separated medially by one or two series of scales and separated from interparietal by 3 or 4 series of scales; 5 or 6 rows of loreals; 6 or 7 supralabials anterior to center of eye. *A. peraccae* is an *Alpha* anole of the *Latifrons* species series.

This small species was found to be relatively common and widely distributed in the lowlands of northwestern Ecuador. A total of 33 were captured in February and March 1975, at Santo Domingo de los Colorados, Río Palenque field station, and vicinity of Tinalandia, Río Pupusa. At least twice that number escaped. Compared with other small species, this one is extremely active and wary. Several were found on trunks of large trees in rain forest, a few others were on trunks of balsa trees and several were on roadside agaves. However, approximately 90 per cent were on banana trees. Most often the lizard was between one and three m above ground on the banana stem, but at any movement in the vicinity it would run higher, having no difficulty in clinging to the smooth, vertical stems. Most ascended beyond reach and were lost in the crowns of the banana trees. Captures were made by using a straight pole, which was slowly extended until it touched the trunk above the anole. Then the pole was lowered along the trunk driving the lizard ahead until it had descended within reach, for capture by hand. Even those driven within reach usually escaped by running back up the stem, by jumping to another stem or leaf, or by finding shelter in a hole beneath the roots.

These anoles are dull and cryptically colored, with little difference between the sexes. The most conspicuous recognition marks were ventrolateral oblique dark streaks forming a fine grid-like pattern. The dewlap is relatively small in the male and absent in the female. Males were seen more often than females, probably because they perch in more exposed places. The 32 captured in late February and early March included 17 adult males, 10 adult females, 3 half-grown and 2 small juveniles. This high ratio of adults indicated a low level of breeding in the months before the sampling. Seven of the adult females were dissected and all but one were reproductive. Two each had oviducal eggs on both left and right sides; three each had one oviducal egg and an enlarged follicle on the opposite side; one had an oviducal egg but no follicle. This high level of reproduction, and scarcity of juveniles (only a little over 6 per cent of the sample) suggested recent increase from a low level of reproduction in fall and early winter.

Anolis princeps

Boulenger (1902) described this giant rain forest species from specimens from Río Lita, Paramba, San Javier, and Salidero, northwestern Ecuador. Peters and Donoso-Barros (1970) described the range as lowlands of northwestern Ecuador, and mentioned the following characters: Dorsal color green with dark brown bars; ventrals not consistently keeled or smooth; extended hind limb reaching beyond snout; 4 or 5 series of scales separating supraorbital semicircles; 9 to 11 rows of loreals; 10 to 12 supralabials anterior to eye.

Two adult males were captured at the Río Palenque field station on 1 and 3 March 1975. In life they were olive green with two dark transverse bands on the neck and five more bands on the body, each consisting of a double series of five or six oval markings on each side (in both the anterior and posterior series). Some of the oval markings were like ocelli, having light centers. The ventrum was greenish white. The area around the eye was divided into alternate paler and darker sectors. The large dewlap was white along its anterior edge, ivory or slightly greenish white on its posterior part.

These large anoles were conspicuous on their low perches, and neither made any attempt to escape as the collector approached and captured them by hand. One was .8 m above ground on a stem .05 m in diameter, the other was 1.2 m high on a trunk of .8 m diameter.

Anolis sp.

In February, 1975, at Tinalandia, Río Pupusa, Pichincha Province, Ecuador, we found a species of anole that was obviously different from any described in published literature. Subsequently, at the Río Palenque field station, another specimen was found and the species was found to have been included in a key to the lizards of the Station, compiled by Kenneth A. Miyata of the Museum of Comparative Zoology, Harvard University. Mr. Miyata (pers. comm.) has informed us that the species is described in manuscript by E. E. Williams, and that it is tentatively associated with *Anolis lemurinus,* a *Beta* anole of the *Chrysolepis* species series.

Distinctive features of the species are the short, blunt head (with rostrum especially shortened), long limbs and tail (Table 1), bold dark dorsal markings including a lyre-shaped occipital mark and a saddle-like sacral blotch and several intervening blotches on the olive ground color; dewlap that is relatively small and scarlet in the male, with a central black spot, about one-fourth as large and pink in the females, with the spot brown.

At Tinalandia an adult male was in a thicket at the base of a steep bank, climbing 1.6 m above ground on the terminal twigs of a shrub. A juvenile of 49 mm S-V was flushed from screening vegetation on the vertical surface of a high rock wall and ran several meters along the wall before capture.

An adult female (73 mm S-V) captured at the Río Palenque field station in early March 1975 was larger than the male (70 mm). This female contained two large oviducal eggs.

One seemingly complete display of the juvenile male from Tinalandia was filmed. It was relatively simple, beginning with a slow (4 sec) high bob which was followed by four that were lower and faster (2.0, 1.3, 1.9 and 2.0 sec). The dewlap was fully spread near the peak of the first bob and was partly retracted with each downward movement.

In view of the suggested relationship of this species to *Anolis lemurinus,* the display is of special interest for comparison with the latter. In five displays of three individuals of *A. lemurinus bourgaei* from Tikal, El Petén Province, Guatemala that were analyzed (A. F. Echelle ms) there were four slow bobs followed by a pause and then a final slow bob, with each elevation of the head accompanied by a dewlap extension—a pattern somewhat similar to that of the present species.

Displays of *A. lemurinus lemurinus* from the vicinity of Escuintla, Guatemala, did not follow this basic pattern and were less similar to *A. l. bourgaei* and to the Ecuadorian species than these two were to each other. In each of four displays of the Escuintla anoles there were six bobs and one dewlap movement beginning at the end of the third bob or during the fourth bob, spreading maximally, then retracting at the end of the bobbing series (duration of display 3.4 ± .52 sec, dewlap exposure 1.51 ± .047 sec). Nine other displays were much more complex, with long ascending series and descending series of rapid bobs, with the dewlap maximally extended most of the time and spread one to three times per display. Display posture of *A. l. lemurinus* is distinctive. The head is pointed upward, and holding this position for long periods, the lizard occasionally flashes the dewlap in erratic fashion. The important differences between *A. l. lemurinus* and *A. l. bourgaei* in display and posture, dewlap, and body size cast some doubt on their supposed conspecificity.

DISCUSSION

The 25 kinds of anoles discussed above are almost equally divided among Mexican, Central American and Ecuadorian species, and the three geographic groups show some significantly different trends. Inasmuch as these three geographic areas are somewhat parallel in their range of climates, plant formations and agricultural crops, and each has many species of anoles, ecological equivalence might be expected among them. Each of the species included in this study and each of the better known common species in the same regions was compared with other species to determine the degree of ecological equivalence between the three regions.

For the common and dominant species of each region, especially, counterparts were sought that were similar in size, appearance, habitat and habits. One example of ecological equivalence is that of the semi-aquatic *Anolis barkeri,* widely distributed in Mexico, and its counterparts *A. lionotus, A. aquaticus* and *A. poecilopus,* that are similar in size, habitat, and habits, in different parts of Central America. However, no other such clear-cut cases of ecological equivalence could be discerned.

In Central America the three most abundant species are *Anolis limifrons, A. humilis* and *A. cupreus.* The former is a species of the humid, Caribbean lowlands in forest and forest-edge. It is found on the ground in leaf-litter and grass, but also is scansorial on shrubs, tree trunks and vines. *A. humilis* of the same area, but extending from the lowlands up into cloud forest, occurs on the forest-floor generally in deep shade, usually in leaf-litter but often climbs on buttressed roots and tree bases. *A. cupreus* of the relatively dry Pacific versant is somewhat more scansorial than *A. humilis* and somewhat less so than *A. limifrons.* It is most typically found in leaf-litter of evergreen gallery forests near streams. All three species thrive in some types of disturbed and altered habitats as well as in primary rain forest and in fact all have been found in near-maximum abundance in cacao groves. Also, they have all been found in banana and coffee groves. *A. limifrons* and *A. cupreus,* but not *A. humilis,* have been found in coconut groves on the tree trunks. None of the three seems to have close counterparts among any of the Ecuadorian species. In Central America, *A. biscutiger* and *A. rodriguezi* are near relatives of *A. limifrons* that seem to replace it ecologically in some areas. *A. dollfusianus* is somewhat like *A. cupreus* and even more like *A. limifrons* in habits and behavior. In southern Mexico, both *A. subocularis* and *A. cuprinus* are much like the Central American *A. cupreus,* but both occur in more open and xeric situations. *Anolis sericeus,* widely distributed in Mexico and Central America, resembles *A. cupreus* somewhat, but it is smaller and more slender and where the two overlap, at least, *A. sericeus* is definitely more scansorial. None of the three commonest Central American species (*A. limifrons, A. humilis, A. cupreus*) has an approximate equivalent in Mexico.

These three species, together with *A. sericeus, A. lemurinus* and *A. tropidonotus* occurring in both Central America and Mexico, and *A. nebulosus* and *A. subocularis* of southwestern Mexico, are all widely distributed and abundant, and sympatric with many additional species. Throughout Mexico and Central America one or another of the seven species mentioned tend to dominate habitats that are suitable for anoles and to exert selective pressure on other kinds that are less widely distributed and usually are less numerous in areas of co-occurrence.

The Ecuadorian species studied occurred in low population densities (only *A. gemmosus* was moderately abundant), were mostly medium to large *Alpha* anoles with little sexual difference in size, with arboreal habits, long tails, and with dewlaps often having white (4), green (3), and less frequently blue (2), red (2), and yellow (1). Most of them were notably shy and elusive.

In contrast the Central American species often occurred in high densities, were mostly *Beta* anoles of both *Chrysolepis* (5) and *Fuscoauratus* (2) series but with one *Alpha.* They ranged from extremely small to very large, were found at ground level or were scansorial low on shrubs and tree-trunks, had relatively short or medium-length tails, dewlaps usually yellow or orange, and had but little sexual dimorphism, with the female larger in several.

In the Mexican species, the trend was again somewhat different. Several kinds were found in high population densities, others were uncommon even in the limited areas where they occurred. All nine species were *Beta* anoles of the *Chrysolepis* series, having short to medium tails, ground-living or rock-living habits (or if scansorial, occurring only on bushes and low on tree-trunks), small or medium size, dewlap often all red or partly red, sexual size-difference extreme in some, with males usually larger than females.

Divergent ecological trends in the three geographic groups may have some phylogenetic basis, with *Alpha* anoles tending to be larger and more arboreal and having longer tails. Also, climatic trends are closely correlated with the ecological trends observed. Most of the Mexican species have small geographic ranges or are even confined to a single locality within a few square kilometers. In those instances it seems that the populations are relicts, surviving precariously in a region that is almost too xeric to support anoles. They have managed to survive only where local conditions mollify the aridity of the climate, and have undergone some adaptive specialization in the process.

In arid climates, such as are inhabited by most of the Mexican species, successful reproduction can occur only in the rainy season. Limitation of breeding to one part of the year intensifies its stresses. Males, needing to establish territories, repel rivals and find and court females, are selected for size, aggressiveness, and effectiveness of display. Sexual dimorphism becomes more pronounced than in the species that live in the relatively uniform and benign environment of a rain forest or cloud forest.

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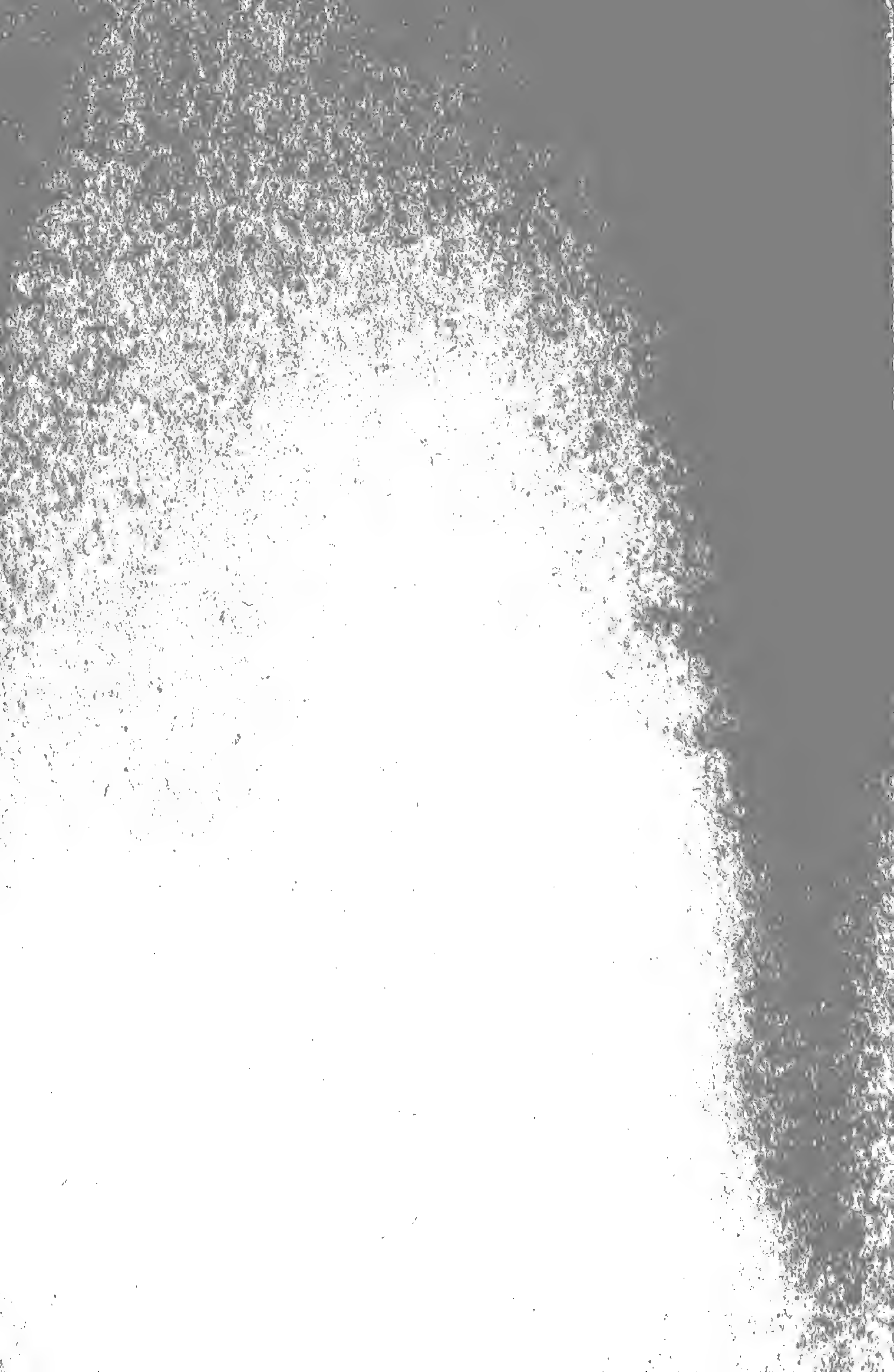

THE UNIVERSITY OF KANSAS

SCIENCE BULLETIN

COMPUTER-AIDED EVALUATION OF SHOOT-GROWTH PATTERNS IN TREES

By

ROLF BORCHERT

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Quantitative data suitable as a base for modeling the rhythmic shoot-growth should comprise as many variables related to shoot-growth as possible and be obtained from a large number of trees. This report deals with an attempt to meet this requirement by measuring relatively few variables per tree in a large number of trees at regular intervals throughout the growing season. Consecutive processing of raw data by the computer involves the following steps: 1. Calculation of derived quantities from the measured variables. 2. Printing of measured and derived data in numerical form. 3. Calculation and printing of mean values for groups of trees growing under identical conditions or subject to the same experimental treatment. 4. Presentation of data for each tree in graphic form.

This computer-aided evaluation of growth-measurements facilitates the analysis of shoot-growth in hundreds of trees with a degree of precision nearly equal to that achieved by detailed growth-measurements of a few trees.

ACKNOWLEDGEMENTS

Support of this work by the University of Kansas General Research Fund, use of the facilities of the University of Kansas Computation Center and the reliable and competent help of Mrs. Louise Wilson and Miss Elizabeth Vacek in making growth-measurements and preparing the data for computer treatment are gratefully acknowledged. Dr. Robert Nunley, Department of Geography, kindly provided use of the MAPS Computer System for measurement of leaf-areas.

MATERIALS AND METHODS

Collection of Data

At the beginning of the growing season, the initial state of each tree was determined, e.g., length and diameter of the stem, number of branches, weight, etc. Because of existing differences in morphology and growth-patterns, different genera of trees may require different evaluation procedures and the initial parameters used for the characterization of trees, the variables to be measured at regular intervals and the derived quantities to be calculated may vary.

Even where repeated measurements of shoot-growth in a population of trees are not possible, the amount and rhythmicity of shoot-growth is reflected in graphs of data from one measurement, each, for shoot, leaf, and internode length taken at the end of the growing season (compare Fig. 1f,g; 3f,g).

Data given and discussed below include measurements of the following variables made at regular intervals throughout the growing season in 1973 or 1974: a. Length of shoot developed in current season. b. Length of leaves exceeding 20 mm. c. Internode length between mature leaves. Leaves were considered mature when weekly increments in length were less than 2 mm.

Also, the state of activity of the apical bud—active growth vs. rest—was observed on the date of each measurement.

Data Processing

At the time of measurement, data were recorded by means of a tape recorder, later being transferred to data sheets containing 80 columns, each line corresponding to one computer card. Data were then punched on cards and evaluated by a program written in Fortran Y (which is available from the author).

Assuming that leaf growth is allometric, the leaf-area can be calculated from leaf-length by the formula for allometric growth:

$$A = b \cdot L^k$$

or

$$\ln A = \ln b + k \cdot \ln L,$$

where A = leaf-area, L = leaf-length, and

b and k are constants (Bonner 1963). For example, 60 leaves of greenhouse-grown pin-oak were collected, their lengths in mm were determined with a ruler and their areas were determined with the MAPS (Multi-Dimensional-Analysis-Processing-Spaces) Computer system, developed at the University of Kansas by Dr. R. Nunley. Any other valid method for determination of leaf area can, of course, be used. The correlation coefficient between $\ln L$ and $\ln A$ was found to be $r = 0.9$, the leaf area could be calculated by $\ln A = 1.93 \cdot \ln L - 6.04$ or $A = 0.00238 \cdot L^{1.93}$, where L is in mm and A is in cm^2.

The following comparison between measured and calculated leaf areas illustrates the quality of the calculations.

Leaf Length mm	*Leaf Area*, meas. cm^2	*Leaf Area*, calc. cm^2
69	9	8.4
92	13.5	14.7
139	32.4	32.5
145	36.4	35.3
166	48.2	45.9

Whereas the formula for leaf-area in pin-oak has been used in the evaluation of data given below, leaf-areas for other species, as given in Table II, were calculated with the assumed formula $A = L^2 \cdot 0.003$, because no empirical formulas were available.

OUTPUT OF MEASURED AND CALCULATED DATA

All variables not mentioned above as being measured are calculated from the measured data. The totality of measured and calculated data reflects the dynamics of shoot-growth much more clearly than measured data alone can do. Necessarily, the quality of the results depends strongly on the frequency and precision of measurements. Weekly measurements done with a ruler are sufficient to determine adequately the shoot-growth patterns and can be done with large samples of trees.

Since the dynamics of shoot-growth manifests itself both in variations of many parameters in time and in variations along the axis of the shoot, data for growth must be shown as related to both.

INITIAL DATA

The record for each tree begins with the following information (Table I): *a.* Tree-species; *b.* Code number for experimental treatment; *c.* Number of tree; *d.* Initial measurements of tree at beginning of growing season; *e.* Key for transformation of calendar date into coded date.

SHOOT AND LEAF GROWTH DATA RECORDED AND PLOTTED FOR EACH TREE

Numeric data of shoot and leaf-growth against time are given in Table I, as printed by the computer. In an additional table (not given here), the output contains the following measured and calculated variables for each leaf: *a.* Maximum leaf length in mm. *b.* Leaf area in cm^2 as calculated from length. *c.* Internode length in mm. *d.* Sum of all internodes below leaf to determine position of leaf along stem. *e.* Highest leaf growth rate achieved in mm/day. *f.* Date when leaf exceeded 40 mm length. *g.* Date when leaf reached maturity. *h.* Days passed between reaching 40 mm and maximum length. *i.* Days passed between consecutive leaves reaching 40 mm (plastochron index).

A graphic representation of data for shoot and leaf-growth is shown in Fig. 1. For any given tree, the information in this graph equals that in conventional graphic presentations of shoot and leaf-growth (compare Greathouse *et al.* 1972, Critchfield 1960, 1970).

Besides the tables and graphs described above, rhythmicity of each tree is numerically characterized by recording, for each growth-flush, the beginning and ending dates of active shoot-growth, the duration of active growth and of the interflush rest-periods and the number of leaves per flush. Other values for the evaluation of shoot-growth are stored during the computation of data and are printed in a final table for each tree, e.g., maximal rates of shoot and leaf-growth, mean leaf-area per shoot, total leaf-area per shoot, etc.

MEAN VALUES FOR GROUPS OF TREES

For use in quantitatively comparing different groups of trees, the means of the following variables are tabulated at the end of each experimental group of trees: *a*. Total shoot length in mm. *b*. Maximum shoot growth rate achieved in mm/day. *c*. Total leaf area per shoot in cm^2 (d,f). *d*. Area per leaf in cm^2. *e*. Maximum leaf growth rate achieved in mm/day. *f*. Number of leaves per shoot. *g*. Number of leaves per growth flush (f,k). *h*. Number of leaves in first flush. *i*. Number of leaves in second flush (h,g). *j*. Days of active shoot growth. *k*. Number of growth flushes. *l*. Days per growth flush (j,k). *m*. Days in first growth flush. *n*. Days in second growth flush (j,m.) *o*. Duration of rest periods in days (j,q). *p*. Duration of first interflush period in days. *q*. Duration of measurement period in days. *r*. Number of trees in treatment. *s*. Vigor of tree as calculated from initial data on stem height and diameter.

Several of these measured (*a,f,j,k,q*) and calculated (*b,d,e,p*) variables appear to be completely independent from each other. Others obviously depend on some of the independent variables (*c,g,l,o*). They have been characterized above by giving in parenthesis the variables they depend upon. Other correlations should become apparent from future multivariate analyses of tree-growth data and should reveal aspects of the mechanisms which control tree-growth.

Data assembled from these tables have been used to prepare Table II.

OBSERVATIONS

EXAMPLES OF RECORDED SHOOT GROWTH PATTERNS

1. *Quercus palustris*—Pin-oak.

Data given in Table I and Fig. 1 were

TABLE I. *Quercus palustris*. Young, single-shoot tree growing in greenhouse. Data of shoot and leaf growth as a function of time. For explanation of letters see legend Fig. 1.

```
                                                                      *** PIN OAK -- QUERCUS PALUSTRIS
     SPECIES   2    TREATMENT NO.  1    PLANT NO.      1

     STEM LENGTH, UPPER AND LOWER STEM DIAMETERS IN MM       278.        3.        5.

DATE/APR 1   5  10  15  20  25/MAY 1   5  10  15  20  25/JUN 1   5  10  15  20  25 JUL 1   5  10  15
CODE     1   5  15  20  20  25      31  35  40  45  50  55      62  66  71  76  81  86      92  96 101 106

** TABLE 1 **

NO  DA SHOOT SHOOT IA  NB L40 LMX   LEAF   LEAVES
     TE       RATE  CT               AREA   1   2   3   4   5   6   7   8   9  10  11  12  13  14  15
k   j    c     e   i   m    a   b    d    f
 1   1   33.   4.1  0   0   4   0    28.  63. 64. 71. 53.
 2  10   35.   0.2  2   0   0   0    66.  83. 94.110.102.
 3  17   35.   0.   1   0   0   0    73.  93. 99.113.105.
 4  24   35.   0.   1   4   0   4    73.   0.  0.  0.  0.
 5  31   56.   3.0  0   4   5   0   102.   0.  0.  0.  0. 60. 61. 76. 56. 42.
 6  39   60.   0.5  2   4   0   0   179.   0.  0.  0.  0.105.111.118.118.104.
 7  46   60.   0.   1   4   0   0   190.   0.  0.  0.  0.115.111.118.123.107.
 8  54   60.   0.   1   9   0   5   190.   0.  0.  0.  0.  0.  0.  0.  0.  0.
 9  58   60.   0.   1   9
10  65   82.   3.1  0   9   0   0   196.   0.  0.  0.  0.  0.  0.  0.  0.  0. 25. 30. 29. 20. 18.
11  73   88.   0.8  0   9   5   0   269.   0.  o.  0.  0.  0.  0.  0.  0.  0. 88.100.105. 88. 83.
12  80   88.   0.   1   9   0   0   308.   0.  0.  0.  0.  0.  0.  0.  0.  0.105.113.124.110.133.
13  86   88.   0.   1  14   0   5   308.   0.  0.  0.  0.  0.  0.  0.  0.  0.  0.  0.  0.  0.  0.
14  93   88.   0.   1  14
15 100   88.   0.   1  14
```

obtained from a 3-year-old, potted, single-shoot tree growing in the greenhouse from March to June 1974. A single look at the graphic presentation of shoot-growth shows that the tree passed through 3 consecutive flushes of growth during the observation-period, and that virtually every aspect of shoot-growth reflects rhythmic growth (Fig. 1). Curves for shoot-elongation and shoot-growth rate show 3 short periods of rapid growth alternating with longer periods of rest (Fig. 1c,e). During rapid shoot-elongation, relatively few leaves per flush begin growth in rapid sequence, almost simultaneously. They rapidly expand and reach maturity at about the same time (Fig. 1a,b,d). The dynamics of leaf-growth during 3 flushes is given in more detail in Fig. 1f, which shows that the major part of growth of each leaf is completed in less than 2 weeks. This rapid, almost simultaneous expansion of a few leaves per flush is characteristic of the so-called "determinate" pattern of shoot-growth, in which only leaves preformed in the bud expand during a growth-flush. Rhythmic growth is also shown by the periodic changes in internode-length (Fig. 1g), although the greater length of the first internode during each flush represents in reality the sum of 2 or 3 internodes, namely those between the first foliage leaf and the preceding bud scales, which do not enter into the record because of their reduced size.

Although numeric data are less useful for analysis of growth-patterns of individual trees, they are indispensable for quantitative comparisons between groups of different trees. Data given in Table II were compiled from numeric output for individual trees and treatment-groups and clearly show the wide variability of growth-patterns for pin-oak and other species.

2. *Tilia platyphylla*—Basswood.

Although Fig. 2 clearly shows that the 3-year-old, potted basswood tree passed through two flushes during the 1973 observation-period, there are significant differences between the growth-patterns of basswood and the oak tree represented in Fig. 1. In *Tilia,* periods of active growth are longer than rest-periods, and even during the rest-period caused by abortion of the shoot-apex and preceding resumption of growth by the uppermost lateral bud, shoot-elongation continues at a low rate (Fig. 2c, Date 70-92). During the first flush, leaves develop and mature over a longer period of time (Date 42-89), growth of individual leaves lasts approximately 3 weeks and there are more leaves per flush than in oak. In contrast to this pattern for young basswood, flushing and leaf-growth of an adult tree were completed within two weeks, showing a growth-pattern similar to that of a mature oak tree (Fig. 1f′, 2f′).

3. *Populus deltoides*—Cottonwood.

The 2-year-old potted cottonwood tree shows typical "indeterminate" growth (Fig. 3): Shoot-growth continues for a long time; a large number of leaves expand and mature consecutively. However, even though growth is never arrested, shoot-growth displays a marked rhythmicity which is reflected in shoot-growth rate, leaf-size and internode length, all of which pass through minima at about the same time (Date 87, leaves 31-33). Corresponding fluctuations of growing conditions in the greenhouse were not observed.

4. *Fraxinus americana*—American ash.

The 2-year-old potted ash grows slowly, but continuously, for a long period (Fig. 4). Shoot-elongation and number of leaves are low, compared to cottonwood (Fig. 3), but—because of the large leaves—leaf area increases rapidly. Data for leaf-growth reflect the decussate position of leaves. The development of consecutive pairs of leaves is similar. In ash, as in

Table II. Means of selected variables characterizing shoot growth in experimental groups of four tree species under different conditions.
A—Potted sapling, one growing shoot, outside greenhouse
B—Potted sapling, one growing shoot, inside greenhouse
C—Lateral branch of approximately 15 m high tree (basswood, oak) or 5 m high tree (cottonwood)

SPECIES	TREATMENT	shoot length in mm	# of leaves formed	leaf area/shoot in cm^2	area/leaf in cm^2	days of active growth	days/flush	# of leaves/flush	# of flushes
Tilia platyphylla	A	359	12	591	50	44	33	10	1.3
(basswood)	B	343	11	816	73	38	27	9	1.4
	C	145	7	374	56	15	15	9	1.0
Quercus palustris	A	188	19	453	25	19	13	10	1.5
(oak)	B	294	24	938	40	33	14	13	2.4
	C	127	11	493	45	19	17	11	1.1
Fraxinus americana	A	112	21	706	34	82	82	24	1.0
(ash)	B	234	19	1262	67	70	70	21	1.0
Populus deltoides	B	726	39	2458	63	81	81	44	1.0
(cottonwood)	C	351	25	1328	54	79	79	24	1.0

Fig. 1. *Quercus palustris,* same tree as in Table I. Shoot and leaf growth data as a function of time (a-e) and as a function of leaf number (f,g). Lines have been drawn by hand.
Explanation of letters:

a—number of leaves having exceeded 40 mm length since last measurement date
b—number of leaves having reached maturity since last measurement date
c—length of current season's shoot in mm
d—total leaf area of shoot as calculated from leaf length in cm^2
e—shoot growth rate in mm/day
f—leaf growth. Total height of each bar gives length of leaf at maturity in mm. Numbers forming bars indicate date (j) at which leaf has reached certain size. For example, leaf # 5 (h) had 60 mm length at date 5(k) = day 31 (j), 105 mm at date 6 = day 39, and 115 mm at date 7 = day 46. Letters A, B, C indicate dates 10, 11, 12.
g—internode length below respective leaf in mm. Scale is 2× that of leaf length (1 space = 1 mm)
h—leaf number beginning with oldest leaf
i—activity of apical meristem. 0—active growth; 1,2—arrested growth
j—coded measurement date (days after April 1)
k—current number of measurement dates
m—total number of mature leaves
f′—leaf growth of mature tree in spring 1973

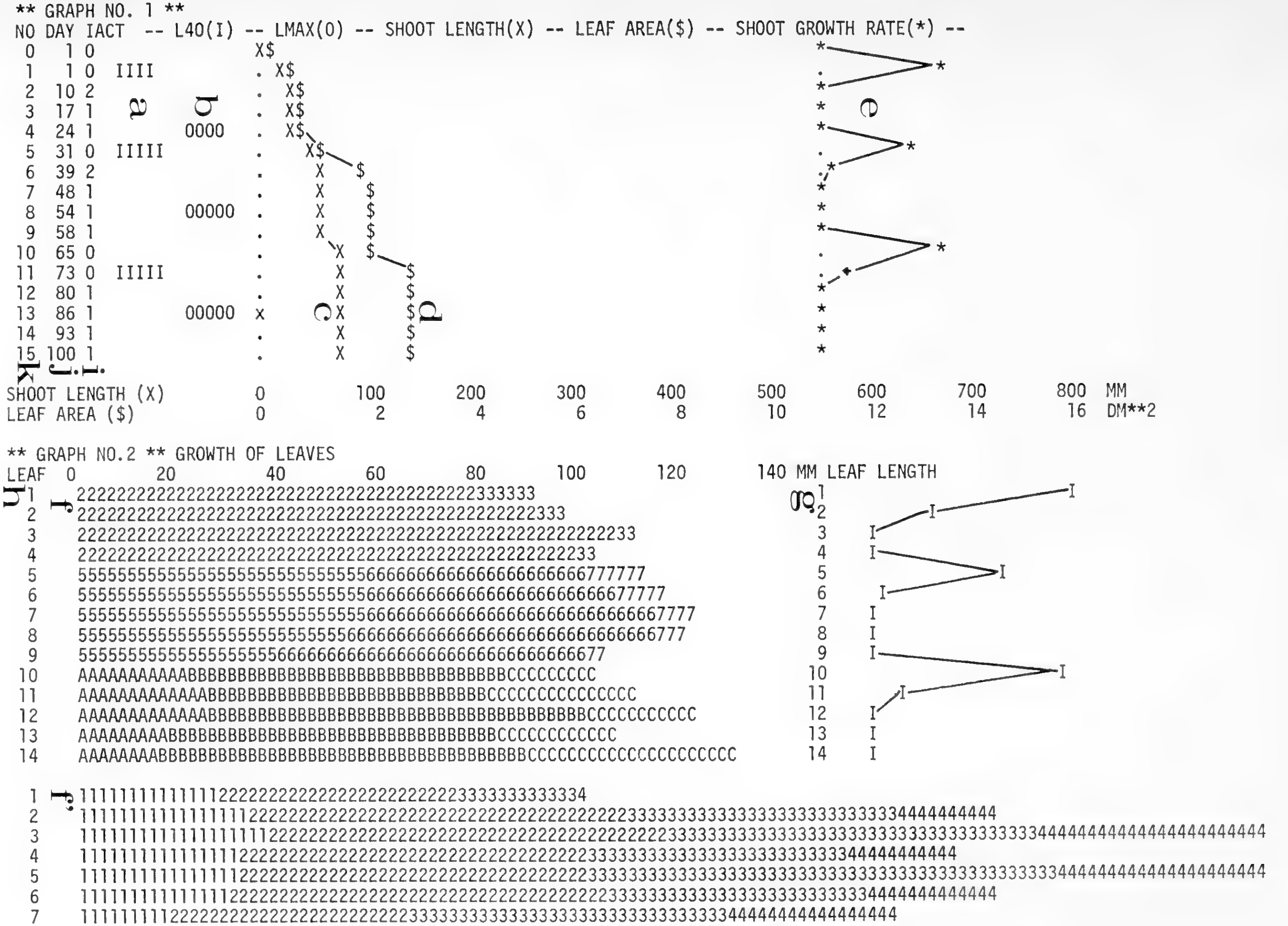

** GRAPH NO. 1 **
NO DAY IACT -- L40(I) -- LMAX(0) -- SHOOT LENGTH(X) -- LEAF AREA($) -- SHOOT GROWTH RATE(*) --
0 1 0
1 1 0 IIII
2 10 2
3 17 1
4 24 1 0000
5 31 0 IIIII
6 39 2
7 48 1
8 54 1 00000
9 58 1
10 65 0
11 73 0 IIIII
12 80 1
13 86 1 00000
14 93 1
15 100 1
a
b
c
d
e
i
j
k
SHOOT LENGTH (X) 0 100 200 300 400 500 600 700 800 MM
LEAF AREA ($) 0 2 4 6 8 10 12 14 16 DM**2
** GRAPH NO.2 ** GROWTH OF LEAVES
LEAF 0 20 40 60 80 100 120 140 MM LEAF LENGTH
1
2
3
4
5
6
7
8
9
10
11
12
13
14
f
f'
g
h

FIG. 2. *Tilia platyphylla.* Young, single-shoot tree growing in greenhouse. Letters as in Fig. 1. f′—leaf growth of adult tree in Spring 1973.

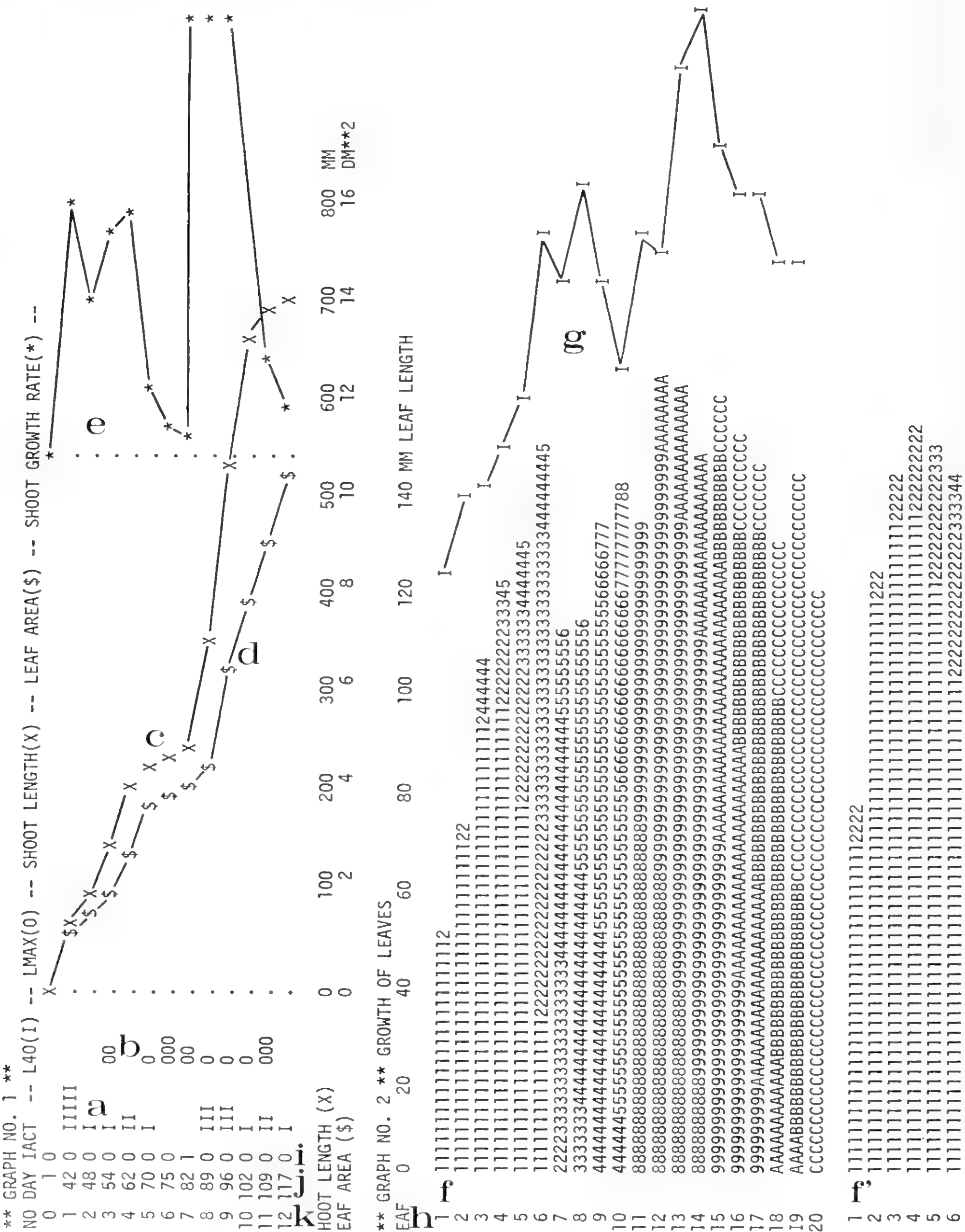


FIG. 3. *Populus deltoides.* Young, single-shoot, potted tree growing in greenhouse. Letters as in Fig. 1. g′—internodes of shoot on 5 m tall tree in the field.

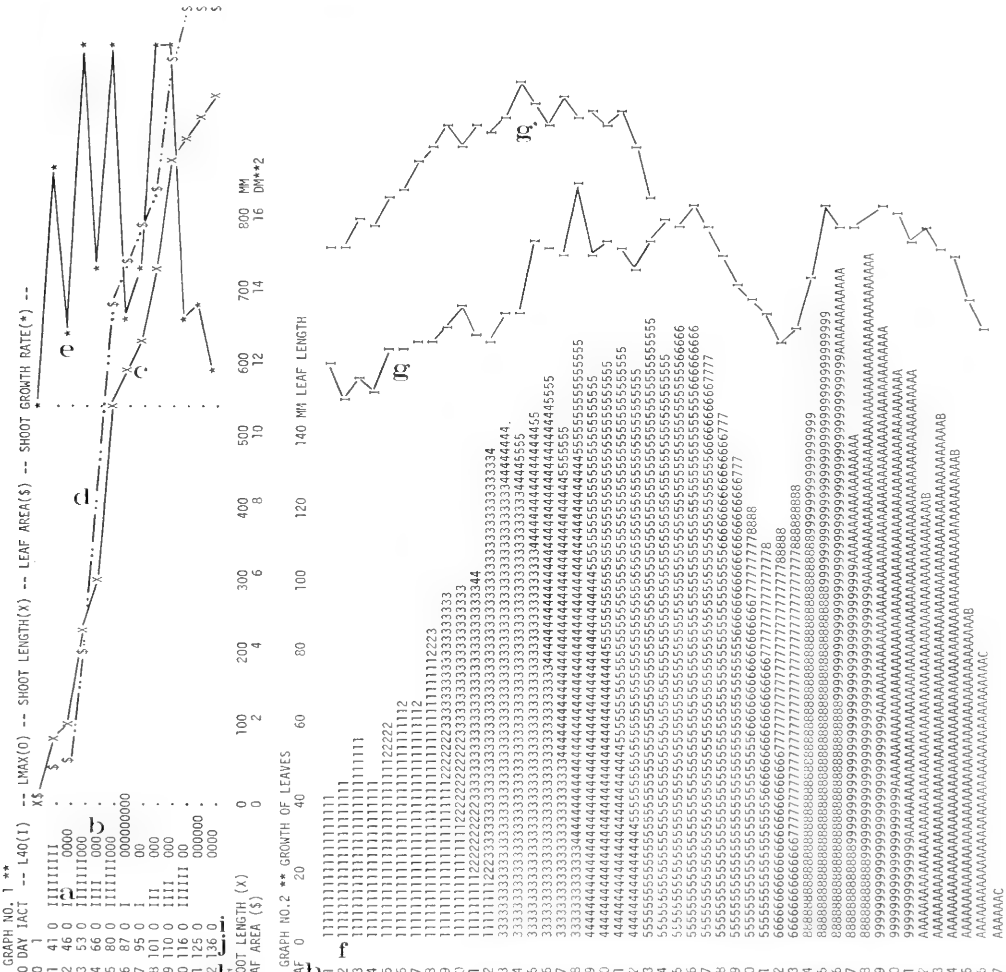
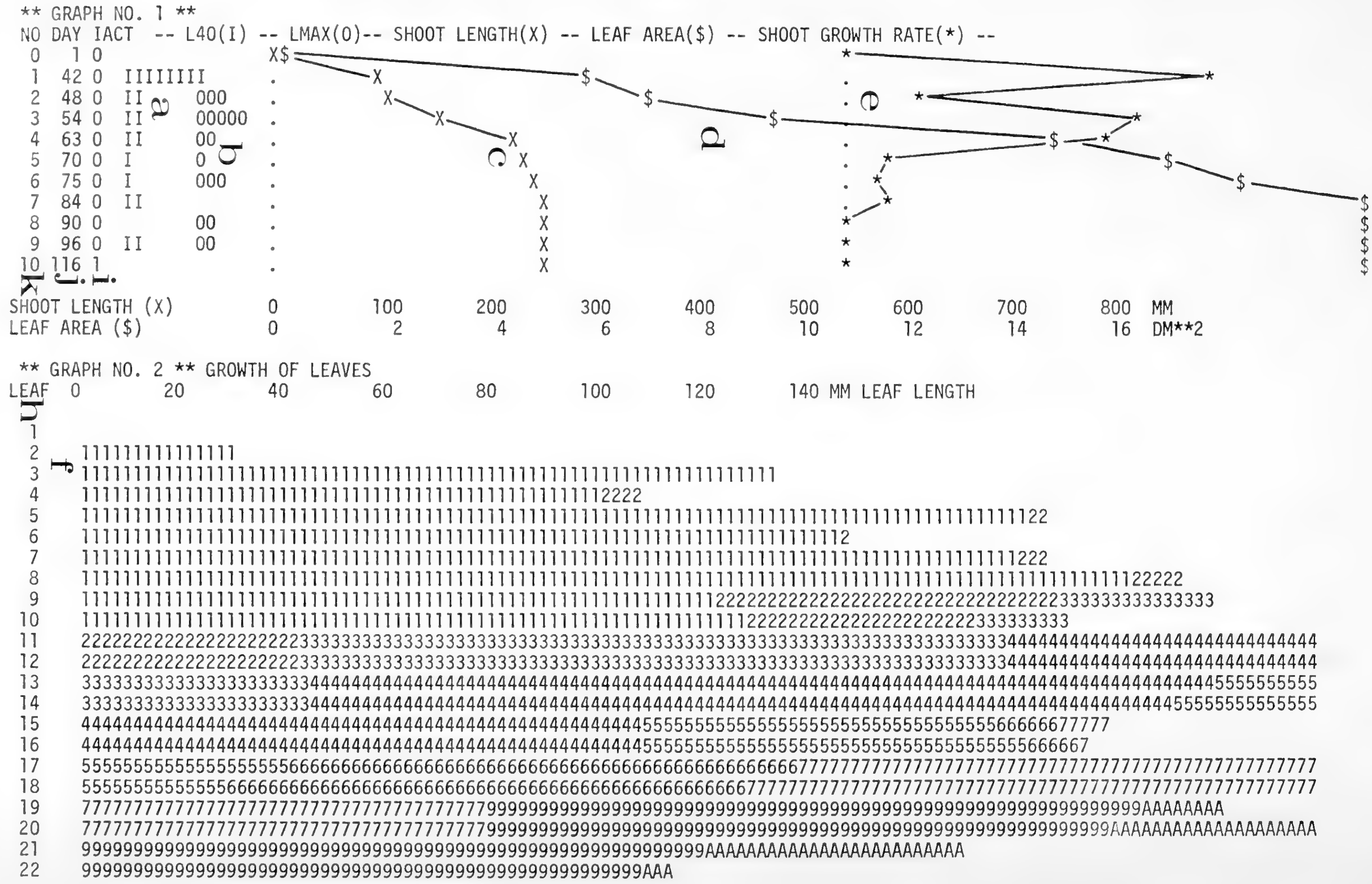


FIG. 4. *Fraxinus americana.* Young, potted tree growing in greenhouse. Letters as in Fig. 1. At date 7, leaf area exceeded the range provided in the graph. Likewise, leaves 11-14 and 17/18 slightly exceeded the maximum length provided for in the graph.



```
 ** GRAPH NO. 1 **
 NO DAY IACT  -- L40(I) -- LMAX(O)-- SHOOT LENGTH(X) -- LEAF AREA($) -- SHOOT GROWTH RATE(*) --
  0   1 0                X$                                                      *
  1  42 0  IIIIIIII      .         X                   $                         .                                 *
  2  48 0  II     000    .          X                        $                   .     *
  3  54 0  II     00000  .               X                               $       .                          *
  4  63 0  II     00     .                      X                                .                  $    *
  5  70 0  I      0      .                       X                               .  *                          $
  6  75 0  I      000    .                        X                              . *                                  $
  7  84 0  II            .                         X                             .  *                                             $
  8  90 0         00     .                         X                             *                                                $
  9  96 0  II     00     .                         X                             *                                                $
 10 116 1                .                         X                             *                                                $
SHOOT LENGTH (X)         0         100       200       300       400       500       600       700       800  MM
LEAF AREA ($)            0           2         4         6         8        10        12        14        16  DM**2

 ** GRAPH NO. 2 ** GROWTH OF LEAVES
LEAF  0        20        40        60        80        100       120       140 MM LEAF LENGTH
  1
  2    111111111111111
  3    1111111111111111111111111111111111111111111111111111111111111111111
  4    111111111111111111111111111111111111111111111111112222
  5    111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111122
  6    11111111111111111111111111111111111111111111111111111111111111111111111112
  7    111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111222
  8    11111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111122222
  9    1111111111111111111111111111111111111111111111111111111111111222222222222222222222222222222222333333333333333
 10    1111111111111111111111111111111111111111111111111111111111111111222222222222222222222233333333
 11    222222222222222222223333333333333333333333333333333333333333333333333333333333333333333334444444444444444444444444444444
 12    222222222222222222223333333333333333333333333333333333333333333333333333333333333333333334444444444444444444444444444444
 13    333333333333333333333344444444444444444444444444444444444444444444444444444444444444444444444444444444444444445555555555
 14    333333333333333333333344444444444444444444444444444444444444444444444444444444444444444444444444444444445555555555555555
 15    444444444444444444444444444444444444444444444444444444555555555555555555555555555555555566666677777
 16    4444444444444444444444444444444444444444444444444444445555555555555555555555555555555555555666667
 17    555555555555555555556666666666666666666666666666666666666666666666667777777777777777777777777777777777777777777777777777
 18    555555555555556666666666666666666666666666666666666666666666666677777777777777777777777777777777777777777777777777777777
 19    777777777777777777777777777777777777777999999999999999999999999999999999999999999999999999999999999999AAAAAAAA
 20    7777777777777777777777777777777777777779999999999999999999999999999999999999999999999999999999999999AAAAAAAAAAAAAAAAAAAA
 21    999999999999999999999999999999999999999999999999999999999999AAAAAAAAAAAAAAAAAAAAAAAAA
 22    999999999999999999999999999999999999999999999999999999AAA
```

basswood and cottonwood, the first set of leaves (1-10), which were enclosed in the resting bud, develop quickly at the beginning of the flush. Thereafter, leaves develop at longer intervals and expand more slowly. Adult ash (not shown here) displays one short annual flush of shoot-growth similar to those of oak and basswood (Fig. 1f′ and 2f′).

COMPARISON BETWEEN DIFFERENT GROUPS OF TREES

As growth-patterns of individual trees growing under identical conditions are variable and the time-course of flushing is not synchronous within a group, an "average shoot-growth pattern" for all trees within one sampled group cannot be calculated. However, if the means of several representative variables are calculated and tabulated, then characteristic, quantitative differences between groups are obtained, useful for statistically treating the data.

VARIATION WITHIN SPECIES

Potted trees of three species (basswood, oak, ash) were grown both outside and inside the greenhouse, the latter growing in environmental conditions characterized by higher average temperature and higher relative humidity. For all three species, overall growth was higher inside the greenhouse, with leaf-size being the single variable showing the greatest increase (Table II, Treatments A and B).

A comparison between seasonal growth of lateral shoots of large trees and greenhouse-grown single-shoot saplings shows significant quantitative differences as well as differences in shoot-growth pattern. Whereas almost all adult trees passed through only one growth flush, young oak and basswood trees usually flushed repeatedly (Table II, Treatments B and C).

If normal intraspecific variability of shoot-growth patterns is as marked as shown in these few examples, even more dramatic differences should be obtained by experimental manipulation of trees. The analysis of such variation should lead to a better understanding of the mechanisms controlling shoot-growth. Variations in shoot-growth of oak as reported in the literature and observed in my experiments have been previously described, interpreted and related to predictions resulting from the model for rhythmic shoot-growth in trees (Borchert 1973, 1975).

VARIATION BETWEEN SPECIES

Interspecific differences in shoot-growth patterns, as shown above for single trees (Fig. 1-4), are equally obvious in the comparison of quantitative data given in Table II.

DISCUSSION

The analysis of shoot-growth data for broad-leaved trees described above offers the following advantages and possibilities:

1. Shoot-growth data for relatively large numbers of trees can be collected and prepared for computer analysis by personnel with little training in tree-morphology and punching of data cards.

2. Data are automatically recorded in numeric and graphic form and can be grouped and rearranged in any desired format.

3. Information contained in the measured raw data is increased as follows: (3.1.) Meaningful subsets of data which are present in the raw data, but not recognized as such, can be extracted and compiled from the raw data, e.g., data on flush-growth and on the time-course of growth in single leaves (Table I and Fig. 1-3). (3.2.) Derived variables, which often mean more than the original ones, can be calculated. For instance, the dynamics of shoot-growth is more clearly reflected in changes of shoot-growth rate over time than in increasing shoot-length. Likewise, leaf-area as calculated from leaf-length is important in determining some principal physiological processes controlling

shoot-growth, especially transpiration and photosynthesis.

4. The automatic representation of data in graphic form is an essential prerequisite for evaluating and comparing shoot-growth patterns in many separate trees by visual scanning. Despite progress in computer technology, the human eye and brain are still the most efficient instruments to evaluate complex patterns. The experienced observer will at a single glance recognize certain growth-patterns in the graphed data; he will detect similarities and discrepancies between trees of different groups and see correlations between or trends in certain variables. This information cannot be obtained as efficiently by observing living plants or by studying numeric growth-measurements. Once detected by visual scanning, such correlations can be analyzed in greater detail in the numeric data and "indicator" variables can be singled out which show differences in growth-patterns between various groups of trees, whose means can be compared statistically, e.g., by multivariate analysis.

5. When physiological measurements have been performed, their results can be treated together with morphologic observations and the combined data used to construct and improve the model for shoot-growth. Predictions from the model may then be compared with measured data, i.e., there will be continuous interaction between observation, description, and interpretation of shoot-growth data.

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THE UNIVERSITY OF KANSAS
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A SYSTEMATIC STUDY OF THE FAMILY BOREIDAE (MECOPTERA)

By

NORMAN D. PENNY

Vol. 51, No. 5, pp. 141-217 April 14, 1977

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A SYSTEMATIC STUDY OF THE FAMILY BOREIDAE (MECOPTERA)

by

Norman D. Penny[1]

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A SYSTEMATIC STUDY OF THE FAMILY BOREIDAE (MECOPTERA)

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NORMAN D. PENNY

ABSTRACT

General aspects of the biology of Boreidae are discussed, including life cycle and immature forms, ecological relationships, geographical and seasonal distribution, external morphology, variation within species, behavior, and adaptations to boreal or winter existence. A phenetic classification is derived by comparison of states of 37 characters. Four possible phylogenies of the family are obtained by application of different methods, and their differences are compared. These systematic analyses yield a distinct group, ***Hesperoboreus*** (new genus), to include *Boreus brevicaudus* Byers (type species) and *B. notoperates* Cooper, of western North America. Revision of the North American species results in the following new synonymy: *B. californicus* Packard (=*B. unicolor* Hine, *B. isolatus* Carpenter, and *B. californicus fuscus* Carpenter), *B. nix* Carpenter (=*B. gracilis* Carpenter). Among Old World species, the following new synonymy is noted: *B. navasi* Pliginsky (=*B. aktijari* Pliginsky). Taxonomic keys and illustrations are provided.

INTRODUCTION

Boreidae (named for Boreas, the Greek god of the north wind) are small, dark colored Mecoptera usually found associated with mosses and infrequently seen except on winter snow. Both sexes are flightless, the wings of females being reduced to tiny, sclerotized flaps and those of males being modified as long, thin hooks used to grasp the female during copulation. The elongate rostrum resembles that of Panorpidae. Female boreids have an ovipositor formed from the fused cerci and elements of the 8th through 11th abdominal segments. The larvae are scarabaeiform and have so far been found only among rhizoids of mosses and club mosses.

The taxonomy of North American boreids has not been studied since Carpenter published descriptions and keys (1935, 1936). Three North American species have been described since that time (Byers, 1955, 1961, and Cooper, 1972), and additional taxonomic characters have been found. In the Palearctic region there has not been a comprehensive treatment of species since Esben-Petersen's (1921) world monograph of the Mecoptera. Six Palearctic species have subsequently been described, primarily in Russian literature.

Crampton (1930) pointed out that terminal abdominal appendages of both male and female Boreidae are distinct from those of other Mecoptera, and since the Boreidae are so specialized they could reasonably be placed in a separate suborder, the Neomecoptera. Hinton (1958) raised this suborder to ordinal level on the basis of nine findings: "Larva: (a) the cranium is without a distinct epistomal suture; (b) the cardo is not fused to the basistipes, and the tentorial adductors of the cardo are present; if homologues of these muscles are present in the Mecoptera they are now tentorial adductors of the cardostipes; (c) the postmentum is well developed instead of lost or reduced to an articulating membrane between the prementum and the cranium; (d) the abdomen lacks prolegs, whereas in the Mecoptera prolegs are present on the first eight abdominal segments; and (e) the larvae feed on moss, whereas those of the Mecoptera are carnivorous. Adult: (a) the ovaries are panoistic instead of polytrophic as in the Mecoptera; (b) the 11th abdominal segment of the female lacks cerci, whereas one- or two-segmented cerci are

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present in the Mecoptera; (c) the 9th and 10th abdominal segments are modified to form a large functional ovipositor but no such 'ovipositor' is found in the Mecoptera; and (d) the adult gut lacks the six especial rectal glands of the Mecoptera."

Although most of Hinton's points are valid, a few inaccuracies occur. Byers (1961) pointed out that the tip of the ovipositor in Boreidae is actually the fused cerci, and recently he discovered that larvae of Panorpodidae lack abdominal prolegs and are probably plant feeders. Hepburn, in his morphological study of the thorax of Mecoptera (1970), concludes that Boreidae are probably closely related to "intermediate families" of Mecoptera, and attempts to remove Boreidae from the Mecoptera are unjustified.

Only one previous attempt has been made to reconstruct phylogeny within the Boreidae (Lestage, 1940). Lestage suggested that Boreidae consisted of two genera: *Boreus,* consisting of Palearctic species with male abdominal tergal ridges and medial lobes of the dististyles, and *Euboreus,* consisting of Nearctic species without tergal ridges and medial dististylar lobes. Lestage further stated that the primitive condition was lack of these structures, therefore making *Euboreus* the more primitive genus and North America the place of origin of the family.

The morphological basis of Lestage's reasoning was faulty. All male Boreidae have medial dististylar lobes and only four western European species have abdominal tergal ridges.

This study was undertaken to bring together recent information on taxonomy, morphology, and ecology of the Boreidae. An attempt has been made to synthesize this information into a better concept of systematics of the family. Specifically, primitive and derived sequences of character states have been used to construct the evolutionary development of Boreidae and this, in turn, has been used to determine genera and species groups. Finally, an attempt has been made to present (sometimes for the first time in the English language) the most comprehensive description available for each species.

METHODS OF PRESERVATION OF SPECIMENS

Specimens should be preserved in alcohol. If specimens are preserved dry on points, the membranous areas tend to contract and the abdominal sclerites telescope within one another. The ninth tergum becomes almost completely enclosed by the eighth tergum, and the dististyles recurve over the abdomen to conceal the caudal surface of the ninth tergum. Retraction and shrinkage make observation of this key structure almost impossible. Preservation in 70 percent alcohol also tends to cause retraction and shrinkage, but if specimens are placed in water for a few minutes, they normally will return to normal size and shape. Even greater detail can be seen if specimens are lightly cleared in a 10% solution of cold potassium hydroxide (KOH) for 24 hours. After clearing, it can be seen that under the tergal hood are recessed pockets into which the tips of the dististyles fit.

MORPHOLOGY AND BOREAL ADAPTATIONS

A. BOREAL ADAPTATIONS—Tweedie (1972) lists four traits frequently noted among northern and alpine insects. Many northern insects are small and dark in color. These two characteristics perhaps allow the insects to absorb radiant heat more readily and warm up much faster than larger and lighter individuals of closely related races or species. However, this situation would create a larger surface area per unit volume, and thus also cool the insect more rapidly when radiant heat is absent (see Salt, 1961). Species of Boreidae range from yellow and brown to russet brown to black in color and 2.0 to 7.4 mm. in length. Whether dark coloration in Boreidae helps maintain thermal regulation has yet to be determined.

Northern insects are frequently more hairy than their more southern counterparts (see Downes, 1965). This allows for an insulating layer of air within the hairy coat. Although no boreids are hairy enough to trap such an insulating air layer, variation in hairiness can be seen even within the genus. Those species living along the west coast of North America in rather mild climates have few setae on the body while such species as *nix* and *pilosus* from mountainous western regions have enough setae over the entire body to give these species a "frosted" appearance.

The fourth trait noticed among northern insects is wing reduction. This characteristic has a three-fold advantage. In such extreme environments, generating enough energy to warm and maintain functioning of wing muscles would be extremely difficult (Heinrich and Bartholomew, 1972). The exposed surface area of wings places the insect in greater danger of freezing. Finally, the frequently windswept, barren environments where northern and alpine insects live make it necessary to reduce surface area to avoid being blown away. Boreidae show marked decrease in wing size, the wings being reduced to small, oval flaps in females (Fig. 1, p. 144) and thin, spiny hooks in males (Fig. 2, p. 145).

Two further winter adaptations of Boreidae are the ability to hop and an extended life cycle. No other mecopteran is known to have the ability to hop. Boreidae will frequently hop when suddenly disturbed on moss or snow. Boreids normally walk while feeding or moving across snow, but it has been noticed that on light, fluffy snow where walking is difficult, an individual will take a few steps and then leap up to 12 inches, even though not disturbed. This action may be repeated several times in rapid succession, allowing Boreidae to cross several feet of soft snow in a few minutes.

Strübing (1950) has found that *B. hyemalis* larvae require two years to mature. This extended life cycle is noted among many northern insects. However, Kaufmann (1971) has shown that a carabid beetle, *Pterostichus brevicornis,* requires from 14 to 36 months to complete its life cycle, depending upon the time of oviposition. It remains to be proven that Boreidae take two years to mature under *all* conditions.

B. General Morphological Description (Adult)—To facilitate the following discussion, it is mentioned here that I have hereinafter separated the Boreidae into two genera, *Hesperoboreus* and *Boreus,* and *Boreus* in turn has been separated into four species groups, the *californicus, hyemalis, nivoriundus,* and *reductus* groups.

Head prolonged into a rostrum, composed anteriorly of clypeus and labrum, laterally of genae, and caudally of maxillo-labial complex (Hepburn, 1969). Labrum short, spatulate, with triangular sclerite at each side. Mandibles slightly longer than labrum, tapering apically, with six stout teeth at apex. Maxillolabial complex much longer than other mouthparts, varying from .44 to 1.00 times length of rostrum. Maxillary palps five-segmented, basal segment much shorter than distal segments. Labial palps two-segmented, arising at apex of maxillolabial complex. Approximately halfway between bases of maxillary and labial palps two areas of pegs, with about 14 pegs on either side. Eyes large, oval, and usually plum to black in living individuals. Antennae long (though short compared to those of other mecopterans), consisting of subcylindrical scape, bulbous pedicel, and 16 to 23 filiform, pedicellate flagellar segments, arising between or just below eyes. Median ocellus between and just dorsad

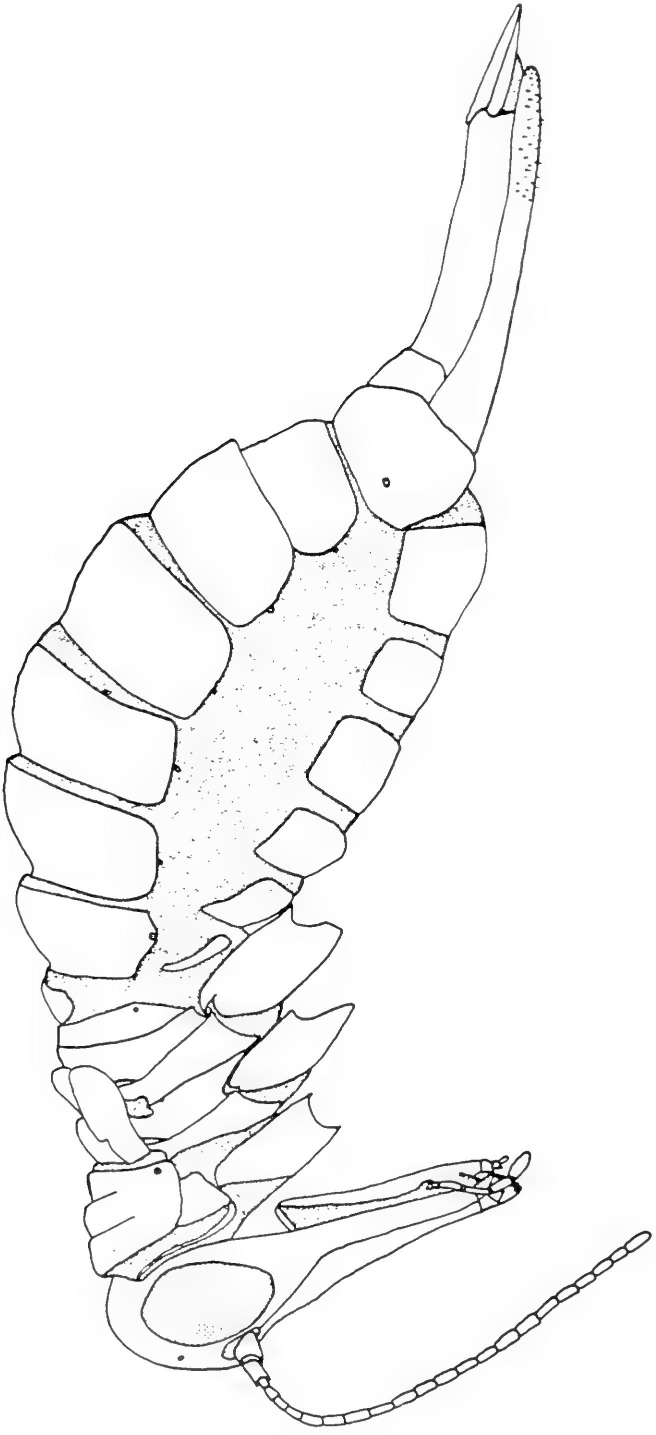


FIGURE 1. *Boreus coloradensis* Byers, female, lateral view, legs removed (39×).

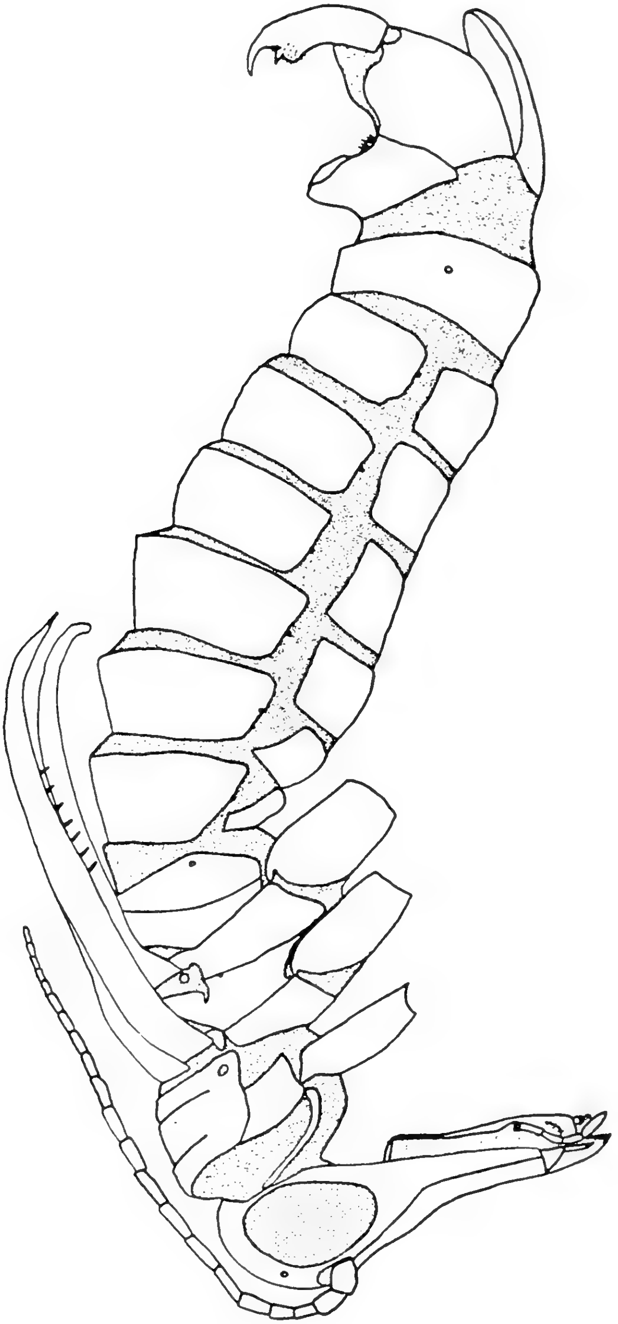


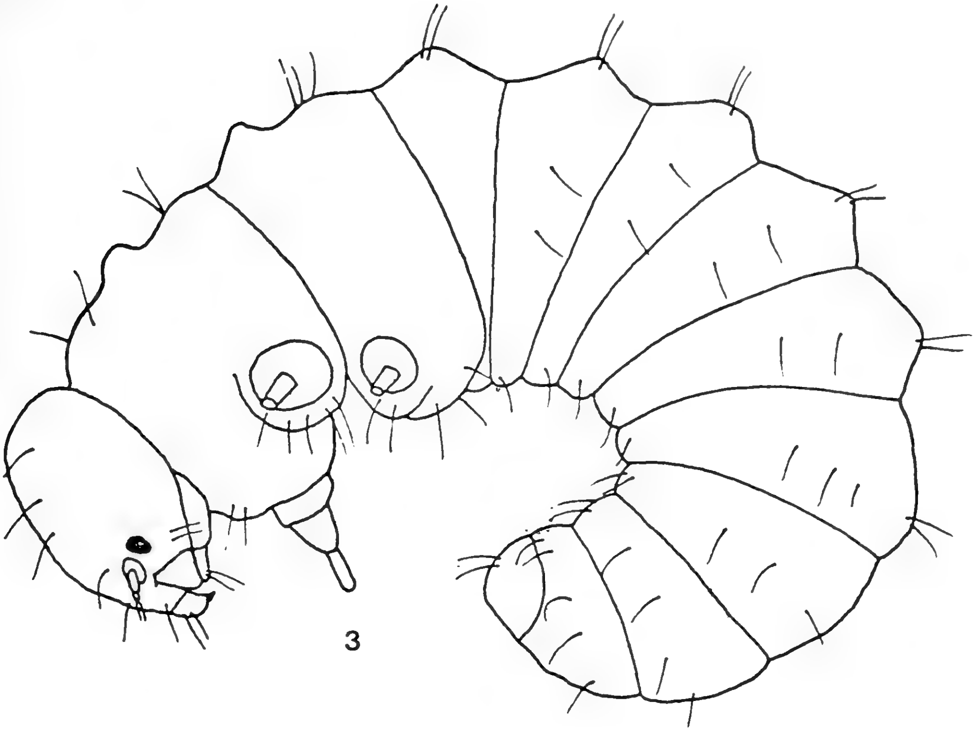
Figure 2. *Boreus coloradensis* Byers, male, lateral view, legs removed (39×).

of antennae. Lateral ocelli close to margins of compound eyes. Anterior tentorial pits just below level of antennae and about halfway between margins of compound eyes and medial line.

A long, thin cervical sclerite articulating with prothoracic episternum (Hepburn, 1970). Pronotum saddle-shaped, frequently with somewhat indistinct medial ridge, bearing small setae, and often with large bristles along anterior and posterior margins. Spiracle at caudo-lateral margin of pronotum. Meso- and metanota with raised, triangular scutella visible between reduced wings. Mesoscutellum frequently bearing two crossed bristles; occasionally metascutellum also with two bristles, varying with individual. Prothoracic basisternum triangular to pentagonal in shape. Preepisternum very thin; coxal cavities occupying almost all of sternal region of thorax. Coxa large, conical; trochanter small; femur long, thin, frequently with subapical dorsal spine; tibia long, thin; tarsus five-segmented, proximal tarsomere about twice as long as each of last four; two smooth tarsal claws. Tibia and tarsomeres with many stout spines. Mesothoracic wings of female reduced to oval, densely sclerotized flaps covering the smaller metathoracic wings, extending to caudal margin of metathorax, except in *B. reductus* and *navasi.* Metathoracic wings reduced to little more than small, irregular folds (Fig. 13, p. 153). Male wings modified as thin hooks. Mesothoracic wings curved ventrad laterally, extending to about fourth abdominal segment, bearing rows of spines along both mesal and lateral margins, and covering metathoracic wings (Fig. 2, p. 145). Metathoracic wings thin, cylindrical structures, extending to about fourth abdominal segment, bearing dense, small setae and frequently several stout spines along ventral side.

Female abdomen composed of 11 segments. First segment closely associated with metathorax. Segments 2 through 7 with terga and sterna separated by membranous pleura. Eighth tergum extending ventrally to sternal area, forming a broken ring. Eighth sternum extending caudally as two long, parallel-sided lower valves (hypovalves) of ovipositor, apical half to one-third of valves bearing numerous spines. Abdominal spiracles in ventral margins of terga 2 through 7; spiracles of eighth segment in mid-lateral surfaces of eighth tergum. Ninth tergum short, quadrate, forming dorsal base of ovipositor. Ninth sternum apparently lightly sclerotized and concealed by lower valves. Tenth tergum in *Boreus* elongate, parallel-sided, forming dorsal surface of ovipositor, in *Hesperoboreus* short with two spine-tipped caudal extensions. Cerci triangular, sclerotized, and fused along midline in *Boreus,* forming acute tip of ovipositor. Cerci incompletely fused distally in *Hesperoboreus,* revealing small, sclerotized eleventh tergum and sternum when raised.

Male abdomen composed of 10 apparent segments. First segment closely associated with metathorax. Segments 2 through 7 with unfused terga and sterna. Terga of segments 2 and 3 in *hyemalis* group bearing flattened ridges. Tergum and sternum of segment 8 fused laterally in *californicus* and *hyemalis* groups, unfused in *nivoriundus* and *reductus* groups and *Hesperoboreus.* Tergum 9 raised in *Boreus* with medial depressions for reception of tips of dististyles. Medial depressions covered anteriorly by thin hood except in *Hesperoboreus;* hood with median septum in *californicus* and *hyemalis* groups. Numerous peg-like denticles caudally and laterally on ninth tergum. Ninth sternum (hypandrium) elongate-triangular, apex rounded, truncate, slightly emarginate, or deeply notched. Tenth tergum and sternum reduced to small, oval sclerites between basistyles. Aedeagus membranous, except for small, thin sclerite along anterior surface. Basistyles (gono-



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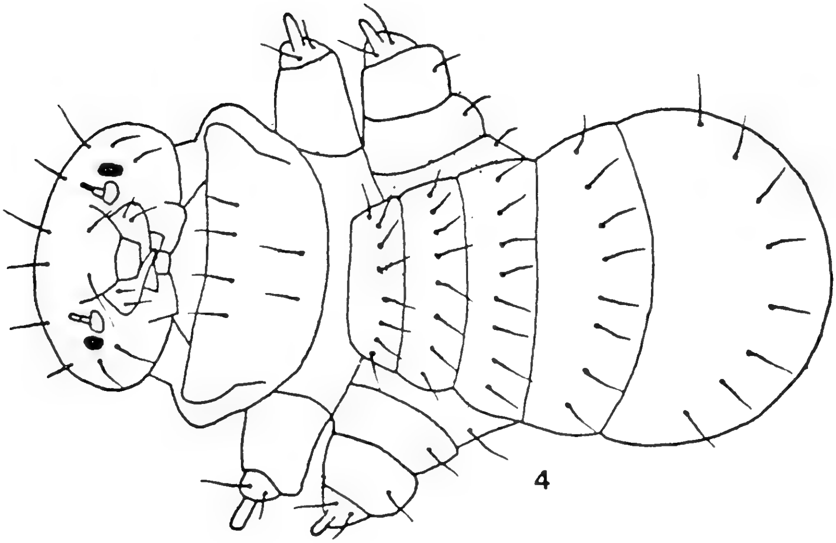

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FIGURES 3,4. *Boreus coloradensis* Byers, larva. Fig. 3, lateral view. Fig. 4, ventral view. Both 42×.

coxites) bulbous, with median dorsal ridge extended anteriorly as two sclerotized, laterally flattened straps, expanding medially to unite and form a thin, broad plate (dorsal gonobase of Cooper, 1974) (see Cooper, 1972, Figure 4). Dististyles claw-shaped with inner, basal lobe and many stout denticles below apex of claw. Dististyles normally recurved over abdomen with apex in ninth tergal depressions and denticles of ninth tergum in contact with similar structures below apex of dististyles.

C. EGG—White, unsculptured, oblong, varying in dimensions from approximately .7 × .5 mm. in *Boreus elegans* to .5 × .3 mm. in *Hesperoboreus notoperates*.

D. LARVA—Overall body length up to 4.83 mm. Head (Figs. 3, 4, p. 147) creamy yellow with prominent, darkened mandibles and darkly pigmented region around stemmata. Pigmentation shifting to position on head where pupal compound eyes will form late in last larval instar (Cooper, 1974). Antennae small, two-segmented, with apical hair, half-way between eyes and mandibles. Mouthparts short, not forming rostrum. Labrum and three-segmented maxillary palpi lightly sclerotized. Many prominent bristles on head and mouthparts (Peterson, 1951), varying among species (Cooper, 1974).

Thin, crescent-shaped sclerite projecting laterally from body wall in cervical region where strong head protractor muscle attaches.

Thorax transparent white, allowing observation of major muscles through body wall. Prothoracic legs small, ventrally directed, two-segmented. Mesothoracic and metathoracic legs large, laterally directed, four-segmented; fourth segment small and transparent. Numerous bristles covering thoracic region.

Abdomen transparent white, 11 segmented, bearing many bristles. No abdominal legs or appendages of any sort. Brauer (1855) mentioned abdominal legs in first instar larvae. This observation has not been repeated.

There are probably four larval instars (see Cooper, 1974; Withycombe, 1922).

E. PUPA—Approximately same length as adults, whitish, with darkened eyes and mandibles. As pupa matures, legs also darken. Pupa exarate, with articulated mandibles (decticous) for movement in subterranean tunnels. Antennae and legs held under body. Male wing sheaths flattened blades along sides of thorax. Female wing sheaths in form of small, dorsal lobes. Both male and female adult structures recognizable in older pupae, although somewhat distorted by enclosing sheaths and without detail. Along with heavily sclerotized mandibles, many setae are lost from body surface at last molt.

F. CHARACTERS USED IN TAXONOMIC DIFFERENTIATION—

a. *Overall size*—Adult Boreidae range in length from 2.0 to 7.4 mm. Although there are distinct differences between species, several other factors also contribute to individual length. Ecological factors such as climate and vegetation probably cause some variation. Method of preservation makes a difference in individual overall length; for instance, males of *B. brumalis* range from 2.0 to 2.7 mm. long preserved dried on points, but from 2.4 to 3.1 mm. preserved in 70 percent alcohol.

Females are invariably larger than males (this is interesting, considering that males carry females on their backs during copulation). Males of *H. brevicaudus* are 2.3 to 2.7 mm. in length in alcohol, while females range from 3.1 to 3.6 mm. in length. In the largest species of Boreidae, *B. elegans,* the differences are even more distinct. Males range from 3.6 to 4.6 mm. in length in alcohol, while females are 6.0 to 7.4 mm. in length.

There is no difference in minimum

length between the two genera, but no species of *Hesperoboreus* has yet been found which can compare with the maximum size attained by *Boreus elegans* or *borealis*.

b. *Coloration*—Previous authors have used coloration as a means of distinguishing species. A simple experiment helped to point out the unreliability of taxonomic use of coloration. On December 1, 1970, Dr. William L. Jellison collected a large number (about 150) of live *Boreus* on the snow near Hamilton, Montana. One-half of the specimens were preserved in alcohol and sent to the Snow Entomological Museum for identification. By use of existing keys (Carpenter, 1935, 1936), all the specimens were identified as *B. californicus fuscus* with yellow legs, wings, and rostrum, and a dark brown (almost black) body. The other half of the collected specimens were placed alive in a large plastic bag together with pine forest detritus, on the shaded north side of Dr. Jellison's home in Hamilton, where they were exposed to seasonal cold temperatures. On January 1, 1971, the bag was opened and live and dead *Boreus* specimens were examined. All specimens were uniformly dark in color, like *B. unicolor*.

In other groups of insects pigmentation is often related to time since eclosion or temperature during development. For example, the grasshopper *Mesopsis* slowly develops a patch of black on the hindwings over a period of about six months (Burtt and Uvarov, 1944) and Goodwin (1952) found that locusts bred at 40° C. were much lighter than the same species bred at 26° C.

B. californicus is particularly variable in coloration. Some specimens are yellow and black; others are light brown, darker russet brown, or dark brown to black. Some russet brown specimens from northeastern California were used in the original species description, causing F. M. Carpenter to describe the more commonly seen forms with light appendages as a subspecies, *B. californicus fuscus*. However, the color differences are sympatric and follow no geographic cline.

Withycombe (1922), Fraser (1943), and Strübing (1950) found that several days to a week were necessary for *B. hyemalis* to darken completely. Brauer (1857, 1863) found the same interval of time necessary for complete pigment deposition to develop in *B. westwoodi*. However, Williams (1916) found that only a half day was necessary for cuticular darkening in *B. brumalis,* and the same time interval is necessary in *H. notoperates* (Cooper, 1974).

Differences in rate of cuticular pigment deposition or in tanning probably do exist among species, but this genetic attribute cannot be used in species identification because rate may be modified by climatic factors, and age of preserved material is rarely known.

c. *Pilosity*—Possibly one of the first things noticed about adult Boreidae when viewed through a microscope is the large number of setae, bristles, spines, and denticles over many parts of the body. These structures are found on all species, most abundantly between the antennae, on the anterior part of the rostrum, along the sides of the thorax, on the wings, coxae, posterior halves of the abdominal segments, male ninth tergum and dististyles, and female eighth sternum. However, two species (*B. nix* and *pilosus*) have more extensive pilosity than others, giving their bodies a "frosted" look. Two other species, *B. brumalis* and *reductus,* have abundant pilosity, but not nearly to the same extent as in *nix* and *pilosus*.

d. *Chromosomes*—Only four species of Boreidae have been studied cytogenetically (Cooper, 1951, 1972, 1974). The haploid number (N) varies from 9 in *H. notoperates* to 11 in *B. brumalis,* to 13 in *nivori-*

undus, to 14 in *hyemalis.* There is an XO sex determining mechanism, except in *B. brumalis* which has X_1X_2Y. Although it is too early to make phylogenetic conclusions from these isolated observations, it does appear that chromosome study holds some promise of adding to our knowledge of the phlogeny of Boreidae.

In two species of *Boreus,* spermatogenesis takes place in the pharate pupa, while in *H. notoperates* spermatogenesis occurs in the mature pupa and pharate adult (Cooper, 1974).

e. *Occipital smoothness*—The occiput of *Hesperoboreus* is rugulose, the uneven surface also covered with many setal pits. In *Boreus* the occipital surface has fine reticulations and setal pits, although these reticulations are barely visible (Fig. 5, p. 151). The surface is much more even than in *Hesperoboreus.* An exception to the occipital reticulation of *Boreus* is the completely smooth occiput of *B. hyemalis* (Fig. 6, p. 151), which has been used to distinguish *hyemalis* from the very closely related *B. westwoodi.* Because I cannot find other characters to separate the species, I doubt the taxonomic significance of the smooth occiput.

f. *Ocelli*—In other mecopteran families, ocelli are arranged in a small triangle just above the antennae. In Boreidae the ocelli are dispersed, the lateral ocelli near the margins of the compound eyes (Figs. 7-10), and the median ocellus, when present, near the antennal bases. In *Hesperoboreus* and the *reductus* group of *Boreus,* the median ocellus is absent. Withycombe (1922) and earlier authors stated that Boreidae possessed no ocelli, but Withycombe later (1926) corrected his earlier statement.

g. *Antennae*—These structures are of use in generic separation. The antennal bases of all *Boreus* lie between the compound eyes (Figs. 8, p. 152; 9, p. 152; 10, p. 152). The antennal bases of *Hesperoboreus* lie at the lower margins of the compound eyes (Fig. 7, p. 152).

Lestage (1940) used number of antennal segments to separate most of the Palearctic species. However, it must be noted that males frequently have one more segment than females, and these is variation among individuals or even between antennae of one individual. For a good statistical analysis of antennal segmentation in *H. notoperates,* see Cooper (1974).

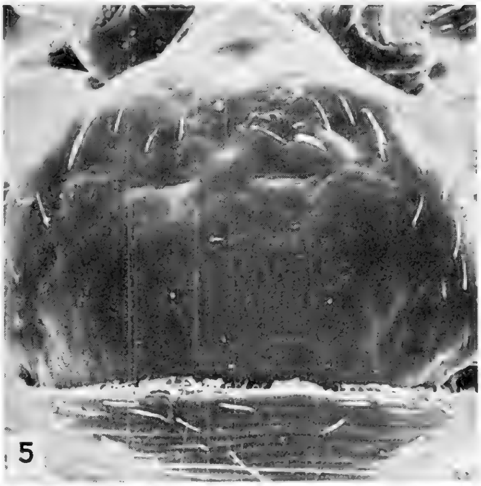
However, the degree of variation differs from one species to another. Males of *H. brevicaudus* consistently have 16 flagellomeres, while males of *B. coloradensis* have flagellomeres numbering from 18 to 22. Thus, the number of flagellomeres can be used taxonomically, as long as the variation is taken into account. The numbers for each species are given below with the species description, but it should be noted that generally *Hesperoboreus* has fewer flagellomeres than *Boreus,* number of flagellomeres varying from 16 to 18 in the former, and 17 to 23 in the latter.

h. *Width of hypostomal bridge*—Variation in hypostomal bridge width makes the maxillo-labial complex appear either shorter or longer. This variation can be expressed as a ratio of the length of the maxillo-labial complex (hypostomal bridge to apex) to the length of the rostrum, as measured from the base of the compound eye to the tip of the labrum. In the genus *Hesperoboreus* this ratio varies from .44 to .71 (Fig. 7, p. 152), while in *Boreus* it varies from .70 to 1.0 (Fig. 10, p. 152). Thus it can be seen that the hypostomal bridge is generally wider in *Hesperoboreus* than in *Boreus.* Within *Boreus,* fluctuation is too great for taxonomic use.

i. *Setae of the maxillo-labial complex*—The maxillo-labial complex of *Boreus* usually has a number of setae along the posterior margins (Fig. 8, p. 152). However, in *Hesperoboreus* these setae are usually completely lacking (Fig. 7, p. 152). Further, *B. nivoriundus* and *elegans* have some setae which are short and so thickened that they are termed spines (Figs. 9, p. 152; 10, p. 152). This character can be used to identify this *Boreus* subgroup.

j. *Notal bristles*—The bristles along the anterior and posterior margins of the pronotum and on the meso- and metanota are so easily visible and so invariable that they should be used for species recognition. Notal bristles are found in *Hesperoboreus* and the *nivoriundus* group of *Boreus* (Figs. 11, p. 153; 12, p. 153). Usually, there are 6 or 8 bristles along the anterior and posterior margins of the pronotum. The scutella of the mesonotum and metanotum may each possess two more bristles, but their presence is much more variable. In all North American species except *B. reductus,* presence of pronotal bristles is correlated with separation of the eighth abdominal tergum and sternum.

k. *Apical femoral spine*—This character is of some value but must be used with caution. The spine is reduced in size in some specimens, and occasionally may be absent entirely. Because smaller setae are also present near the distal ends of the femora, the specimens frequently must be rotated until the spine stands out against a lighted background from the femur and other setae. This spine is present in all North American boreids (Fig. 14, p. 155) except *B. coloradensis* (Fig. 15, p. 155), *reductus,* and sometimes *californicus*. *B. californicus* is very similar to *coloradensis* and no known character differentiates females. In a large collection of specimens from Helena, Montana, *all* female specimens without apical femoral spines were preserved *in copula* with males of *B. coloradensis,* while none of the female specimens with femoral spines and no males of *californicus* were mating when collected. It was hoped that the apical femoral spine could be used for identification, as it seemed reliable for the large number of specimens collected in western Montana, Oregon, and Washington. However, recent collections of *californicus* from California and Arizona created problems because these individuals did not possess the apical femoral spine. Still, I am reluctant to discard this character because of its usefulness in northern regions.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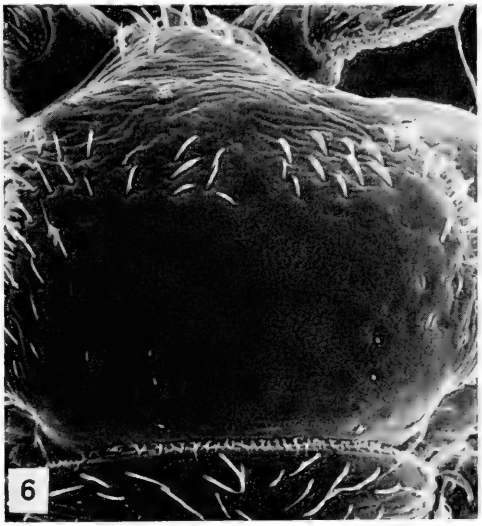
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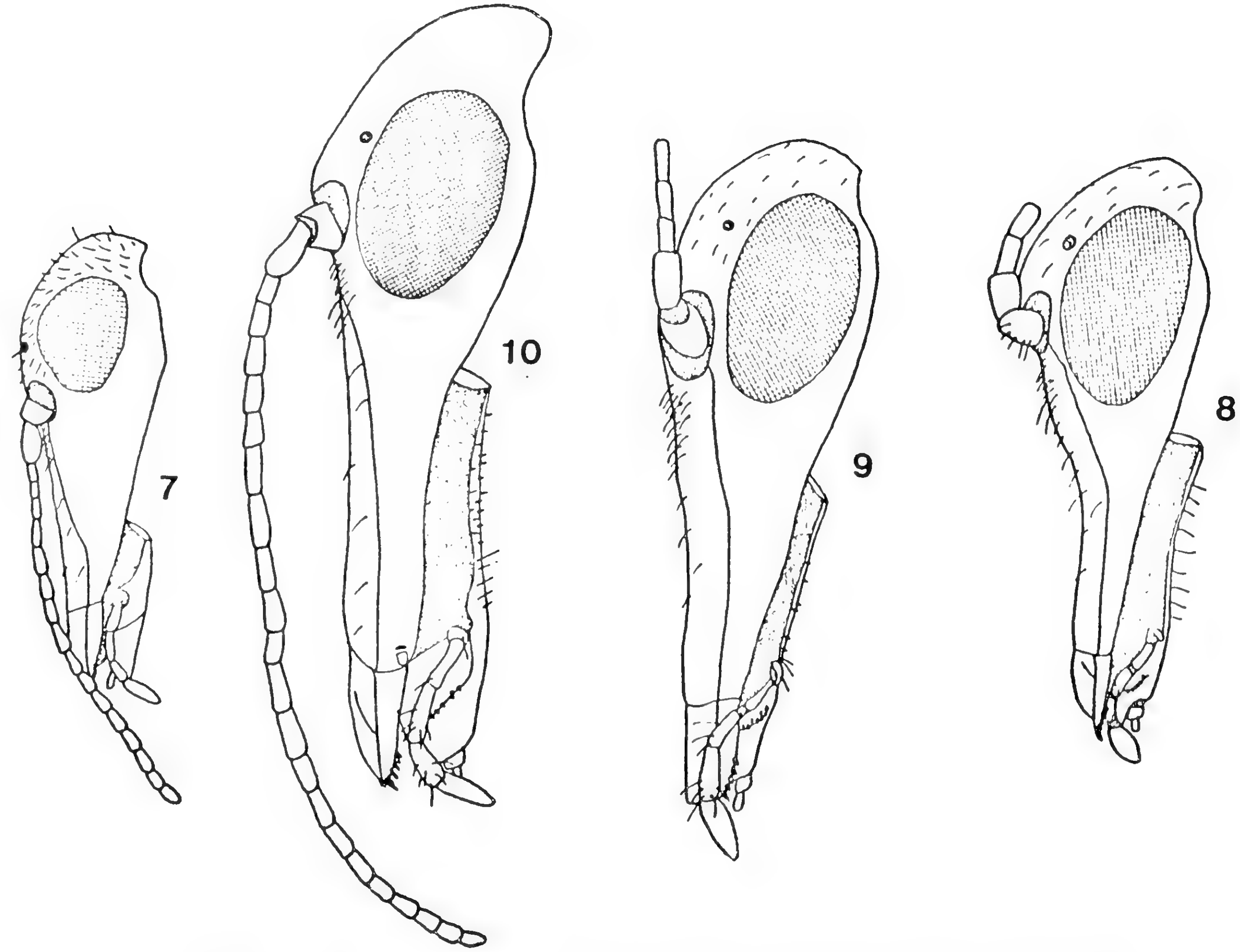
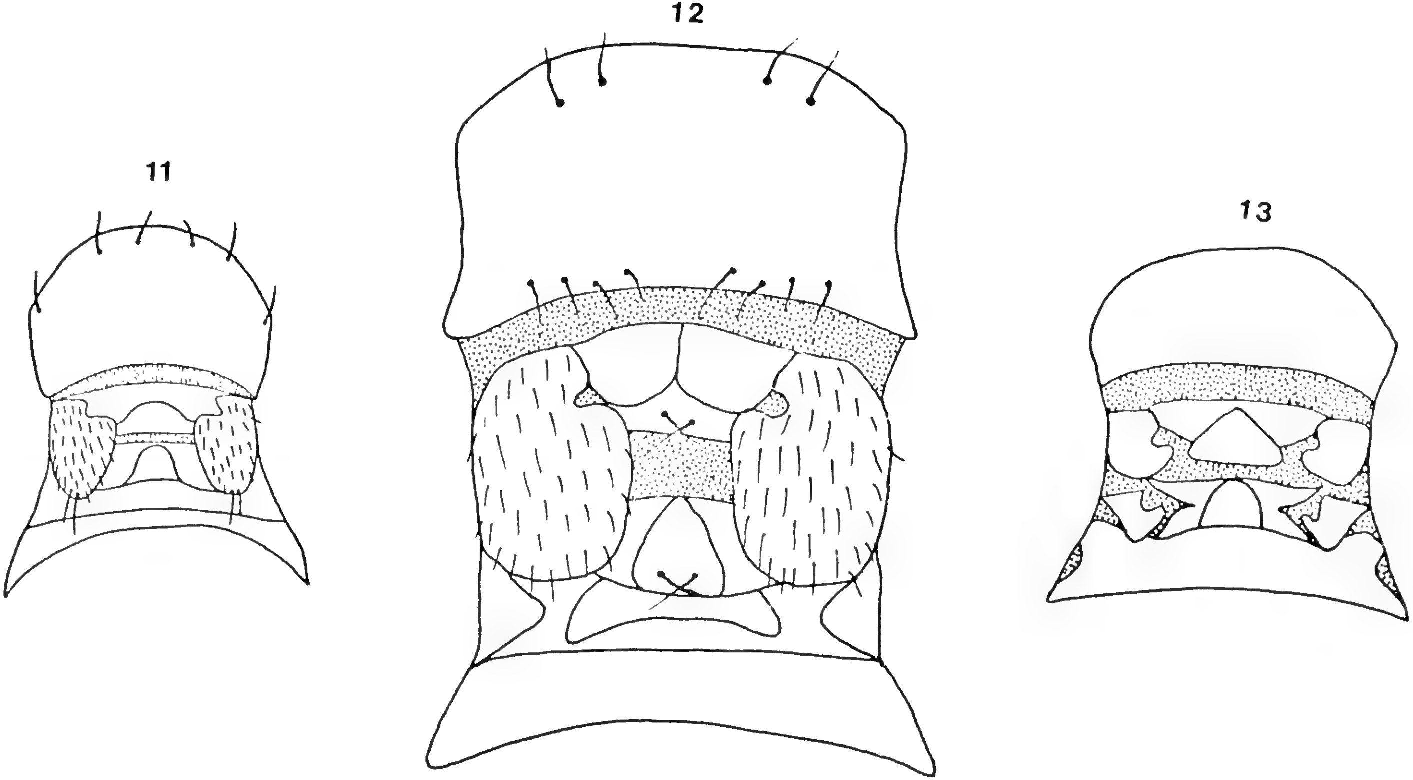
FIGURE 5,6, dorsal view. Fig. 5, *Boreus coloradensis* Byers. Fig. 6, *Boreus hyemalis* (L.). Both 175×.

l. *Male wings*—Forewings of male boreids have two rows of spines. One row along the anal margin projects mesally (inner forewing spines), while a second row projects ventrally from the costal mar-



FIGURES 7-10, head, lateral view. Fig. 7, *Hesperoboreus brevicaudus* (Byers). Fig. 8, *Boreus coloradensis* Byers. Fig. 9, *Boreus nivoriundus* Fitch. Fig. 10, *Boreus elegans* Carpenter. All 53×.



Figures 11-13, thorax, dorsal view. Fig. 11, *Hesperoboreus brevicaudus* (Byers), 56×. Fig. 12, *Boreus elegans* Carpenter, 50×. Fig. 13, *Boreus reductus* Carp., 50×.

gin (outer forewing spines). The tip of the forewing extends caudally as a spine larger than the others. Apparently there has been a reduction in the number of outer forewing spines in the European species. Lestage (1941) mentioned that outer forewing spines in each of these species were grouped in a consistent pattern: six spines (2+2+2) for *westwoodi,* eight spines (1+1+4+2) for *hyemalis,* and eleven spines (5+1+1+3+1) for *kratochvili.* Among specimens of these species that I have examined, this pattern is not consistently found. North American species have more spines than the European species; the spines are arranged in uniform rows; and the number of spines varies both between species and within species. These appears to be a pattern of reduction in outer forewing spines as one looks from the *nivoriundus* group (Fig. 16, p. 158) to the *californicus* group (Fig. 17, p. 158) of species of *Boreus.* The number of spines among species of the *nivoriundus* group ranges from 14 to 19, in the *reductus* group from 11 to 19, in the *californicus* group from 7 to 13, and in the *hyemalis* group from 6 to 11. However, greatest reduction is seen in *Hesperoboreus* which has no outer forewing spines (Fig. 18, p. 158).

In *Boreus* the number of inner forewing spines ranges from 15 in several species to 36 in *borealis,* the greatest variation being in *californicus,* with 15 to 22 inner forewing spines. In *Hesperoboreus* the range is from 13 in *brevicaudus* to 16 in *notoperates.*

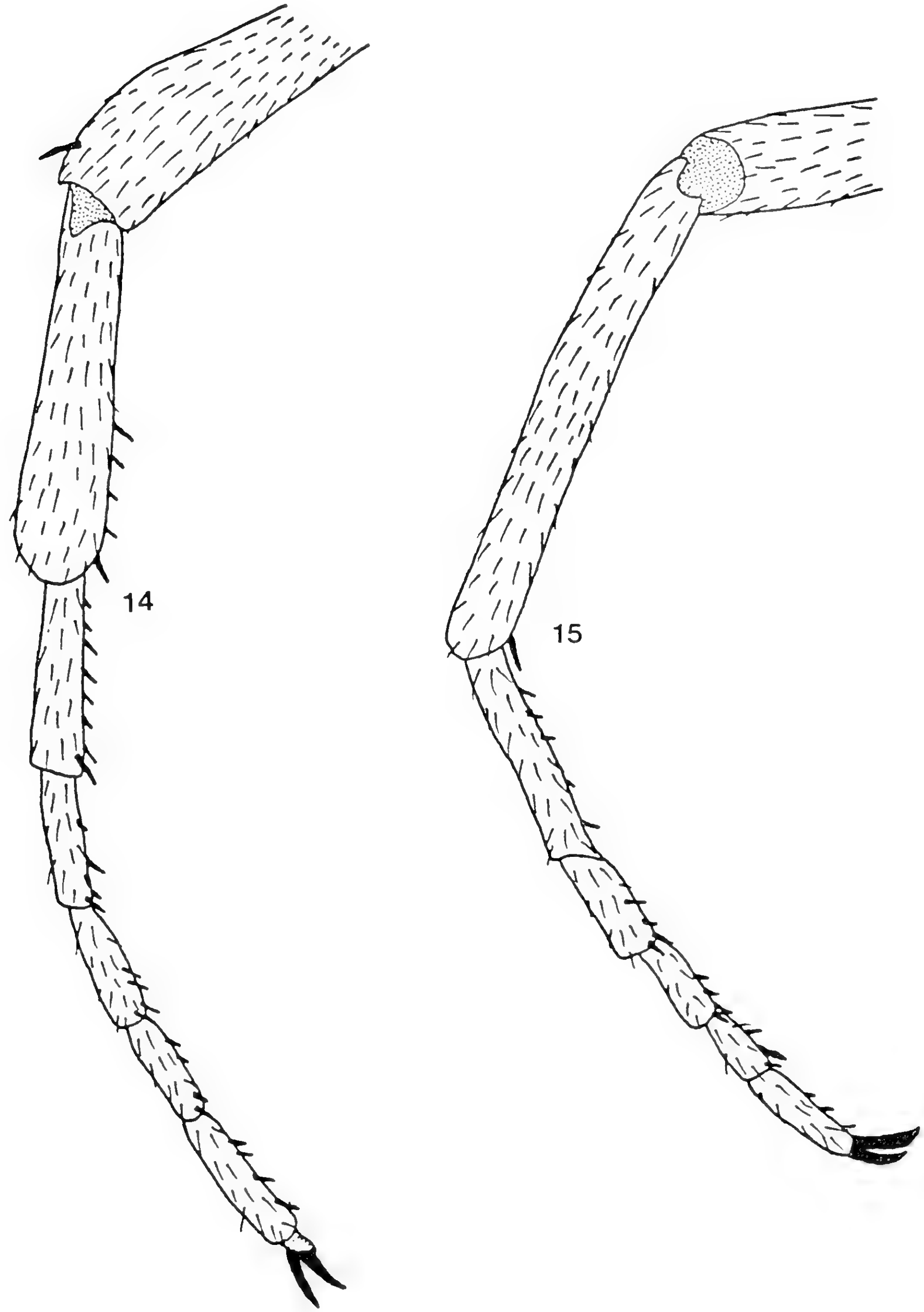
There is a reduction in hindwing spines similar to that in outer forewing spines. These spines are much smaller than those of the forewing, and project ventrally in a row. In the *nivoriundus* group, the number of hindwing spines varies from 9 to 16 (Fig. 16, p. 158), in the *reductus* group, it varies from 3 to 4, and frequently there are no spines at all in species of the *californicus* and *hyemalis* groups (Fig. 17, p. 158), although very small spines are occasionally present. Apparently, there has been little reduction of hindwing spines in *Hesperoboreus,* where there are from 10 to 17 (Fig. 18, p. 158).

Great taxonomic emphasis has in the past been placed on curvature of the outer margins of male wings, as seen in dorsal aspect. In most species of *Boreus,* there is a rather abrupt narrowing of the wing about halfway to the tip (Fig. 19, p. 159). Two species, *B. elegans* and *nivoriundus,* do not show this abrupt narrowing and their wings are wider near the tip than in other species (Fig. 20, p. 159). Carpenter (1936) mentioned that *B. intermedius* possesses this broader wing; however, I could see distinct narrowing at mid-length in the same specimens. Abruptness of narrowing varies according to how the specimen is positioned for viewing, for if viewed from too far laterally, an abruptly narrowed costal margin appears almost straight. Thus, shape of male wings can be used, if done with great caution.

m. *Female wings*—Although all species of boreids have an abundance of fine setae covering the dorsum of the female mesothoracic wings, only one species, *Hesperoboreus brevicaudus,* has yet been noted to possess several larger bristles at the caudal margin (Fig. 11, p. 153).

The female boreid's metathoracic wings are normally reduced to little more than wing vestiges, but in *B. reductus* this condition is found in both pairs of wings (Fig. 13, p. 153). The reduced mesothoracic wings are also found in other species of the *reductus* group from the Crimean region of U.S.S.R., but not in any other groups.

n. *Male tergal ridges of second and third abdominal segments*—Lestage (1940) used two characters to separate the Boreidae into two genera. Nearctic species (plus *B. semenovi*) were placed in the genus *Euboreus,* having no transverse ridges on the



Figures 14,15, left foreleg, dorsal view. Fig. 14, *Boreus elegans* Carpenter, 86×. Fig. 15, *Boreus coloradensis* Byers, 80×.

second and third abdominal terga (Fig. 21, p. 162) and lacking a medial tooth on the diststyles. Palearctic species (minus *B. semenovi*) were retained in the genus *Boreus,* having tergal ridges (Fig. 22, p. 162) and the medial tooth. Lestage was wrong, however, about both characters. The medial tooth (basal lobe) is found on the dististyles of *all* male boreids. And the tergal ridges are present only in four closely related European species. The ridges are not found in *any* of the Asiatic Boreidae for which males are known. The phylogeny presented later in this paper and Cooper's (1972) discussion of the status of *Euboreus* give further reasons why this classification should not be followed.

Species which do have transverse ridges on the male second and third abdominal terga are: *B. hyemalis, kratochvili, lokayi, westwoodi,* and possibly *chadzhigireji.* Martynova (1954) mentions that tergal ridges of *chadzhigireji* are almost not present, and her illustration of the terminal segments of the male suggest that this species has no fusion of eighth tergum and sternum. Fusion of eighth tergum and sternum probably occurred long before acquisition of the tergal ridges within the Boreidae. Thus, it is probable that only the first four species mentioned have tergal ridges.

Lestage (1941) illustrated the tergal ridges of three of the four European species. The ridge of the second tergum in *B. hyemalis* is wide and lobed near its lateral ends. The ridge of tergum 3 is also lobed laterally, but varies in width. In *B. westwoodi* the second tergal ridge is very similar to that of *hyemalis,* but the third tergal ridge is triangular to convex (lacking the lateral lobes). The second tergal ridge of *B. kratochvili* is deeply notched medially, giving the ridge a bipartite appearance. The third tergal ridge of *kratochvili* is obtusely angled to an ill-defined peak. Lestage's key to Palearctic boreids states that the third tergal ridge of *B. lokayi* is reduced to a small tubercle.

These character states can apparently be used to differentiate species. Not enough specimens were available for me to study the tergal variation within these four species, although considerable variation is apparent from Lestage's drawings and from specimens I have examined (Figs. 23-30).

o. *Fusion of male eighth abdominal tergum and sternum*—Mickoleit (1971) first mentioned interspecific variability of the male eighth abdominal segment. Cooper (1972) expanded upon this statement by listing many of the Palearctic and Nearctic species and noting whether fusion of the tergum and sternum had occurred. He based many of his decisions on illustrations Martynova (1954) made of species from the U.S.S.R. I can do little better, as I have seen only *B. hyemalis* and *vlasovi* from the Asiatic region. Therefore, until more material can be obtained, analysis of Palearctic species must rely on often-times incomplete descriptions and inadequate illustrations.

This character of fusion of the eighth abdominal tergum and sternum in males appears to be a very strong one, and it has been used to separate major groups within *Boreus.* Fusion in this segment is correlated with expansion of the ninth tergal hood, presence of a large medial septum within the hood, loss of some outer forewing spines, and usually complete loss of hindwing spines. Fusion of the eighth abdominal tergum and sternum (Fig. 31, p. 165) is found in all species of the *californicus* and *hyemalis* groups. It is not found in *Hesperoboreus* or the other two groups of *Boreus* (Fig. 32, p. 165).

p. *Male ninth tergum*—Carpenter (1931) stated that "The male genitalia are also useless because they are constant in all our species." However, there is more diversity of the male ninth tergum than anywhere else on the external surface of Boreidae (Figs. 34-49).

The male ninth tergum is narrow laterally, expanding caudally toward the dorsal surface of the body. On the dorsal surface, the tergum is cleft medially for a short distance at its caudal end. On either side of this cleft are apical areas of peglike setae, which I shall refer to as denticles. The number of denticles varies from about eight on each side in *Hesperoboreus* (Fig. 34, p. 166) to over a hundred in some species of *Boreus* (Fig. 40, p. 167). In the genus *Hesperoboreus* the cleft is large and no tergal hood is present. In *Boreus* the cleft is smaller and at least a remnant of a hood is present in all species. In the *nivoriundus* subgroup of the *nivoriundus* group, the tergal hood is very small, enclosing only the very tips of the dististyles (Fig. 40). Within the *brumalis* subgroup the tergal hood is more than twice the size of that of the *nivoriundus* subgroup (Fig. 37, p. 166) and there may be an indication of a medial ridge within the hood (Fig. 46, p. 170).

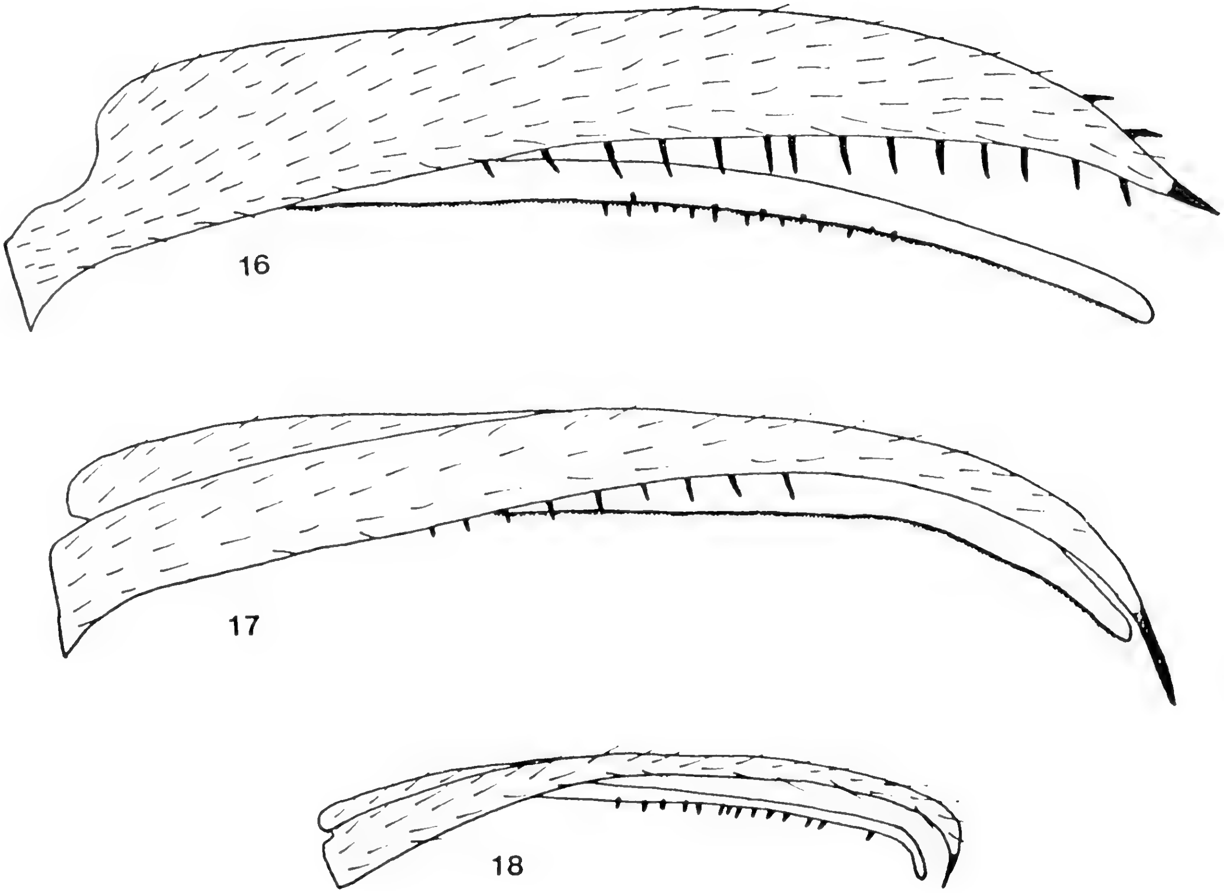
The *reductus* group is characterized mainly by differences in the caudal edge of the hood. In *B. vlasovi* this edge has symmetrical points on either side of the midline (Fig. 48, p. 170). In *B. reductus* the edge comes to one large peak in the middle of the hood (Fig. 47, p. 170). This group is largely composed of little-known species, so that further variation is quite possible.

Within the *californicus* and *hyemalis* groups, the tergal hood is broadly expanded dorsally and caudally to laterally almost engulf the area of denticles, and medially does cover over the cleft (Fig. 42, p. 167). A large medial septum supports this expanded hood in both groups. The medial septum may be either broad or narrow, and sometimes there are so many setae along the septum that observation of the interior of the hood area is difficult.

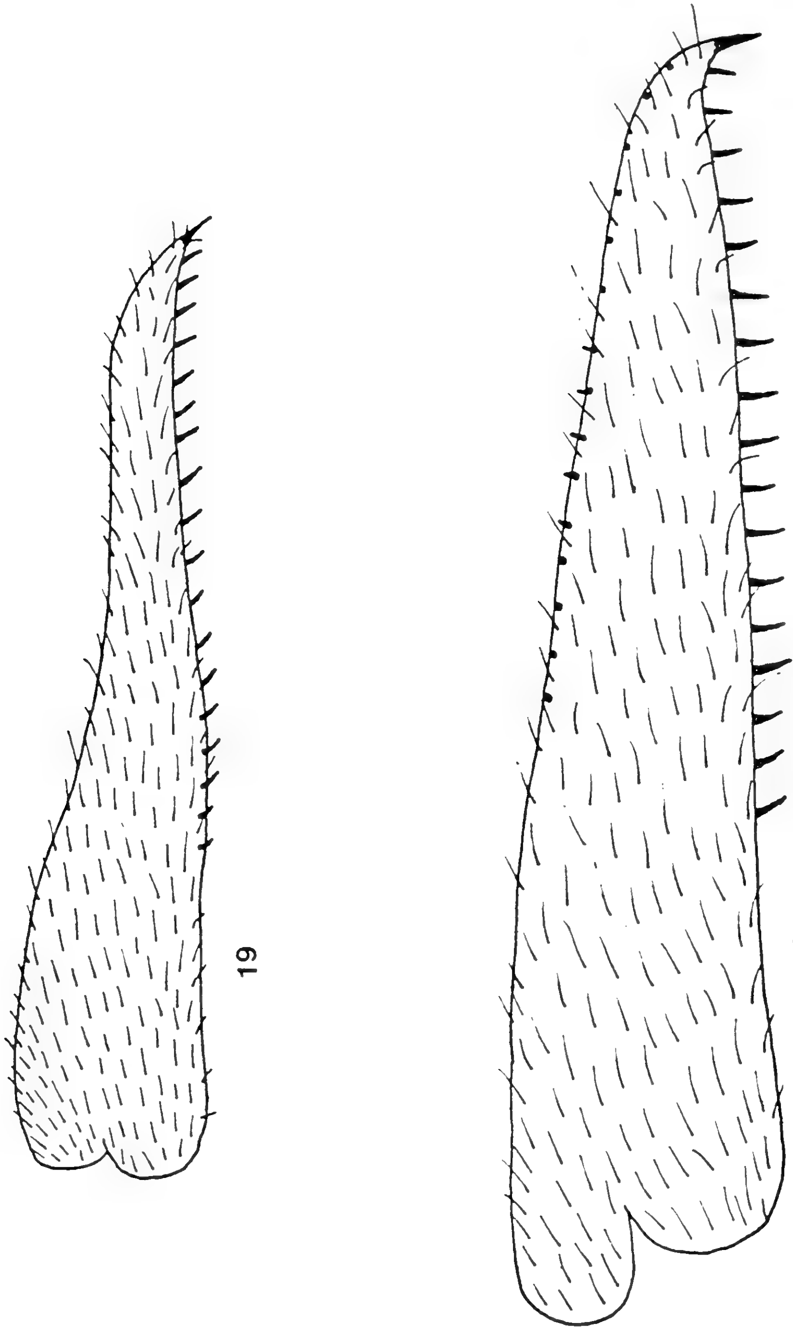
q. *Fusion of male ninth tergum and sternum*—Cooper (1972) mentioned that any revision of the Boreidae would necessarily include fusion of tergum and sternum in the eighth and ninth abdominal segments as key taxonomic characters. The fusion of the eighth segment has been used by me to separate the *nivoriundus* and *reductus* groups from the *californicus* and *hyemalis* groups within *Boreus.*

The fusion of male ninth tergum and sternum may be of less importance taxonomically, but it still has some value. The ninth tergum tapers laterally to a narrow strip. Often it is either retracted within the eighth segment or overlapping the ninth sternum, making observation of a membranous gap between the sclerites difficult. North American and European species do not possess this fusion; however, my study of *B. vlasovi* and examination of the literature indicate that some Asiatic species of *Boreus* possess the potential for fusion of male ninth tergum and sternum (Fig. 33, p. 165). In *B. vlasovi* some male specimens have the fusion, and some do not. These Asiatic species can all be placed in a subgroup of the *reductus* group on the basis of this character state. Thus, this character state is too variable for use in species identification.

r. *Male ninth sternum (hypandrium)*—In males of most Boreidae, the ninth sternum is broadly triangular, being broadest basally and gradually tapering caudally to a broadly rounded apex between the bases of the dististyles (Fig. 50, p. 172). In *B. reductus* this triangle is much narrower, forming an acute apex (Fig. 51, p. 172). As Byers (1955) pointed out for the species *B. coloradensis,* the apex varies intra-specifically from smoothly rounded to truncate to shallowly emarginate. In no case, however, does a species with a rounded ninth sternal apex also include individuals with a *deeply* emarginate apex. In the *brumalis* subgroup, the ninth sternal apex is deeply notched (Fig. 51).



Figures 16-18, male, left wing, lateral view. Fig. 16, *Boreus elegans* Carp., 86×. Fig. 17, *Boreus coloradensis* Byers, 86×. Fig. 18, *Hesperoboreus brevicaudus* (Byers), 50×.



Figures 19,20, male, left forewing, dorsal view. Fig. 19, *Boreus coloradensis* Byers. Fig. 20, *Boreus elegans* Carpenter. Both 86×.

s. *Male diststyles*—These structures hold the female's eighth sternum in place during copulation. Observed differences in the shape of the diststyles may have a direct relationship to differences in mating posture between the two genera. In *Boreus* the basal lobe has a rather blunt, obtuse apex. There is a deep, narrow cleft between the basal lobe and the diststyle proper. Denticles occur only from the basal lobe to the base of the diststylar claw (Figs. 53-56). In *Hesperoboreus* the basal lobe has an acute apex. There is no cleft between the basal lobe and the diststyle proper. Finally, denticles occur from the basal lobe to very near the apex of the diststylar claw (Figs. 57, p. 172; 58, p. 172). Variation within each genus is too slight to be of taxonomic value. The number of denticles does vary, but their size is so small and the number so variable within a species that differences are difficult to detect.

t. *Length of the ovipositor*—This character varies, as do measurements of the structure. The fused cerci form an apical triangle which articulates with the tenth segment. In preserved specimens, the fused cerci may be directed straight posteriorly or deflected posteroventrally. As Carpenter (1935) pointed out, measuring the ovipositor on the dorsal surface will yield a different length than measuring the same specimen on the ventral surface, because the eighth sternum normally projects farther anteriorly than the tenth tergum. length of ovipositor therefore is measured as length of tenth tergum plus length of cerci, rather than from base of tenth tergum to tips of cerci.

Since overall length of specimens varies with method of preservation, it is helpful to compare the length of the ovipositor to that of some other relatively stable structure. The ratio gives an index of ovipositor length. Carpenter (1931) first used the rostrum as the second structure. Rostral length is measured from the ventral edge of the compound eye to the tip of the labrum.

By using the ovipositor/rostrum index, a distinct difference is noted between *Boreus* and *Hesperoboreus*. In *Boreus* the index ranges from 1.00 to 1.43 (Figs. 59, p. 173; 60, p. 173). Variation within and between species is considerable, making this index useless below the generic level. For instance, the index varies from 1.10 to 1.30 in *B. californicus*. In *Hesperoboreus* the index ranges from .33 to .63 (Fig. 61, p. 173). This means that the ovipositor of *Hesperoboreus* is much shorter than that of *Boreus*, a fact readily discernible when females of both genera are seen side by side.

u. *Process of tenth abdominal segment of female*—As noted by Byers (1961), the shortened tenth abdominal segment of the female in *Hesperoboreus brevicaudus* is prolonged posteriorly as spine-tipped extensions on either side of the partially unfused cerci (Fig. 61, p. 173). This structure is also found in *H. notoperates* (Fig. 62, p. 173), but has not been noted in *Boreus* (Figs. 59, p. 173; 60, p. 173). This caudal extension is a good character for separating genera, but it does not vary appreciably within *Hesperoboreus*.

v. *Basal notch of female eighth sternum*—Cooper (1974) noted that in *H. notoperates* copulation is reciprocal, meaning that in addition to normal coition the female eighth sternum is held in the male's endoandrium (of Cooper, 1974) by his diststyles. In this species, a basal notch on the eighth sternum of the female facilitates the diststylar hold (Fig. 62, p. 173). This basal notch is also found (although much smaller) in *H. brevicaudus* (Fig. 61, p. 173) but is lacking in all species of *Boreus*. Cooper observed that this mechanism helps *H. notoperates* maintain the unusual perpendicular mating position.

w. *Spines of the eighth abdominal sternum of the female*—All female boreids have some spines at the tip of the eighth sternum. Variation in number and placement of spines differs within species and between species, but there are consistent differences between the two genera. Spines only occur on the apical one-third in *Boreus,* while spines occur over the apical half in *Hesperoboreus.*

x. *Fusion of the female cerci*—Byers (1961) first reported that not all species of boreids had fully fused cerci (Fig. 64, p. 174). Until that time it was thought that Boreidae lacked cerci and that the apex of the ovipositor was the eleventh abdominal tergum. Byers separated the partially fused cerci of *H. brevicaudus* (Fig. 63, p. 174) and observed the sclerites of the eleventh segment below them. The same lack of complete cercal fusion has since been noted in *H. notoperates.* Incomplete fusion of the cerci is another taxonomically reliable generic character state.

PHENETICS

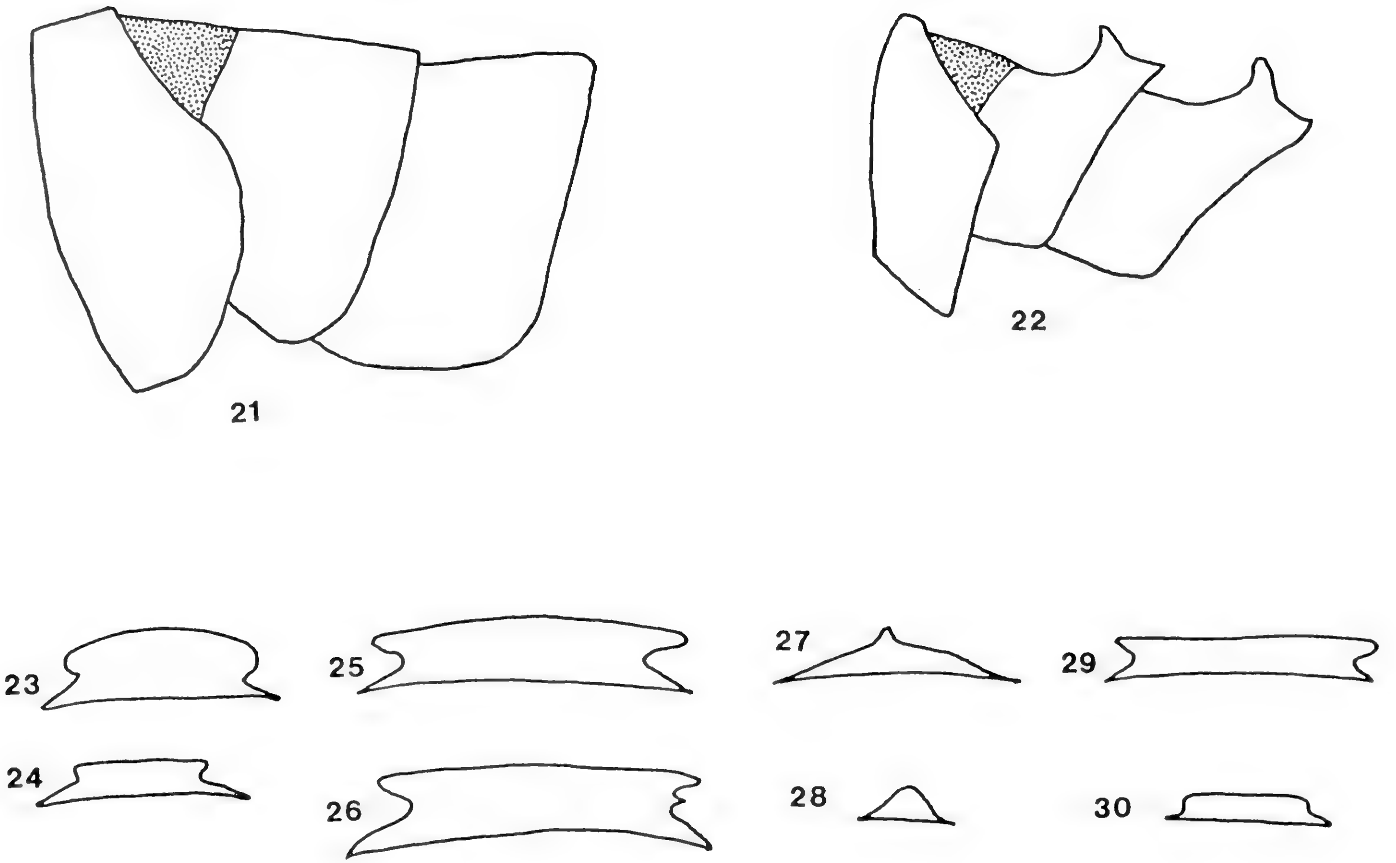
The subsequent discussion of phylogeny of the Boreidae is based on the author's subjective judgement of whether a given character state is primitive or derived. Much reliance is placed on the opinion that character states cannot be lost and then regained within the evolutionary history of the group. To assess whether the judgments and the emphasis placed on certain characters have distorted the degree of difference among species, a phenetic analysis of the Boreidae was also made of all species for which I had enough information. All characters that could be found to vary between species, but that varied little or not at all within a species, were recorded and compared. In all, 37 characters were used. The comparison of species was tabulated (Table 3, p. 176) in a scaled similarity matrix (Sneath and Sokal, 1973). This scaled similarity matrix was constructed by giving each character state (Table 4) a plus or minus, depending upon whether the species has (+) or lacks (—) the character state listed in Table 5, p. 178. The species were then compared with one another and the number of differences (mismatches) listed in the matrix. The absolute number of differences was then divided by the total number of character states used, and this fraction of difference was also entered in the scaled similarity matrix.

From this matrix a phenogram was constructed (Fig. 69, p. 182) by comparing the differences between each pair of species separately (Sneath and Sokal, 1973). The two species showing the least difference are linked together at the degree of difference indicated. This linked couplet is then compared with each other species, and the differences with the pair averaged. The smallest degree of difference is then linked to this couplet at the averaged degree of difference, or new couplets are formed, if this is the smallest degree of difference. Increasingly larger groupings are then compared. Using this technique, the phenogram is formed of these species showing the most similarity.

After constructing the phenogram, the levels for genus, group, and subgroup were set at .30-.40, .20, and .10, respectively. As can be seen by comparing the phenogram and phylogenies, phenetic and phylogenetic groupings are very similar. The same species repeatedly occur together in distinct groups. The *hyemalis* group is not quite as distinct as the other groups, but characters of the male tergum used to separate this group are quite discernible. These results may be due to the high degree of correlation in characters, an unconscious phenetic bias on the part of the author in choosing characters to study, or both.

PHYLOGENY

There are no fossils to help clarify the evolutionary development of Boreidae. The best indicator of a nearest sister group relationship (Hennig, 1965) is the scarabaeiform larva, because most other morpho-



FIGURES 21-30. Figs. 21,22, male, 1-3 abdominal terga, lateral view. Fig. 21, *Boreus coloradensis* Byers. Fig. 22, *Boreus hyemalis* (L.). Figs. 23,25,26, and 29, male, 2nd abdominal tergum, caudal view. Figs. 24,27,28, and 30, male, 3rd abdominal tergum, caudal view. Figs. 22-24, *Boreus hyemalis* (L.). Figs. 25-28, *Boreus lokayi* Klp. Figs. 29,30, *Boreus westwoodi* Hagen. All 100×.

logical traits are either unique or shared by several other mecopterous families.

Most mecopterous larvae are eruciform. Only one other family, the Panorpodidae, has scarabaeiform larvae. Within the Panorpodidae females are moderately to extremely short-winged and flightless, or nearly so. Adults generally live at elevations between 3000 and 8000 feet in the mountains of eastern and western North America, Japan, and Korea. Severe climatic conditions could have forced a population of panorpodid-like ancestors to express the genetic capability for additional cold tolerance with corresponding morphological modifications of size and structure. Comparisons between the two families indicate that within the Boreidae cerci and the tenth abdominal segment of the female fused into a heavily sclerotized ovipositor; adults and larvae adapted to feeding on moss, while panopodid larvae feed on roots and adults on leaf tissue; size became reduced; dark pigmentation increased; wings became reduced to heavily sclerotized flaps in the females and elongate, thin hooks in the males; the ocelli became more dispersed; and the life cycle increased to two years. The length of the life cycle is unknown in Panorpodidae, although in other mecopterous families where such information is available, the life cycle never exceeds one year.

The long rostrum of Boreidae is very

TABLE 1

LIST OF PRIMITIVE CHARACTER STATES.

1. Presence of median ocellus
2. Occiput not rugulose
3. No occipital reticulations
4. 21 or more antennal segments
5. Antennal bases between compound eyes
6. Narrow hypostomal bridge
7. Only fine setae on posterior surface of rostrum
8. Setae on body uniformly short
9. Thoracic bristles present
10. Forewings narrowed abruptly at mid-length-male
11. Presence of outer forewing bristles-male
12. Female forewings covering hindwings-female
13. Absence of bristles at caudal margin of wing pad-female
14. No transverse ridges on second abdominal tergum-male
15. No transverse ridges on third abdominal tergum-male
16. No fusion of eighth tergum and sternum-male
17. No ninth tergal hood present-male
18. No fusion of ninth tergum and sternum-male
19. Ninth sternum smoothly rounded apically-male
20. Tenth abdominal segment short-female
21. No posterior process of tenth abdominal segment-female
22. Cerci not fused-female
23. Cerci evenly tapering to apex-female
24. Eighth sternum not notched basally-female

LIST OF DERIVED CHARACTER STATES.

1. Loss of median ocellus
2. Gain of rugulose occiput
3. Loss of occipital reticulations
4. Loss of antennal segments
5. Movement of antennal bases to below eyes
6. Widening of hypostomal bridge
7. Gain of rostral spines
8. Gain of 25 rostral spines
9. Gain of long pilosity
10. Loss of thoracic bristles
11. Broadening of forewings at mid-length-male
12. Loss of outer forewing spines-male
13. Forewings reduced until they no longer cover hindwings-female
14. Gain of bristles at caudal margin of wing pad-female
15. Gain of transverse ridge on second abdominal tergum-male
16. Gain of transverse ridge on third abdominal tergum-male
17. Transverse ridge of third segment reduced to a tubercle-male
18. Fusion of eighth tergum and sternum-male
19. Development of small tergal hood-male
20. Tergal hood expanded to middle of denticular area-male
21. Tergal hood expanded to lateral margin of
22. Development of projections along lip of tergal denticular area-male
    hood-male
23. Development of medial projections along lip of tergal hood-male
24. Gain of medial septum to tergal hood-male
25. Development of narrow median septum-male
26. Gain of short median septum with ventral fork-male
27. Development of numerous setae covering interior of hood-male
28. Fusion of ninth tergum and sternum-male
29. Development of notched ninth sternum-male
30. Lengthening of tenth abdominal segment-female
31. Development of posterior process on tenth abdominal segment-female
32. Complete fusion of cerci-female
33. Gain of abruptly narrowing of cerci at mid-length-female
34. Development of eighth sternal notch-female
35. Expansion of eighth sternal notch-female

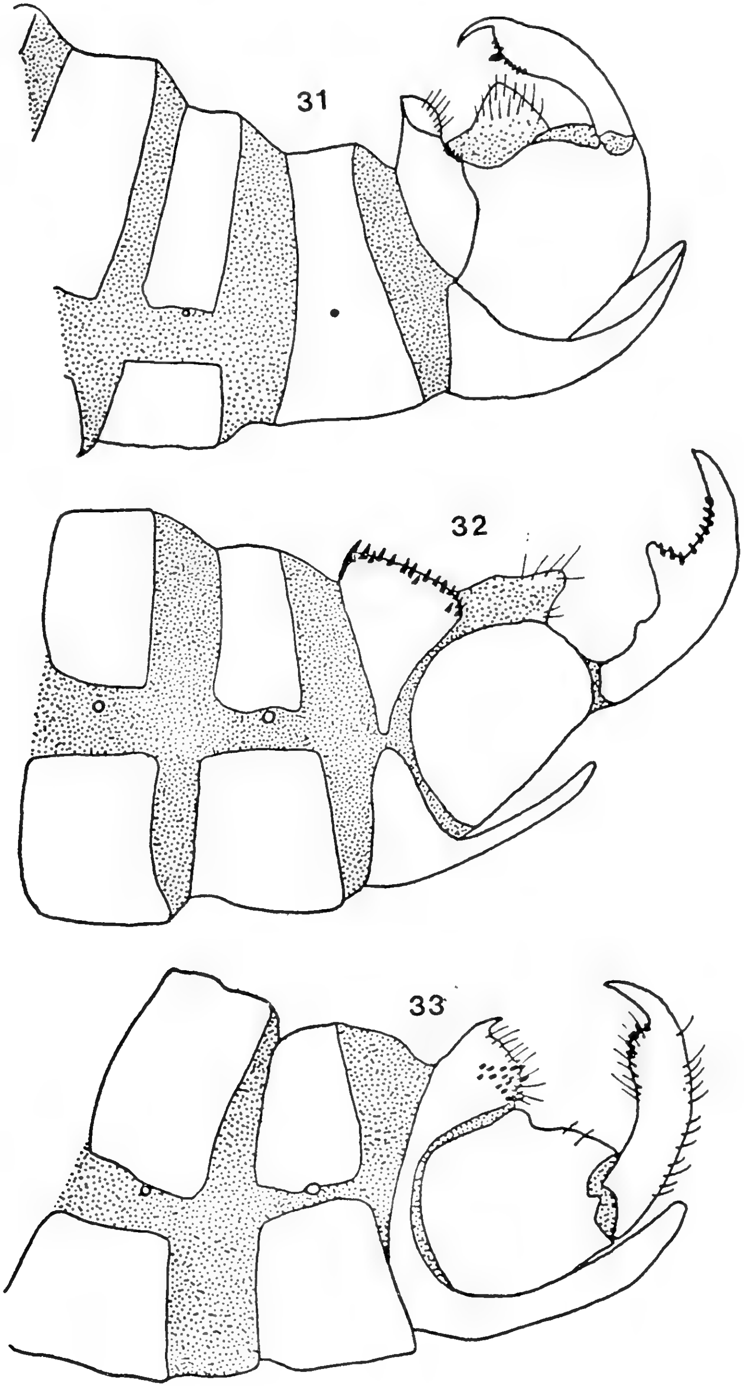
similar to that found in Panorpidae and indicates that ancestral boreids and panorpodids were distinct groups before secondary reduction of the rostrum began in Panorpodidae.

Many different ways can be used to depict diagrammatically the supposed evolution of Boreidae. Four methods are used here. The first (Fig. 66, p. 175) represents a phylogeny in which 35 derived character states (Table 1, p. 163) were chosen which varied between species, but were relatively constant within a species. These 35 character states were then analyzed to determine the probable primitive state for each (Table 1, p. 163) and subsequent development. They were then arranged on an unweighted branching sequence which would give the minimum number of changes in the characters. Although evolution may not always have taken the simplest course, the most parsimonious evolutionary diagram is presumably the best.

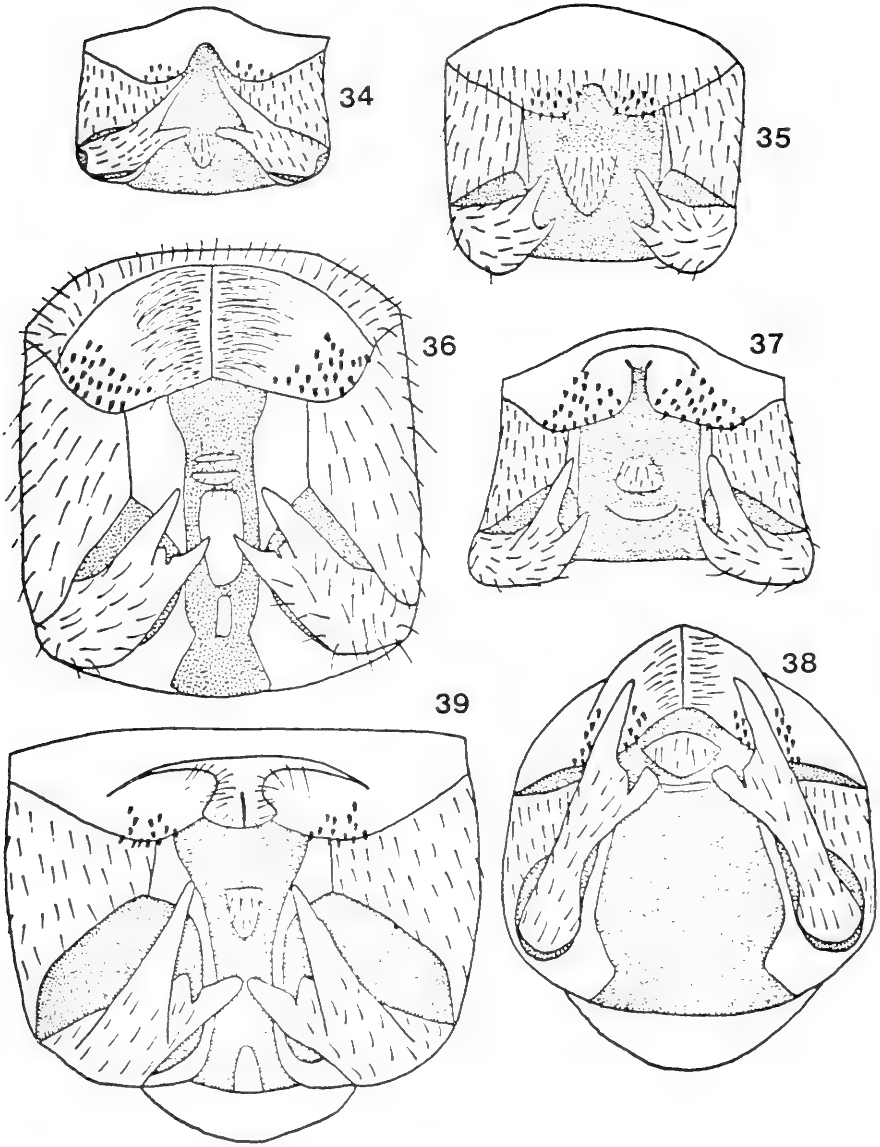
Many of the character states in this list are shared with the rest of Mecoptera, and are, therefore, considered primitive. Almost all Mecoptera have three ocelli, a smooth occiput without fine reticulations, antennal bases between the eyes, a narrow hypostomal bridge, fine setae on the posterior surface of the rostrum (if any setae at all) and prothoracic bristles, as well as unfused eighth tergum and sternum and no elaboration of the ninth tergum, in males, and in females a short tenth segment without caudal processes, unfused cerci which taper uniformly to the apex, and a basally unnotched eighth sternum. Mecoptera have long, filiform antennae with flagellomeres varying in number from about 60 in *Chorista* to 18 in *Bittacus*, with 40 or more being common in most families. Therefore, the largest number of flagellomeres found in Boreidae (23) is considered closest to the ancestral condition. Setation of Mecoptera usually consists of very small hairs on all areas of the body. Some boreids also have small hairs on most areas of the body, but two species (*Boreus nix* and *pilosus*) have developed extensive areas of thick, long pilosity, which I consider derived. Broad wings in the male are found only in *B. elegans* and *nivoriundus* and probably arose in a common ancestor of those two species. Likewise, reduction of the female forewings to vestiges not covering the hindwings is only found in the *reductus* group and is probably derived. A similar process was used to recognize as primitive the absence of bristles on the wing vestiges of females (bristles only in *H. brevicaudus*), absence of abdominal tergal ridges in males (ridges only in *hyemalis* group), the lack of fusion of ninth tergum and sternum of males (fusion only in *vlasovi* subgroup), and the smoothly rounded ninth sternum in males (deeply notched only in *H. notoperates* and the *brumalis* subgroup). Almost all Mecoptera have setae along the costal and anal margins of the wings, and enlargement of these setae could have led to the rows of spines along costal and anal margins of boreid forewings. Absence of these spines along the costal margins of forewings in *Hesperoboreus* is considered derived. The complex tergal hood of the *californicus* and *hyemalis* groups is derived through a progression of steps from no hood in *Hesperoboreus* to increasingly more complex structures in *nivoriundus* and *reductus* groups.

A conventional two-dimensional diagram depicting boreid phylogeny becomes too clustered around certain points to provide a clear idea of branching sequences. Therefore, a three-dimensional diagram was employed to allow more directions for progression. Displacement from one plate to the next above it of one millimeter in any horizontal plane (0°, 45°, 90°) corresponds to a change in one character state. However, direction of displacement has no biological significance.

A second phylogeny (Fig. 67, p. 180)



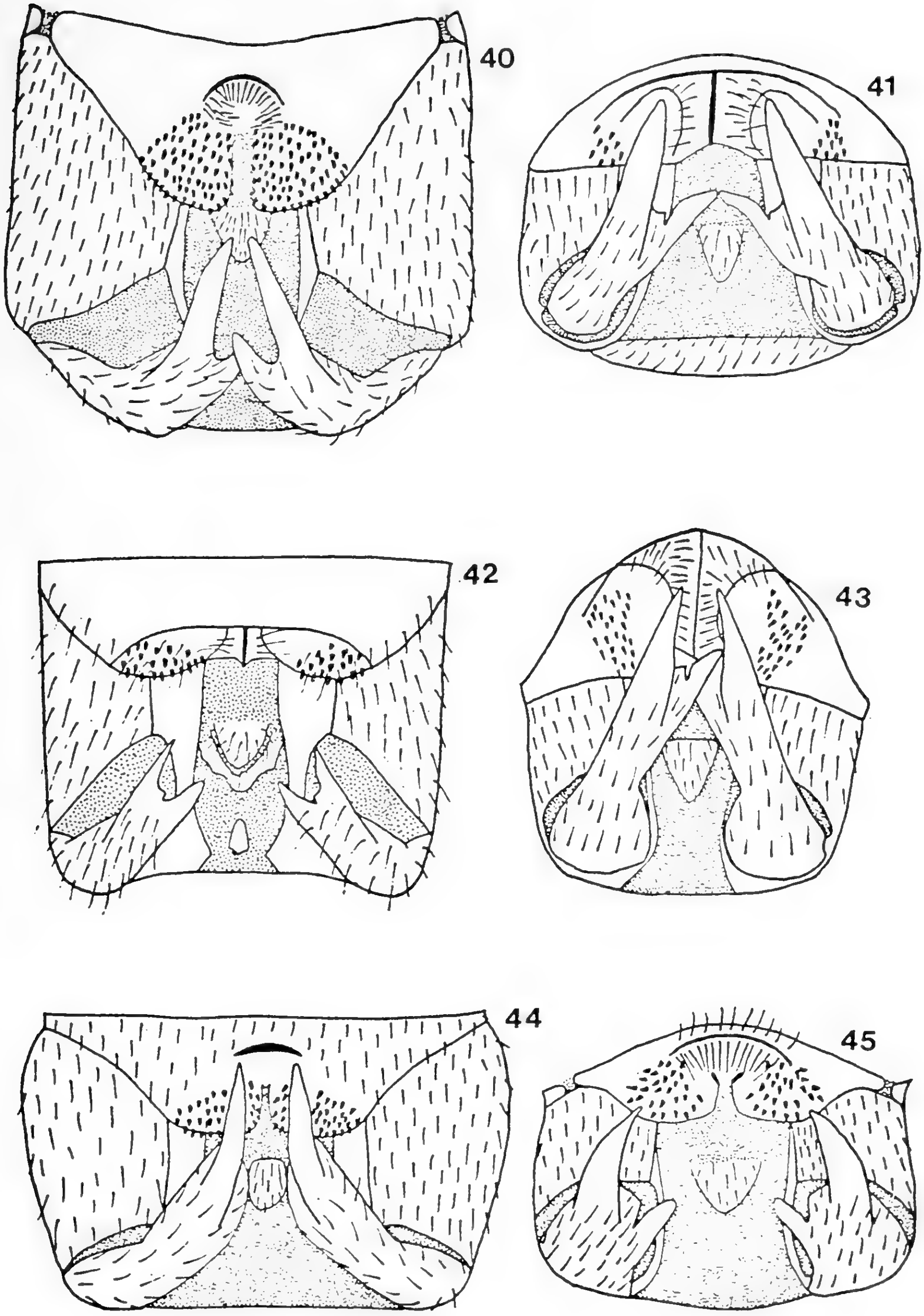
Figures 31-33, male, tip of abdomen, lateral view. Fig. 31, *Boreus coloradensis* Byers. Fig. 32, *Boreus reductus* Carpenter. Fig. 33, *Boreus vlasovi* Martynova. All 78×.



FIGURES 34-39, tip of abdomen, dorso-caudal view. Fig. 34, *Hesperoboreus brevicaudus* (Byers). Fig. 35, *Hesperoboreus notoperates* (Cooper). Fig. 36, *Boreus borealis* Banks. Fig. 37, *Boreus brumalis* Fitch. Fig. 38, *Boreus californicus* Packard. Fig. 39, *Boreus coloradensis* Byers. All 66×.

was constructed by weighting each character state in the unweighted phylogeny according to the number of species involved (Ashlock, unpublished method). This would give more value to those character states which help to unify groups of species. The final horizontal distance between species gives a measure of how closely related the species are. Character states on the weighted phylogenies are listed by branching sequence in Table 2, p. 169.

The third phylogeny (Figure 68, p. 181) illustrates a weighted phylogeny which



Figures 40-45, tip of male abdomen, dorso-caudal view. Fig. 40, *Boreus elegans* Carpenter. Fig. 41, *Boreus hyemalis* (L.). Fig. 42, *Boreus intermedius* Carp. Fig. 43, *Boreus lokayi* Klp. Fig. 44, *Boreus nivoriundus* Fitch. Fig. 45, *Boreus nix* Carpenter. All 66×.

uses not only the number of species involved but also the number of times a character state appears (Brothers, 1975). By assignment of only half value to a character state which has evolved twice, these character states lose much of their value. This is done because we are trying to determine the most probable line of evolution, and character states which appear to have evolved twice are more doubtfully correct and should be given less weight. By reducing their value such lines of evolution which use these character states appear to have diverged less. Figure 68 agrees with my own intuition as to the evolution of this group.

In all three phylogenies, the two genera, *Boreus* and *Hesperoboreus,* appear quite distinct, as do most of the groups and subgroups mentioned earlier. However, it will be noted that in the two weighted phylogenetic diagrams the *vlasovi* subgroup and *hyemalis* group do not appear to be very distinct, while the *nivoriundus* group is very distinct. This is due in part to the material available. All *nivoriundus* group species are represented, while *kratochvili* is lacking from the *hyemalis* group, and the only one *vlasovi* subgroup species is represented. Only one synapomorphous character (Hennig, 1965) separates the *nivoriundus* subgroup from the rest of *Boreus,* but because of the primitive position of this subgroup in the phylogeny and the large number of species involved, the two subgroups of the *nivoriundus* groups appear quite distinct from each other.

Boreids evolved in two directions. One group, given the new generic name *Hesperoboreus,* and containing *H. brevicaudus* and *notoperates,* lives in areas of rather warm climate along the west coast of the United States. These species possess two ocelli; large bristles are present along the anterior and posterior margins of the pronotum; the eighth tergum and sternum are not fused in males; females possess a very short ovipositor with cerci incompletely fused; and no ninth tergal hood development or outer forewing spines are found in males.

All species of *Boreus* have outer forewing spines in the males, and a long ovipositor and fused cerci among females. These species can in turn be divided into one Nearctic group, two Holarctic groups, and one Palearctic group.

The first group (*nivoriundus* group), containing *B. beybienkoi, brumalis, elegans, nivoriundus, nix,* and *pilosus,* consists of both North American and Asiatic species. These species possess pronotal bristles, and in males have unfused eighth and ninth abdominal terga and sterna, and small tergal hoods. This group can be further divided into the *nivoriundus* subgroup, having males with entire ninth sterna and gradually tapering forewings, and the *brumalis* subgroup, having males with deeply notched ninth sterna and wings abruptly narrowed at mid-length.

The second group (*reductus* group), containing *B. reductus, vlasovi,* and probably most Asiatic boreids, is found both in western North America and Asia. These species agree in possessing no pronotal bristles, unfused male eighth tergum and sternum, and a small tergal hood in males. This group also can be subdivided into two subgroups. The *reductus* subgroup has unfused ninth tergum and sternum in males, while the *vlasovi* subgroup usually has fused male ninth tergum and sternum. Most Asiatic species belong in this second subgroup.

B. orientalis may be an exception among Asiatic species. Martynova (1954) has illustrated part of the eighth abdominal segment of this species, showing it as fused. This would be the only known Asiatic species with fusion in both eighth and ninth segments. Until more is known about this species, I feel that it should be considered as a part of the *vlasovi* subgroup of the *reductus* group. Other Asiatic species which Martynova illustrated with fused ninth segment are *chadzhigireji, vlasovi,* and *semenovi.* Cooper (1973) stated that the ninth tergum and sternum of *vlasovi* were unfused, but this varies with the individual. Since *navasi* is very similar to *chadzhigireji,* it probably belongs in this subgroup. Although little is known about *sjoestedti,* perhaps it too belong to the *vlasovi* subgroup. To know with certainty, it will be necessary to collect males of these species.

The third group (*californicus* group) includes *B. borealis, californicus, coloradensis, and intermedius.* These species all possess no pronotal bristles, show fusion of eighth terga and sterna among males but no fusion of male ninth terga and sterna,

TABLE 2

Phylogenetic Character State Sequence.

Between points 1 and 2
1. Loss of median ocellus
2. Gain of rugulose occiput
4. Loss of antennal segments
5. Movement of antennal bases to below eyes
6. Widening of hypostomal bridge
12. Loss of outer forewing spines-male
31. Development of posterior process on tenth abdominal segment-female
34. Development of eighth sternal notch-female

Between point 2 and H. brevicaudus
14. Gain of bristles at caudal margin of wing pad-female

Between point 2 and H. notoperates
29. Development of notched ninth sternum-male
35. Expansion of eighth sternal notch-female

Between points 1 and 3
19. Development of small tergal hood-male
30. Lengthening of tenth abdominal segment-female
32. Complete fusion of cerci-female

Between points 3 and 4
7. Gain of rostral bristles
11. Broadening of forewings at mid-length-male

Between point 4 and B. elegans
8. Gain of 25 rostral bristles

Between point 4 and B. nivoriundus
none

Between points 3 and 5
20. Tergal hood expanded to middle of denticular areas-male

Between points 5 and 6
29. Development of notched ninth sternum-male

Between point 6 and B. brumalis
none

Between points 6 and 7
9. Gain of long pilosity

Between point 7 and B. nix
none

Between point 7 and B. pilosus
Loss of some denticles

Between points 5 and 8
10. Loss of thoracic bristles

Between points 8 and 9
1. Loss of median ocellus
4. Loss of antennal segments
22. Development of projections along lip of hood

Between point 9 and B. reductus
13. Forewings reduced until they no longer cover hindwings-female
23. Development of medial projections along lip of hood-male

Between point 9 and B. vlasovi
28. Fusion of ninth tergum and sternum-male
33. Gain of abruptly narrowed cerci at mid-length-female

Between points 8 and 10
18. Fusion of eighth tergum and sternum-male
21. Tergal hood expanded to lateral margin of denticular areas-male
24. Gain of median septum to tergal hood-male

Between points 10 and 11
none

Between point 11 and B. borealis
27. Development of numerous setae covering interior of tergal hood-male

Between point 11 and B. californicus
25. Development of narrow median septum

Between 11 and B. coloradensis
none

Between point 11 and B. intermedius
26. Gain of short median septum with ventral fork-male

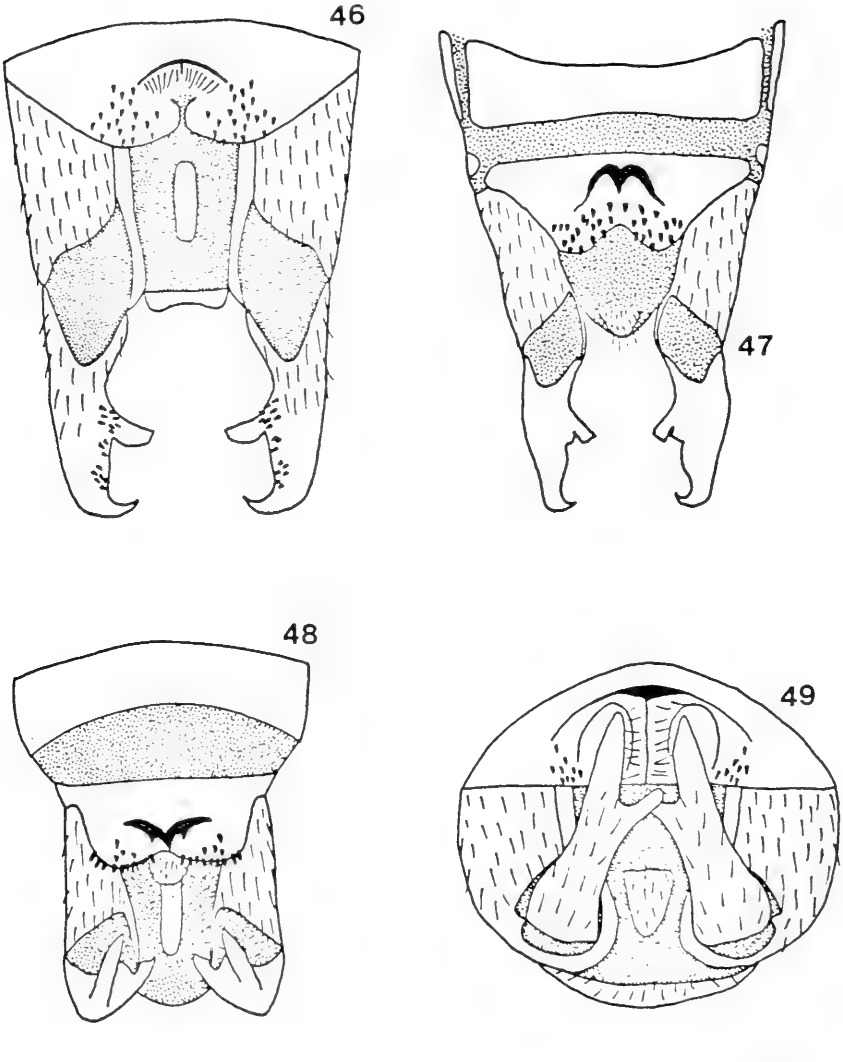
Between points 10 and 12
15. Gain of transverse ridge on second abdominal tergum-male
16. Gain of transverse ridge on third abdominal tergum-male

Between point 12 and B. hyemalis
3. Loss of occipital reticulations

Between points 12 and 13
none

Between point 13 and B. westwoodi
none

Between point 13 and B. loḳayi
17. Transverse ridge of third segment reduced to a tubercle-male
26. Gain of short median septum with ventral fork-male



FIGURES 46-49, tip of abdomen, dorso-caudal view. Fig. 46, *Boreus pilosus* Carp. Fig. 47, *Boreus reductus* Carpenter. Fig. 48, *Boreus vlasovi* Martynova. Fig. 49, *Boreus westwoodi* Hagen. All 66×.

and have a large male tergal hood with median septum. All species of this group are Nearctic.

In the Palearctic region a fourth group of species occurs, the *hyemalis* group, consisting of *B. hyemalis, kratochvili, lokayi,* and *westwoodi.* These are similar to the *californicus* group but have transverse ridges on the second and third abdominal terga.

The picture that emerges from the morphology and distribution of these species is the following: ancestral boreids developed in the Nearctic region from a panorpodid-like ancestor, with flightless females, prothoracic bristles, and unfused eighth and ninth abdominal segments in the males. As is the *Hesperoboreus* species, females had incompletely fused cerci, and no elaboration had occurred on the male ninth abdominal tergum. This ancestral stock then split. *H. notoperates* and *brevicaudus* represent the remnant of an ancestral species which further split into two populations as glaciers retreated after the ice ages. One population (*notoperates*) remained in southern California and survived the warming trend by becoming adapted to warmer temperatures and moving to the higher elevations of Mount San Jacinto (and perhaps associated ranges). The other population *(brevicaudus)* remained at a lower elevation and moved or remained northward in western Oregon and Washington.

In the other ancestral stock, i.e., exclusive of *Hesperoboreus,* the female cerci fused entirely and the tenth abdominal segment became more elongate. This stage of development is exemplified by the *nivoriundus* group. This group is trancontinental in distribution in North America and is also found in the Ala-Too Range, north of the Himalayas. Although no specimens are now known from the Rocky Mountains of Colorado to southern Illinois, it seems likely that at one time environmental conditions permitted an east-west movement of *Boreus* across northern North America. Perhaps in the cooler regions of northern Canada this distribution is still contiguous, although there are no specimens to verify this. The presence of this group in Asia indicates a possible early movement into the Palearctic region.

The *nivoriundus* group is here subdivided into the *nivoriundus* subgroup (*elegans* and *nivoriundus*) and *brumalis* subgroup (*brumalis, nix,* and *pilosus*). *B. beybienkoi* is probably in this group, since the original description mentions prothoracic bristles. However, I have not seen specimens of this species and its position within the *nivoriundus* group is still not known.

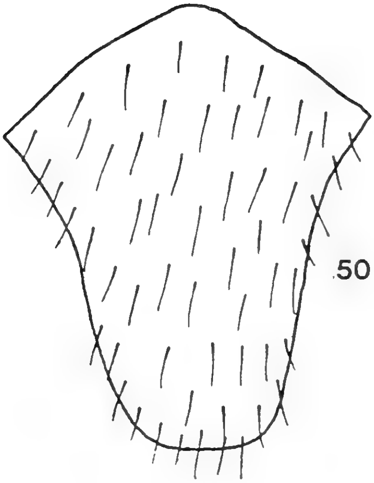
The next step in evolution of the Boreidae was loss of thoracic bristles, as seen in the *reductus* group. The only member of this group in the Nearctic region is *reductus,* distributed in the arid mountain regions of western North America.

There are some character states in this group that cause problems for phylogeneticists. Species of the *reductus* group have no median ocellus, in which character they resemble *Hesperoboreus.* The *vlasovi* subgroup has the shortest ovipositor found in any group or subgroup of *Boreus;* and the number of antennal segments is reduced to 19 or 20, as in some specimens of *Hesperoboreus.* However, these character states probably were independently achieved through reduction, because males of the *reductus* group have a well-developed ninth tergal hood, a relatively elaborate structure which seems unlikely to have evolved twice. There are other indications, as well, of the relatively advanced state of evolution of the *reductus* group, such as the absence of thoracic bristles in both sexes and reduced number of hindwing spines in males.

Fusion of the eighth abdominal tergum and sternum in males of a population of an ancient *reductus* group species later occurred. This condition created the ancestral species of the *californicus* group, which later disepersed in or into the Nearctic region. *B. borealis* became isolated on St. Paul Island, probably at a time when land connections existed, or possibly when permanent ice covered the Bering Sea. The closely related species *californicus* and *coloradensis* became widely distributed in the relatively arid mountain regions of western North America from California to central Colorado and from central Arizona to northwestern British Columbia. *B. intermedius* is a more northern counterpart of these western species in Alaska.

In Europe, the *hyemalis* group arose from species in which there evolved an enlargement of the male second and third abdominal terga into flat ridges. These ancestors dispersed into the Carpathian Mountains and western Europe.

Martynova (1954) stated that *B. chadzhigireji* had tergal ridges but that they were almost absent. The figures accompanying her description showed no fusion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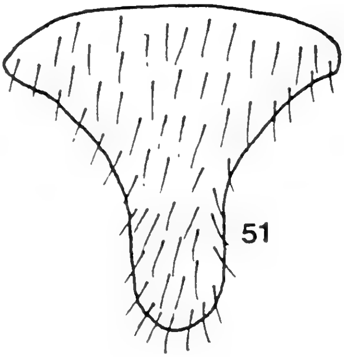
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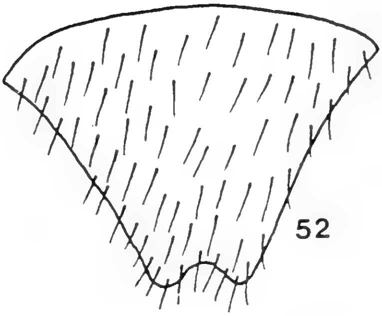
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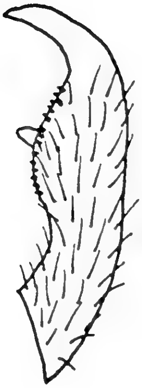
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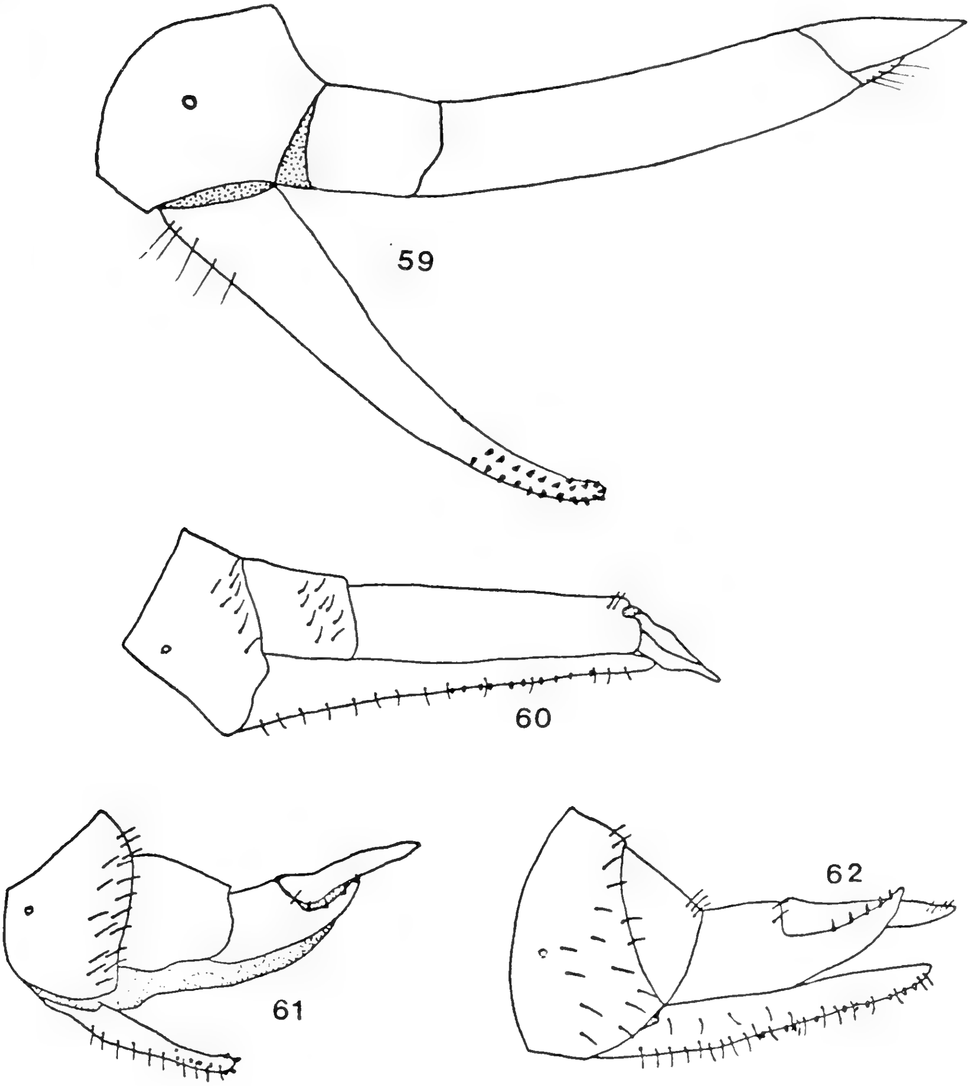
58

FIGURES 50-52, male, *ninth sternum,* ventral view. Fig. 50, *Boreus coloradensis* Byers. Fig. 51, *Boreus reductus* Carp. Fig. 52, *Boreus brumalis* Fitch. Figs. 53-58, male, dististyle. Figs. 53-54, *Boreus coloradensis* Byers. Figs. 55,56, *Boreus elegans* Carp. Figs. 57,58, *Hesperoboreus brevicaudus* (Byers). Figs. 53,55, and 57, caudal view. Figs. 54,56, and 58, lateral view. All 88×.



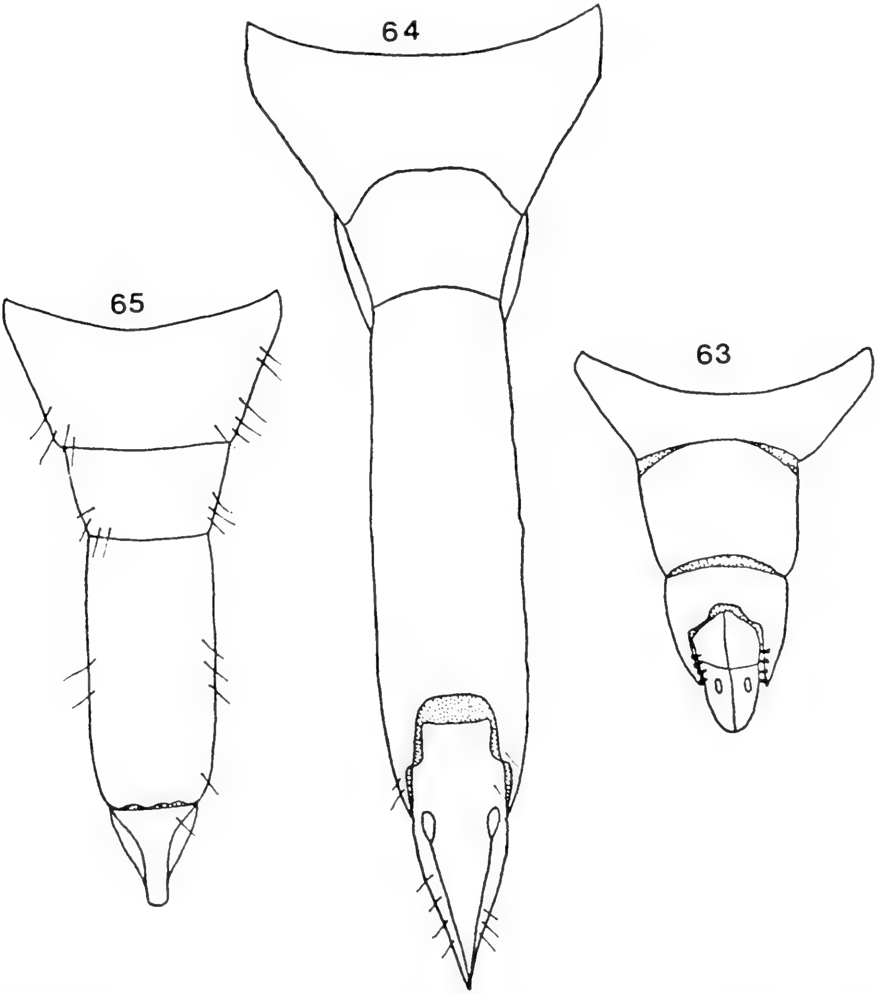
Figures 59-62, female ovipositors, lateral view. Fig. 59, *Boreus coloradensis* Byers, 50×. Fig. 60, *Boreus vlasovi* Martynova, 57×. Fig. 61, *Hesperoboreus brevicaudus* (Byers), 57×. Fig. 62, *Hesperoboreus notoperates* (Cooper), 57×.

of the eighth tergum and sternum, but fusion in the ninth segment. These two character states indicate that this species is most likely a member of the *vlasovi* subgroup of the *reductus* group, and has no tergal ridges (cf. Cooper, 1972:276-277).

Both the *nivoriundus* and *reductus* groups are Holarctic, and little evidence is available to indicate the direction of their movement between continents. However, there may well have been multiple movements between the Palearctic and Nearctic regions.

ECOLOGY

A. Plant Associations—Boreidae have been taken from many mosses. *Boreus brumalis* larvae from eastern North America has been collected from *Dicranella heteromalla* and *Atrichum angustatum* (Webb et al., 1975), and Byers (1954) mentioned that J. W. Leonard had found adults of this species in *Sphagnum*. *Hesperoboreus notoperates* has been recorded from *Grimmia apocarpa, G. laevigata, G. montana, Rhacomitrium sudeticum, Orthotrichum rupestre, Tortula princeps, T. ruralis, Homalothecium aeneum, H. nevadense, H. pinnatifidum,* and *Campothecium amesiae* in southern California (Cooper, 1974). *Boreus reductus* larvae and adults have been collected on club mosses (*Selaginella* sp.) in southeastern Washington. It appears that the species of moss is of less importance than the moss texture. Mosses which grow in low, compact cushions and whose rhizoids are tightly matted more frequently contain adult and larval Boreidae than do mosses that grow upright or are more loosely matted. It has been my experience that upright or loosely matted mosses more frequently contain predaceous carabid beetle larvae. Perhaps, larval boreids survive predation better in the more tightly compacted mosses.



Figures 63-65, female ovipositors, dorsal view. Fig. 63, *Hesperoboreus brevicaudus* (Byers). Fig. 64, *Boreus coloradensis* Byers. Fig. 65, *Boreus vlasovi* Martynova. All 66×.

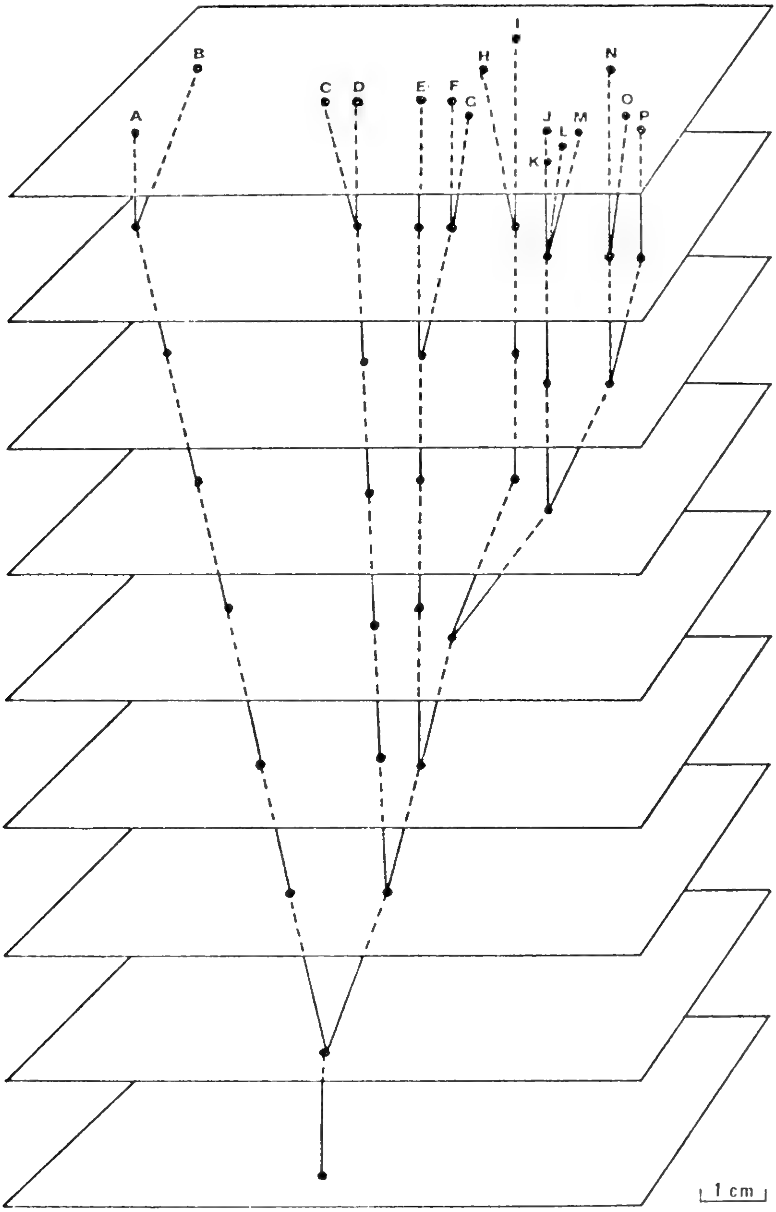


Figure 66. Three dimensional unweighted phylogeny. Movement between plates in any direction of 1 cm indicates one character state change. (Direction of change in position between plates has no biological significance.) A is *H. notoperates,* B is *H. brevicaudus,* C is *B. elegans,* D is *B. nivoriundus,* E is *B. brumalis,* F is *B. nix,* G is *B. pilosus,* H is *B. reductus,* I is *B. vlasovi,* J is *B. coloradensis,* K is *B. borealis,* L is *B. californicus,* M is *B. intermedius,* N is *B. lokayi,* O is *B. westwoodi,* and P is *B. hyemalis.*

B. Feeding—Withycombe (1922) mentioned keeping one female of *Boreus hyemalis* alive for 37 days on juices of crushed flies, although in a later paper (Withycombe, 1926) he states that the diet of *Boreus* is moss. Other authors (Brauer, 1855, and Steiner, 1937) have speculated that *Boreus* feeds on collembolans, although no evidence has been presented to support this. The European *B. hyemalis*

TABLE 3

SCALED SIMILARITY MATRIX.

	H. brevicaudus	*H. notoperates*	*B. borealis*	*B. brumalis*	*B. californicus*	*B. coloradensis*	*B. elegans*	*B. hyemalis*	*B. intermedius*	*B. lokayi*	*B. nivoriundus*	*B. nix*	*B. pilosus*	*B. reductus*	*B. vlasovi*	*B. westwoodi*
H. brevicaudus	....	3	18	16	18	17	18	18	18	22	17	17	16	17	16	20
H. notoperates	.08	....	19	15	19	18	19	19	19	23	18	16	15	18	18	21
B. borealis	.49	.51	....	8	2	1	10	4	2	6	9	9	8	11	11	4
B. brumalis	.43	.41	.22	....	8	7	6	10	8	10	5	1	2	7	7	10
B. californicus	.49	.51	.05	.22	....	1	10	4	2	6	9	9	8	11	11	4
B. coloradensis	.46	.49	.03	.19	.03	....	9	3	1	5	8	8	7	10	10	3
B. elegans	.49	.51	.27	.16	.27	.24	....	12	10	12	1	7	8	11	11	12
B. hyemalis	.49	.51	.11	.27	.11	.08	.32	....	4	4	11	11	10	13	13	2
B. intermedius	.49	.51	.05	.22	.05	.03	.27	.11	....	4	9	9	8	11	11	4
B. lokayi	.60	.63	.16	.27	.16	.14	.32	.11	.11	....	11	11	12	13	13	2
B. nivoriundus	.46	.49	.24	.14	.24	.22	.03	.30	.24	.30	....	6	7	10	10	11
B. nix	.46	.43	.24	.03	.24	.22	.19	.30	.24	.30	.16	....	1	8	8	11
B. pilosus	.43	.41	.22	.05	.22	.19	.22	.27	.22	.32	.19	.03	....	9	9	10
B. reductus	.46	.49	.30	.19	.30	.27	.30	.35	.30	.35	.27	.22	.24	....	4	13
B. vlasovi	.43	.49	.30	.19	.30	.27	.30	.35	.30	.35	.27	.22	.24	.11	....	13
B. westwoodi	.54	.57	.11	.27	.11	.08	.32	.05	.11	.05	.30	.30	.27	.35	.35	....

Number of Differences

Ratio of Differences/Total of Characters Used

has been found to feed as larvae on *Dicranella heteromalla, Byrum atropurpureum, Mnium hornum* (Withycombe, 1926) and *Pylaisia* sp. (Boldyrev, 1914). Strübing kept larvae of *B. hyemalis* alive to pupation on *Polytrichum piliferum.* I have observed larvae of *B. brumalis* feeding on the rhizoids of *Dicranella heteromalla* in the field. In the laboratory, adults I observed placed the long rostrum among the moss leaves, as if to feed, although the tip of the rostrum could not be seen. Stomach contents of adults reveal only small globules of a liquid substance, possibly because of masticating activity of the proventriculus (see Richards, 1965). That adult boreids do indeed feed on mosses and occasionally other substances has been recorded by numerous other observers.

C. LIFE CYCLE—Both Brauer (1855) and Steiner (1937) found large larvae of *Boreus hyemalis* in terraria within a few months of initial collection of adults. However, in both cases no mention was made of initially checking the moss for larvae. Withycombe (1922) claimed to have reared the same species to adulthood in one year, although he gave few details of his technique. Doubts were raised when Syms (1933) found larvae of *hyemalis* of two distinct sizes. He postulated a two-year life cycle. Strübing (1950) was able to rear this species and confirmed a two-year life cycle. Cooper (in litt.) reports early and late instar larvae occurring together for *B. brumalis, B. nivoriundus, B. elegans, H. brevicaudus* and *H. notoperates.*

This two-year life span seems reasonable in light of other boreal adaptations. Other cold-adapted insects have increased the length of the life cycle. In the high arctic environment most Lepidoptera spend two or more years in the larval stage (Downs, 1964), and even northerly or

TABLE 4

List of Presence (+) vs. Absence (—) of a Character State.

Character no.	*H. brevicaudus*	*H. notoperates*	*B. borealis*	*B. brumalis*	*B. californicus*	*B. coloradensis*	*B. elegans*	*B. hyemalis*	*B. intermedius*	*B. lokayi*	*B. nivoriundus*	*B. nix*	*B. pilosus*	*B. reductus*	*B. vlasovi*	*B. westwoodi*
1	—	—	+	+	+	+	+	+	+	+	+	+	+	—	—	+
2	+	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—
3	—	—	+	+	+	+	+	—	+	+	+	+	+	+	+	+
4	+	+	—	—	—	—	—	—	—	—	—	—	—	+	+	—
5	+	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—
6	+	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—
7	—	—	—	—	—	—	+	—	—	—	+	—	—	—	—	—
8	—	—	—	—	—	—	+	—	—	—	—	—	—	—	—	—
9	—	—	—	—	—	—	—	—	—	—	—	+	+	—	—	—
10	+	+	—	+	—	—	+	—	—	—	+	+	+	—	—	—
11	+	+	+	+	+	+	—	+	+	+	—	+	+	+	+	+
12	+	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—
13	+	+	+	+	+	+	+	+	+	+	+	+	+	—	+	+
14	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
15	—	—	—	—	—	—	—	+	—	+	—	—	—	—	—	+
16	—	—	—	—	—	—	—	+	—	+	—	—	—	—	—	+
17	—	—	—	—	—	—	—	—	—	+	—	—	—	—	—	+
18	—	—	+	—	+	+	—	+	+	+	—	—	—	—	—	+
19	—	—	+	+	+	+	+	+	+	+	+	+	+	+	+	+
20	—	—	—	—	—	—	+	—	—	—	+	—	—	—	—	—
21	—	—	—	+	—	—	—	—	—	—	—	+	+	+	+	—
22	—	—	+	—	+	+	—	+	+	+	—	—	—	—	—	+
23	—	—	—	—	—	—	—	—	—	—	—	—	—	+	+	—
24	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—
25	—	—	+	—	+	+	—	+	+	+	—	—	—	—	—	+
26	—	—	—	—	+	—	—	—	—	—	—	—	—	—	—	—
27	—	—	—	—	—	—	—	—	+	+	—	—	—	—	—	—
28	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—
29	—	—	—	+	—	—	+	—	—	+	+	+	—	+	+	—
30	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—
31	—	+	—	+	—	—	—	—	—	—	—	+	+	—	—	—
32	+	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—
33	+	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—
34	—	—	+	+	+	+	+	+	+	+	+	+	+	+	+	+
35	+	+	+	+	+	+	+	+	+	+	+	+	+	+	—	+
36	+	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—
37	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—

montane races of one species may have a prolonged life cycle (Downes, 1965). Thus, finding this adaptation within another group of holometabolous insects is not surprising. However, Kaufmann (1971) has shown that an arctic carabid beetle, *Pterostichus brevicornis,* can have a variable length of life cycle. A two-year life cycle needs to be confirmed for other populations and species of Boreidae.

The pupal and adult stages of the life cycle usually occur during the cool or cold months of the year, yet pupae of a few species have been found as early as mid-August. Pupae of *B. brumalis* have been collected only from September 30 until October 18. Pupae collected on October 13 were maintained in the laboratory until the adults emerged from November 24 to December 4. Adults of this species have been collected from November 19 until April 24. Two adult specimens in the

TABLE 5

LIST OF CHARACTER STATES USED IN TABLE 4.

1. Presence of median ocellus.
2. Occiput very rugulose.
3. Occiput with fine reticulations.
4. 19 or 20 antennal segments.
5. Antennal base below eyes.
6. Wide hypostomal bridge.
7. Spines on caudal margin of rostrum.
8. More than 24 rostral spines.
9. Body covered with long pilosity.
10. Thoracic bristles present.
11. Forewings abruptly narrowed at mid-length-male.
12. Complete loss of outer forewing spines-male.
13. Forewings covering hindwings-female.
14. Bristles on caudal margin of wing pad-female.
15. Transverse ridge on second abdominal tergum-male.
16. Transverse ridge on third abdominal tergum-male.
17. Third tergal ridge reduced to a tubercle-male.
18. Eighth abdominal tergum and sternum fused-male.
19. Tergal hood on ninth abdominal segment-male.
20. Lateral margin of hood reaching only medial margin of denticular areas-male.
21. Lateral margin of hood reaching only middle of denticular areas-male.
22. Lateral margin of hood reaching lateral margins of denticular areas-male.
23. Projections along lip of tergal hood-male.
24. Medial projections along lip of tergal hood-male.
25. Tergal hood with median septum-male.
26. Median septum narrow-male.
27. Median septum short and forked ventrally-male.
28. Interior of tergal hood obscured by numerous setae-male.
29. More than 25 denticles on either side of ninth tergum-male.
30. Ninth tergum and sternum fused-male.
31. Presence of deeply notched ninth sternum-male.
32. Tenth segment as short dorsally as ninth-female.
33. Posterior process on tenth abdominal segment-female.
34. Complete fusion of cerci-female.
35. Cerci tapering evenly-female.
36. Eighth sternal notch present-female.
37. Eighth sternal notch large-female.

Ohio State University Collection are labelled August 15, 1935, but surely these are atypical. Adults of other species have also been collected generally from November until April; however, adults of *B. coloradensis* have been collected as late as May 27 in the mountains around Logan, Utah, and those of *B. borealis* have been collected in the Pribilof Islands only during May, July, and August.

Emergence appears to be delayed until moderate weather conditions exist for species living in montane and high latitudinal environments. The populations of *B. coloradensis* at 2,134 to 3,657 m. in Boulder County, Colorado, have only been collected in April, whereas this same species is collected from November until May at 1,676 m. around Logan, Utah. *Boreus nix* is found from November to February in Montana and British Columbia, but has only been collected in April in Alaska. *B. intermedius* also has only been collected in April in Alaska. Thus, emergence is to be expected later in northern and montane regions.

In the laboratory, I maintained adults of *B. coloradensis* and *nivoriundus* for 48 and 51 days, respectively. This is possibly shorter than natural adult longevity, yet the rigors of the laboratory environment may have been offset by protection from predation or severe cold.

D. MATING AND OVIPOSITION—The mating behavior of Boreidae has been discussed by Cooper (1940, 1974) and various other authors. Briefly, the mating behavior is as follows: In *Boreus,* the male upon encountering a female, attempts to clasp her with his dististyles; if he is successful, the female becomes quiescent and the male uses his long, thin hook-like wings to pull the female upon his back. The female tucks her rostrum and antennae under her thorax and between her legs while the male's wings clasp her forelegs; the hypovalves of the female's eighth sternum are inserted into the male endoandrium, where they are held in place by the basal lobes of the male dististyles. The male carries the female upon his back for an extended period of time; Marechal (1939) used the figure of 55 hours, although the duration is usually much shorter than that. During this time the female moves very little. Later, the female places small, white oval eggs among the moss rhizoids and the bases of the leafy stems.

In *Hesperoboreus,* the male approaches and leaps at the female, grasping whatever part of her anatomy he can with his dististyles. The female actively tries to escape, dragging the male with her. When she rests, he tries to grasp her with his wing hooks. If successful, he clutches her between her head and mesonotum, holding her body parallel to his own. When the female becomes submissive, the male moves his dististyles to the ovipositor, and the wing grip is released. The valves of the female's eighth sternum are pried down and apart. The male holds the valves down by hooking the basal notch of the valves with the basal lobe of his dististyles. The valves are forced into the subepandrial pockets and held there. The female then rocks backwards 90°, and rests with rostrum and antennae folded between the forelegs. She remains perpendicular to the male in a "female perpendicular pose" that contrasts with the copulatory position of *Boreus* which Lamb (1922) has termed "female vertical pose," but in which the final copulatory position of the female is above and parallel to the male.

E. Moisture—The water required for boreid survival can probably be obtained from the food. However, the relative humidity requirements of the microhabitat may be a major limiting factor. The humidity must be high enough to support a good growth of moss, and the luxuriance of moss banks where most specimens of *Boreus* have been collected indicates high humidity most of the year. On the other hand, boreid larvae have sometimes been found in mosses that appeared desiccated and friable (Cooper, 1974). There has even been one collection of adults of *B. coloradensis* in sagebrush desert at Promontory, Utah. *H. notoperates* survives in *Grimmia,* a moss of dry, rocky habitats. Therefore, no one statement can cover the moisture requirements of all species of Boreidae.

F. Elevation—Elevation greatly influences such climatic conditions as moisture and temperature; however, its effects on the distribution of Boridae have not been determined. *B. brumalis* is found in eastern North America from sea level to 4,000 feet (1,220 m). *H. brevicaudus* has been collected from the bottom of the Columbia River gorge at 100 feet (31 m.) and on Spencer Butte near Eugene, Oregon, from 1,200 to 1,900 feet (366 to 580 m.). On the other hand, *B. coloradensis* is normally found in mountainous regions from 4,700 feet (1,457 m.) around Logan, Utah, up to 12,000 feet (3,660 m.) near Boulder, Colorado.

G. Temperature—The effect of temperature, like that of moisture, can only be guessed at because of the insects' behavior in selection of microhabitat. However, various species' distributions do appear to be governed to some extent by differences in average temperature. The distributions of *H. brevicaudus, B. elegans,* and possibly *H. notoperates* appear to be influenced by the mild, modifying effects of the Pacific Ocean. None of these species has been collected more than 90 miles from the Coast. The mildness of temperatures in this region can be seen in monthly means at Mount San Jacinto, California, Portland, Oregon, Seattle, Washington,

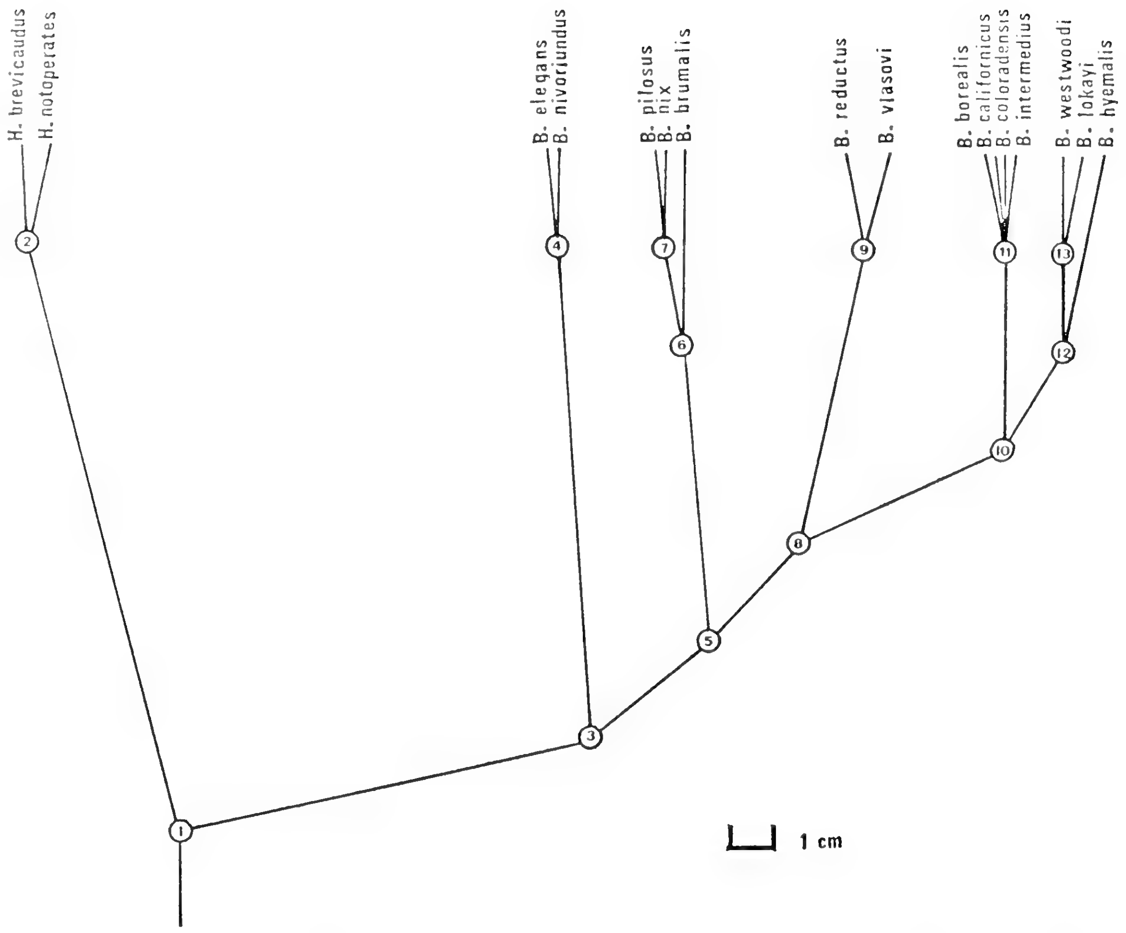


FIGURE 67. Phylogeny weighted by number of species involved. (Number of character state changes × number of species involved equals horizontal distance.)

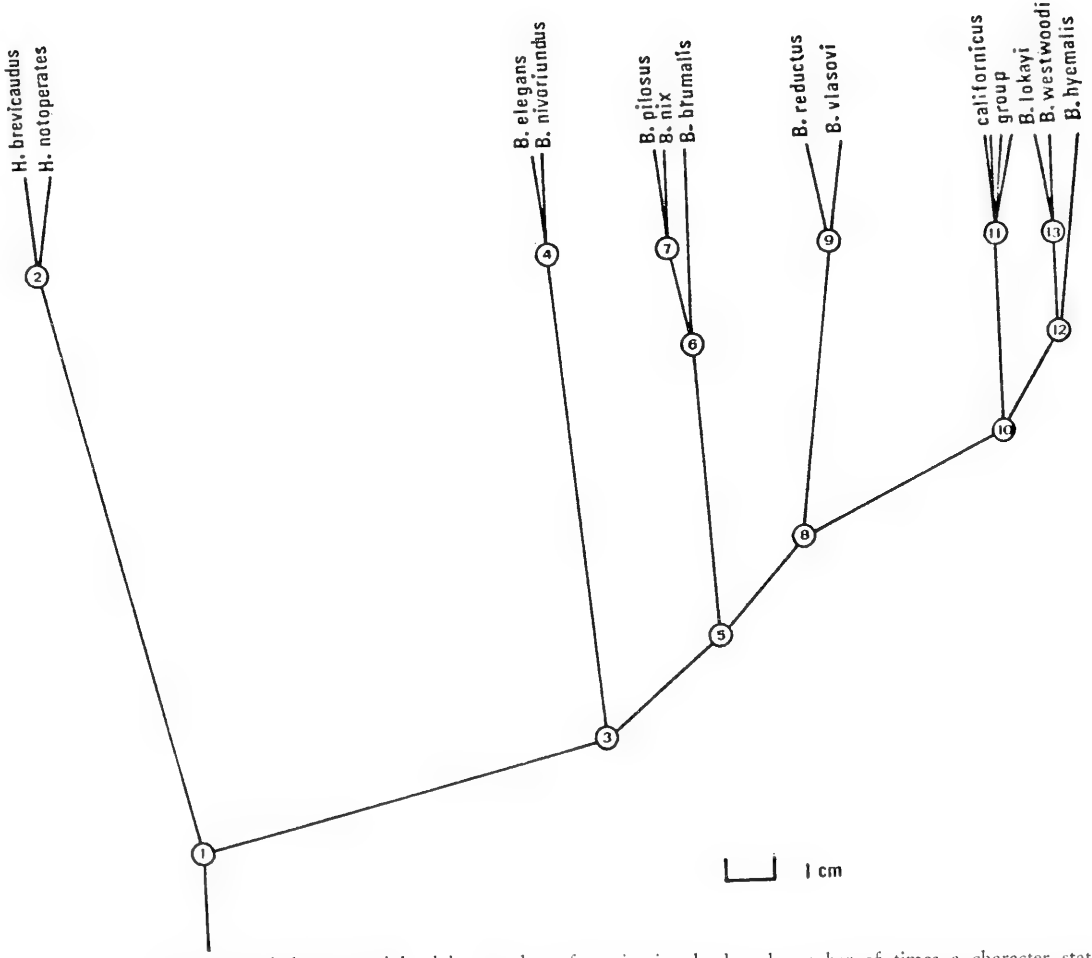


Figure 68. Phylogeny weighted by number of species involved and number of times a character state appears. [(Number of character state changes—½ for each change occurring twice) × number of species involved equals horizontal distance.]

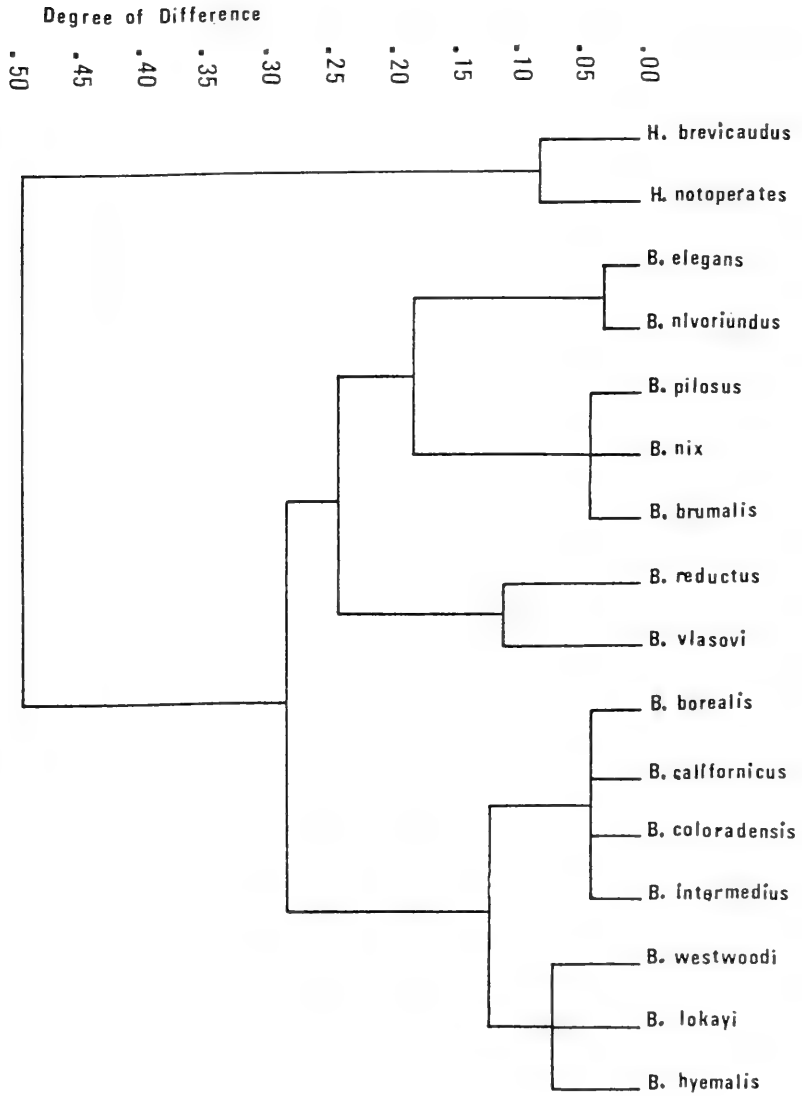


FIGURE 69. Phenogram.

and Vancouver, British Columbia—all localities close to places where these three species of Boreidae have been found. The low mean monthly temperatures for these four localities range from 0° to 8°, and the high mean monthly temperatures range from 18° to 28° C. The high temperature recorded for these cities in 1971 was 46° and the low temperature was —13° C. This contrasts sharply with temperature tolerances of species from the western plateau region and the East Coast. *B. brumalis* has been collected from Duluth, Minnesota, to Washington, D. C., with low mean monthly temperatures varying from —13° to 3°, and high mean monthly temperatures ranging from 19° to 26° C. High and low temperatures for these two localities in 1971 were 34° and —32° C. Helena, Montana, is within the range of three western species, and it, too, has severe changes in temperature with high and low monthly mean temperatures of 20° and —7° C. The change in species composition with climatic zone seems to be particularly abrupt in Oregon and Washington, where *B. californicus* is found from the Cascade Range eastward, and *H. brevicaudus* is found from the western foothills of the Cascades westward.

Microhabitats offer climatic diversity in these extreme environments. Bliss (1969) noted that "In these severe environments, where day-time temperatures at 0.7 m seldom exceed 13° to 18° C. and more frequently are 5° to 8° C., it is of considerable interest to note that soil surface temperatures in excess of 38° C. have been recorded by the writer in arctic Alaska as well as in the alpine tundras of Wyoming and Mt. Washington. Night-time soil-surface temperatures for the same dates were 4° to 7° C." Wilson (1957) found that air temperatures near a small clump of arctic *Saxifraga oppositifolia* were 0.5° C. at 2 m, 3.5° C. at 1 cm above the clump, and 6° C. inside two flower buds. Wulff (cited in Porsild, 1951) recorded temperature readings of 3.5° C. among dead leaves of a saxifrage and 10° C. in a clump of mosses in northern Greenland when air temperature was —12° C. Thus, through behavioral preferences boreids can select microenvironmental temperatures far different from local air temperatures.

One collection of *B. brumalis* larvae was made on a day when air temperatures were about 24°, but the soil temperature where they were collected was only 10° C.

The activity of adult boreids is clearly influenced by temperature. At 0° C., adults of *B. coloradensis* are active on the snow surface; however, this temperature appears to be close to the minimum for most boreid activity. Below this temperature, they can be seen lying on the snow but will not move, even when picked up. Overnight temperatures of —37° C. in British Columbia killed specimens of *B. elegans* and *H. brevicaudus* I was transporting in plastic cartons for study. The maximum temperatures of adult activity are not known, but adults of *B. brumalis* survived a temperature of 20° for a few hours time. Herter (1943) recorded maximal survival temperatures of 32-32° C. for *B. hyemalis* and 34-37° C. for *B. westwoodi*.

H. TIME OF ACTIVITY AND LIGHT REACTION—During a collecting trip in northern Utah, I noticed that adults of *B. coloradensis* were far more abundant on the snow surface at dusk than during the day. One active individual was even found by flashlight more than an hour after dark. This observation led to speculation that Boreidae are mainly crepuscular, or possibly nocturnal. Fraser (1943) made the same observation for *B. hyemalis*. While observing *H. brevicaudus* in Washington, I noted that the insects on snow did not move, even though the air temperature was 5° C. and the area was in bright sunlight. However, about three hours later (2:00 P.M.), at another collecting site 2° warmer, individuals of *H. brevicaudus* were active. In the laboratory, adults of *B. brumalis* occasionally move at night when temperatures are 7° C.; but most often remain immobile, clinging to moss stems. The two isolated observations of numerous boreids at dusk may have been due to chance, and more observations should be made.

Marechal (1939) mentioned that *B. hyemalis* was attracted to electric lights, and Lestage (1940) speculated that this reaction explained why *Boreus* was more frequently collected on bright, sunny days. Lestage's suggestion is contrary to my own observations, although I recognize it applies to a species I have not observed alive. All North American species I have collected are as abundant on cloudy days as on sunlit days. Temperature appears to be a more important factor than light in their activity.

TAXONOMY

Key to the Genera of Boreidae

1. Males with no outer forewing spines; females with tenth abdominal tergum as short as ninth, bearing caudal, spiniferous extensions; female eighth abdominal sternum notched basally; cerci not fused apically .... *Hesperoboreus* n. gen.
   Males with outer forewing spines; females with long tenth abdominal segment without caudal extensions; female eighth abdominal sternum not notched basally; cerci completely fused .... *Boreus* Latreille

Hesperoboreus, new genus

Hesperoboreus (from the Greek *hesperus* = western and *boreus* = boreal) describes the western Nearctic distribution of this genus. Type species: *Boreus brevicaudus* Byers.

This genus can be separated from *Boreus* by the following characters: Hypostomal bridge wide; ratio of length of maxillo-labial complex to rostrum less than .60. Male forewings with no outer row of spines. Female eighth sternum with basolateral notch. Female tenth segment as short as ninth, bearing spiniferous caudal extensions; cerci not fused apically. Mating posture perpendicular.

Key to Species of *Hesperoboreus*

1. Apex of male ninth sternum smoothly rounded; forewing of female with apical bristles .... *brevicaudus*
   Apex of male ninth sternum deeply notched; forewing of female without apical bristles .... *notoperates*

SPECIES DESCRIPTIONS

Hesperoboreus brevicaudus (Byers), new combination.

Boreus brevicaudus Byers, 1961, J. Kansas Entomol. Soc. 34:73-78, Figs. 1-6.

Holotype and allotype in Oregon State University collection, Corvallis.

Present description based on 1 female pinned, 6 males and 18 females in alcohol.

Head: Occiput dark brown shading to light brown at base of rostrum to yellowish-brown at tip of rostrum. Occiput rugulose with many fine setae. Median ocellus absent. Antenna light brown, with 16 flagellomeres. Viewed in profile, anterior surface of rostrum with few setae; hind margin of hypostomal bridge with none. Ratio of length of maxillo-labial complex to rostrum = .44.

Thorax: Tergum and pleuron dark brown. Anterior margin of pronotum with 6 to 8 bristles, posterior margin with 4 bristles. Meso- and metanotum usually without bristles, occasionally 2 to 4 bristles on mesothorax.

Legs: Yellowish-brown with numerous dark brown setae and apical femoral spine. Two tibial spurs light brown.

Male wing: Light brown, abruptly narrowed at mid-length, with 13 inner spines at anal margin; covering hindwings.

Female forewing: Dark brown, oval, with large bristles at caudal margin; covering hindwing.

Male abdomen: Dark brown changing to yellowish-brown on last two segments. No tergal ridges on second and third segments. No fusion of eighth tergum and sternum or ninth tergum and sternum. Ninth tergum without hood; median partition between denticular areas; 13 denticles on either side of partition. Dististyle with about 6 spines arising from below basal lobe almost to apex of dististylar claw. Ninth sternum broadly rounded apically, not reaching bases of dististyles.

Female abdomen: First seven segments dark brown, last three visible segments light brown. Ratio of length of ovipositor to rostrum = .33. Caudal extensions of tenth segment each bearing 3 to 4 apical spines. Cerci dark brown with transparent tip. Eighth sternum with shallow basolateral notch.

Body length, male, 2.3 to 2.7 mm. in alcohol (holotype 2.6 mm., pinned); female, 3.1 to 3.6 mm. in alcohol (allotype 2.7 mm., pinned).

Intraspecific variation: Females from northern Washington vary from those from southern Oregon by occasionally lacking bristles on the forewings, having fewer spines on the eighth sternum and having only 3 spines on the extensions of the tenth segment.

Holotype male, 3 miles south of Eugene, Lane Co., OREGON, 427 m., 27 Nov. 1959. Allotype female, 1 male, 4 females, and 7 larvae, same locality, but dates of 23 Nov. 1959 (for allotype) and 26 Dec. 1971. This locality is a small park on Spencer's Butte overlooking the city of Eugene. Specimens have been collected on moss from 366 to 579 m. on this butte. Additional collections (Fig. 70) are: OREGON: Multnomah Co., 7 mi W of Bonneville, 16 Oct. 1955, K. M. Fender, 1 female (paratype); Yamhill Co., near McMinnville, 8 Nov. 1946, K. M. Fender, 1 female (paratype); Josephine Co., 7 mi SW of Williams, 23 Dec. 1971, N. D. Penny, 3 males, 5 females; Benton Co., Yew Creek, 27 Dec. 1971, N. D. Penny, 1 male, 1 female; Clatsop Co., 2 mi E of Elsie, 28 Dec. 1971, N. D. Penny, 2 females; WASHINGTON, Clallam Co., 4 mi S of Port Angeles, 31 Dec. 1971, N. D. Penny, 1 male, 6 females.

This species has only been collected at low elevations between 30 and 579 m.

H. brevicaudus is very similar to *H. notoperates,* but can be separated by the smaller number of flagellomeres, by the smoothly rounded male ninth sternum, and apical bristles on the female forewings. *H. brevicaudus* usually is not as dark as *H. notoperates,* lives at lower elevations, and is found in a moister, more northern climate.

Hesperoboreus notoperates (Cooper), new combination

Boreus notoperates Cooper, 1972, Psyche 79:269-283, Figs. 1-9.

Holotype and allotype in Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

Present description based on 3 males and 1 female pinned, 1 male and 1 female in alcohol.

Head: Black shading to dark brown near tip of rostrum. Occiput rugulose, with many fine setae. Median ocellus absent. Antenna dark brown, with 16 to 18 flagellomeres. Viewed in side profile, anterior surface of rostrum with few setae; posterior margin of hypostomal bridge with none. Ratio of length of maxillolabial complex to rostrum = .52.

Thorax: Nota and pleura dark brown. Pronotum with two transverse incisions, anterior margin with 6 bristles, middle of notum with 2 to 8 bristles, posterior margin with 4 bristles. Meso- and metanotum sometimes with bristles. Numerous smaller setae cover thorax.

Legs: Dark brown with numerous paler setae and dark brown apical femoral spine. Tibial spurs light brown.

Male wings: Light brown and abruptly narrowed at mid-length; 16 inner forewing and 17 hindwing spines.

Female forewing: Oval, light brown, covering hindwing, with many setae, without large bristles at apical margin.

Male abdomen: Dark brown throughout. No tergal ridges on second and third abdominal segments. No fusion of eighth tergum and sternum or ninth tergum and sternum. Ninth tergum without hood; 8 denticles on either side of medial partition. Dististyle with about 10 spines arranged from below basal lobe to near apex of diststylar claw. Ninth sternum deeply notched, not reaching base of dististyles.

Female abdomen: All segments dark brown. Ratio of length of ovipositor to rostrum = .63. Caudal extensions of tenth segment each bearing 5 apical spines. Cerci dark brown with semitransparent tips. Eighth sternum with deeply incised, basolateral notch.

Body length: Male—about 2.7 mm. in alcohol (holotype 2.5 mm., pinned); female, about 3.9 mm. in alcohol (allotype 3.6 mm., pinned).

Intraspecific variation: Antennae vary from 18 to 20 segments, with 19 being the most common number.

Holotype male, allotype female, and all known specimens from Coldwater and Black Canyons, near town of Mountain Center on Mt. San Jacinto, Riverside Co., CALIFORNIA, from 27 Dec. to 22 Jan., collected by K. W. Cooper and family (Fig. 70).

A detailed study of the habitat, life history, and behavior of this species has been published by Cooper (1974). Among his observations are that this species forms a larval cell in dry weather to conserve moisture, that many species of moss are used as food, and that mating is perpendicular (Cooper's terminology) rather than parallel, as in *Boreus*. This species is aided in this unusual mating position by reciprocal locking of genitalia and the basal notch of the female eighth sternum (a structure also found in *H. brevicaudus*).

In his original description Cooper went beyond a mere external morphological description, including in the paper excellent comparisons of this species' male and female reproductive systems with those of other species and giving further notes on boreid chromosomes.

H. notoperates can be separated from *H. brevicaudus* by a deeply notched male ninth sternum, lack of apical bristles on the female forewings, and larger notch to the female eighth sternum. *H. notoperates* is usually darker in color than *H. brevicaudus,* lives at a higher elevation, in a drier, more southern climate.

Boreus Latreille (1816)

Boreus Latreille. 1816. Nouveau dictionnaire d'histoire naturelle 4:152-153. Type species: *Panorpa hyemalis* L.

Ateleptera Dalman. 1823. Analecta Entomologica. Holmiae, Lindholm. 104 p. Type species: *Ateleptera hiemalis* L.

Euboreus Lestage. 1940. Pour l'histoire des *Boreus* (Stegopteres-Mecopteres). Annales de Societe royale zoologique de Belgique 71:5-22. Type species: *Euboreus nivoriundus* Fitch.

This genus can be separated from *Hesperoboreus* by the following characters: Hypostomal bridge narrow; ratio of length of maxillo-labial complex to rostrum more than .61. Male forewings with an outer row of spines. Female eighth sternum without basal notch. Female tenth tergum at least twice as long as ninth, bearing no caudal extensions. Cerci fused completely. Mating posture parallel.

Key to Males of Nearctic *Boreus*

1. Bristles on pronotum 2
   No bristles on pronotum 6
2. Apex of ninth sternum deeply notched 3
   Apex of ninth sternum smoothly rounded, truncate, or shallowly notched 5
3. Pilosity of thorax and abdomen half as long as thoracic bristles (western North America) 4
   Short pilosity on thorax and abdomen (eastern North America) .... *brumalis*
4. Ninth tergum bearing 25 or fewer denticles at each side of median partition .... *pilosus*
   Ninth tergum bearing 26 or more denticles at each side of median partition .... *nix*
5. Posterior surface of rostrum bearing 25 or more stout setae (western North America) .... *elegans*

Posterior surface of rostrum bearing 24 or fewer stout setae (eastern North America) .... *nivoriundus*

6. Eighth abdominal tergum and sternum fused 7
   Eighth abdominal tergum and sternum not fused .... *reductus*
7. Interior of hood of tergum IX obscured by numerous setae (Alaska) .... *borealis*
   Interior of hood visible 8
8. Median septum of hood short, forked ventrally (Alaska) .... *intermedius*
   Median septum of hood long, unforked ventrally (western North America) 9
9. Median septum of hood with only a narrow crest .... *californicus*
   Median septum of hood wide, with raised area between crest and tergal pockets .... *coloradensis*

KEY TO FEMALES OF NEARCTIC *Boreus*

1. Bristles on pronotum 2
   No bristles on pronotum 6
2. Stout setae on posterior (ventral) surface of rostrum 3
   No stout setae on posterior (ventral) surface of rostrum, only fine setae 4
3. Posterior surface of rostrum bearing 25 or more spines (western North America) .... *elegans*
   Posterior surface of rostrum bearing 24 or fewer spines (eastern North America) .... *nivoriundus*
4. Pilosity of thorax and abdomen as long as thoracic bristles (western North America) 5
   Pilosity of thorax and abdomen shorter than thoracic bristles (eastern North America) .... *brumalis*
5. Legs black or dark brown .... *nix*
   Legs yellowish-brown .... *pilosus*
6. Forewings reduced to small vestiges not covering hindwings .... *reductus*
   Forewings oval; covering hindwings .... *borealis, californicus, coloradensis,* and *intermedius*

SPECIES DESCRIPTIONS

Boreus borealis Banks

Boreus borealis Banks, 1923, North American Fauna 46:158, pl. IX, Fig. 8.

One male syntype (labelled paratype) in Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts. Although Banks originally described *borealis* from both sexes, all that remains is one male. Apparently four specimens composed the original collection (Banks, 1923). Carpenter (1931) mentioned the lone remaining male (as cotype), as well as the absence of any females. This male bears the following five labels: "St. Paul Id., Bering Sea, May 23, 1914," "A. G. W. Lot No. 157," "A. G. Whitney Collector," "Type, 11277" (red), and "*Boreus borealis* Bks, paratype." Since this is actually a syntype and is the only remaining specimen of the type series, it is hereby designated lectotype.

Present description based on 1 additional male (teneral) and 1 female pinned.

HEAD: Occiput reticulately striated (Fig. 5), without setae. Occiput and vertex dark brown shading to light brown on rostrum; tip of rostrum dark brown. Median ocellus present. Antenna light brown, with 18 flagellomeres (missing from present specimens, but one antenna glued to base of point holding male specimen). Numerous setae on anterior surface of rostrum near antennal bases, also on posterior surface, but sparse elsewhere on rostrum. Ratio of length of maxillo-labial complex to rostrum = .84.

THORAX: Pronotum dark brown, with two lateral incisions and no bristles. Meso- and metanotum light brown, without bristles. A few small setae on dorsum and pleuron.

LEGS: Light brown with numerous lighter colored setae and dark brown apical femoral spine. Tibial spurs light brown.

MALE WINGS: Yellowish-brown, abruptly narrowed at mid-length, with 36 inner and 13 outer forewing spines, no hindwing spines.

FEMALE FOREWING: Yellowish-brown, oval, covering hindwing.

MALE ABDOMEN: Glossy black with some blue reflections. No tergal ridges on second and third terga. Eighth tergum and sternum fused; ninth tergum and sternum not fused. Ninth tergum with large hood extending laterally to outer edge of denticular area; median septum long, thin; long setae almost completely covering median septum and tergal pockets, smaller setae on dorsal surface of hood. Denticles about 15 in number, of equal size. Dististyle with about 21 spines arranged from below basal lobe to base of dististylar claw; covered with many setae, except on dististylar claw and basal lobe; basal lobe with blunt tip and cleft between it and base of dististyle. Ninth sternum smoothly rounded at apex, reaching to bases of dististyles.

FEMALE ABDOMEN: Dark brown dorsally, lighter brown ventrally; ninth and tenth segments yellowish-brown. Ovipositor to rostrum ratio = 1.05. Cerci dark brown, evenly tapering to apex.

BODY LENGTH: Male, 5.0 mm. pinned; female, 5.4 mm., pinned. Syntypes from St. Paul Island, Bering Sea, ALASKA, 16-23 May 1914, A. G. Whitney. Two other known specimens (1 male, 1 female) from same locality as types, July-Aug. 1925, A. Christofferson.

INTRASPECIFIC VARIATION: Banks (1923) mentioned wings as well as overall size of both male and female as being larger than those of other North American species. Carpenter (1931) mentioned that the female wing pad is about as long as in other *Boreus,* and speculated that the original female may have been somewhat shriveled. The male I have examined also appears not to have wings longer than in other species. Carpenter, in the same paper, mentioned that the body color had a bronzy sheen. Although the specimens I examined did not display this bronzy color, the male was obviously teneral and may not have displayed the full color of the species.

This species has been collected only from St. Paul Island in the Pribilofs (Fig. 80) which has a maximum elevation of 203 feet and dominant vegetation of cottonsedge tundra. Sage (1973) has characterized the area as follows: "Most of the Bering Sea islands are remote and this fact, coupled with the formidable combination of frequent fog, gales, and violent seas, means that opportunities to visit most of them even in summer are few."

This species appears to emerge at a different time than all other boreids, probably due to the severity of climatic conditions. All specimens were also collected at a lower elevation than any other species of the *californicus* group.

B. borealis is structurally similar to *californicus, coloradensis,* and *intermedius,* but males can be identified by the large number of setae lining the tergal hood. Females cannot be positively identified, except by locality. Banks (1923) mentioned that this was the only species with pale coxae and pleura, but some individuals of *californicus* and *pilosus* also have pale coxae and pleura.

Boreus brumalis Fitch

Boreus brumalis Fitch, 1847, Amer. J. Agr. Sci., 5:278.

One male and one female, both syntypes, in Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts. The male bears the labels "316," "Hagen," "*B. brumalis* Fitch, ♂" (green), "Type, 11118" (red), "*Boreus brumalis* Fitch." It is in good condition and is hereby designated lectotype.

Present description based on 189 males, 246 females.

HEAD: Dark brown, shading to light brown on rostrum. Occiput smooth, except for fine reticulations and setal pits. Median ocellus present. Antenna light brown, with 20 to 21 flagellomeres. Numerous setae on anterior surface of rostrum near antennal bases, also on posterior surface, but sparse elsewhere on rostrum. Ratio of length of maxillo-labial complex to rostrum = .83.

Thorax: Pronotum dark brown, with two transverse incisions; anterior and posterior margins each with four bristles. No bristles on meso- and metanotum. Small setae covering thorax.

Legs: Light brown to dark brown with numerous lighter-colored setae. Dark brown apical femoral spine. Tibial spurs light brown to translucent.

Male wings: Dark brown to light brown, abruptly narrowed at mid-length, with 20 inner and 15 outer forewing spines, three hindwing spines.

Female forewing: Dark brown, oval; covering hindwing.

Male abdomen: Dark brown to glossy black. No tergal ridges on second and third abdominal segments. No fusion of eighth tergum and sternum or ninth tergum and sternum. Ninth tergum with small medially cleft hood, extending laterally only to medial margins of denticular areas; median septum absent. Denticles about 29 in number on each side, smaller toward pockets of hood. Dististyle with about 15 spines arranged from below basal lobe to base of dististylar claw; basal lobe blunt tipped, separated from base of dististyle by cleft. Ninth sternum deeply notched at apex, extending to bases of dististyles.

Female abdomen: Dark brown to glossy black. Ratio of length of ovipositor to rostrum = 1.00. Cerci dark brown, evenly tapering to apex.

Body length: Male, 2.4 to 3.1 mm., in alcohol, 2.0 to 2.7 mm., pinned; female 3.6 to 4.1 mm., in alcohol, 2.9 to 3.8 mm., pinned.

Intraspecific variation: Overall color varies. Most brown specimens are from the more southern parts of the range.

B. brumalis has generally been collected from 19 Nov. to 24 April, but 1 male and 1 female in the Ohio State University Collection are labelled 15 Aug. 1935.

This species is widespread over eastern North America (Fig. 71), from the Smoky Mountains (Cole, 1938) and Cumberland Mountains (Goslin, 1950) of TENNESSEE to southern ILLINOIS (Stannard, 1957) to Sauk County, WISCONSIN and Duluth, MINNESOTA, to Brownsburg, QUEBEC. Specimens have been collected in almost all states within these boundaries. The southern Illinois population is 370 miles from the nearest known population in central OHIO. Stannard (1957) suggested that the Illinois population is a remnant of a once widespread population living in the mesophytic forest that stretched from eastern Tennessee to the Ozark Plateau and that is now only tenuously linked through southern Illinois. Despite intensive searching, no specimens have been found in nearby Missouri or the lower Ohio River Valley.

The elevational records vary from sea level in New England to 4000 feet (1220 m.) in the Cumberland and Smoky Mountains of Tennessee.

There are no records to indicate that northern populations emerge earlier or later in the winter than southern populations.

B. brumalis larvae can be collected at any time of the year in their southern Illinois habitats, where they are found tunneling just beneath the rhizoids of *Dicranella heteromalla* and *Atrichum angustatum*. This species apparently does not form the dry weather cells, such as Cooper (1974) described for *H. notoperates*. In the same area, larvae and adults are most frequently collected on moss on sandy loam soil rather than mossy rocks, as are other species in other areas.

The deeply notched ninth sternum of separate this eastern species from all other the male and bristles of the pronotum species of *Boreus,* except *nix* and *pilosus.* The pilosity of *brumalis* is shorter than in either of these latter two western species.

Boreus californicus Packard

Boreus californicus Packard, 1870, Proc. Boston Soc. Nat. Hist. 13:408.

Boreus unicolor Hine, 1901, Bull. Sci. Lab., Denison Univ. 11:256. New synonymy.

Boreus isolatus Carpenter, 1935, Psyche 42:115, Fig. 11. New synonymy.

Boreus californicus fuscus Carpenter, 1935, Psyche 42:117-118. New synonymy.

Three male, three female syntypes of *californicus* are in the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts. (These are the types originally deposited in the Museum of the Peabody Academy of Science.) All six specimens bear the following three labels: "Ft. Bidwell, Siskiyou Calif.," "Type, 11119" (red), and "californicus." As Lattin (1956) mentioned, Ft. Bidwell is in Modoc Co. The best preserved male is hereby designated lectotype. Two female syntypes of *unicolor* are in the United States National Museum of Natural History, Washington, D.C. (In 1931 Carpenter designated a male in the Museum of Comparative Zoology as allotype.) Both specimens are labelled "Helena, Mon. 26.4" "Coll. Hubbard & Schwarz" "Type No. 5743 U.S.N.M." The better specimen is hereby designated lectotype. Holotypes of *isolatus* and *californicus fuscus* are in the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

All previous authors have referred to *B. californicus* as having been originally described in 1871 in volume 8 of the *Proceedings of the Boston Society of Natural History.* Actually, it was described in 1870 in volume 13.

Present description based on 372 males, 432 females.

Head: Occiput dark brown to black shading to lighter brown on rostrum. Occiput smooth. Median ocellus present. Antenna light brown basally to dark brown apically, with 20 to 23 flagellomeres. Numerous setae on anterior surface of rostrum near antennal bases, also on posterior surface, but sparse elsewhere on rostrum. Ratio of length of maxillo-labial complex to rostrum = .70 to .90.

Thorax: Pronotum dark brown, with indistinct medial transverse ridge and no bristles. Meso- and metanotum dark brown, without bristles. Many small setae covering thorax.

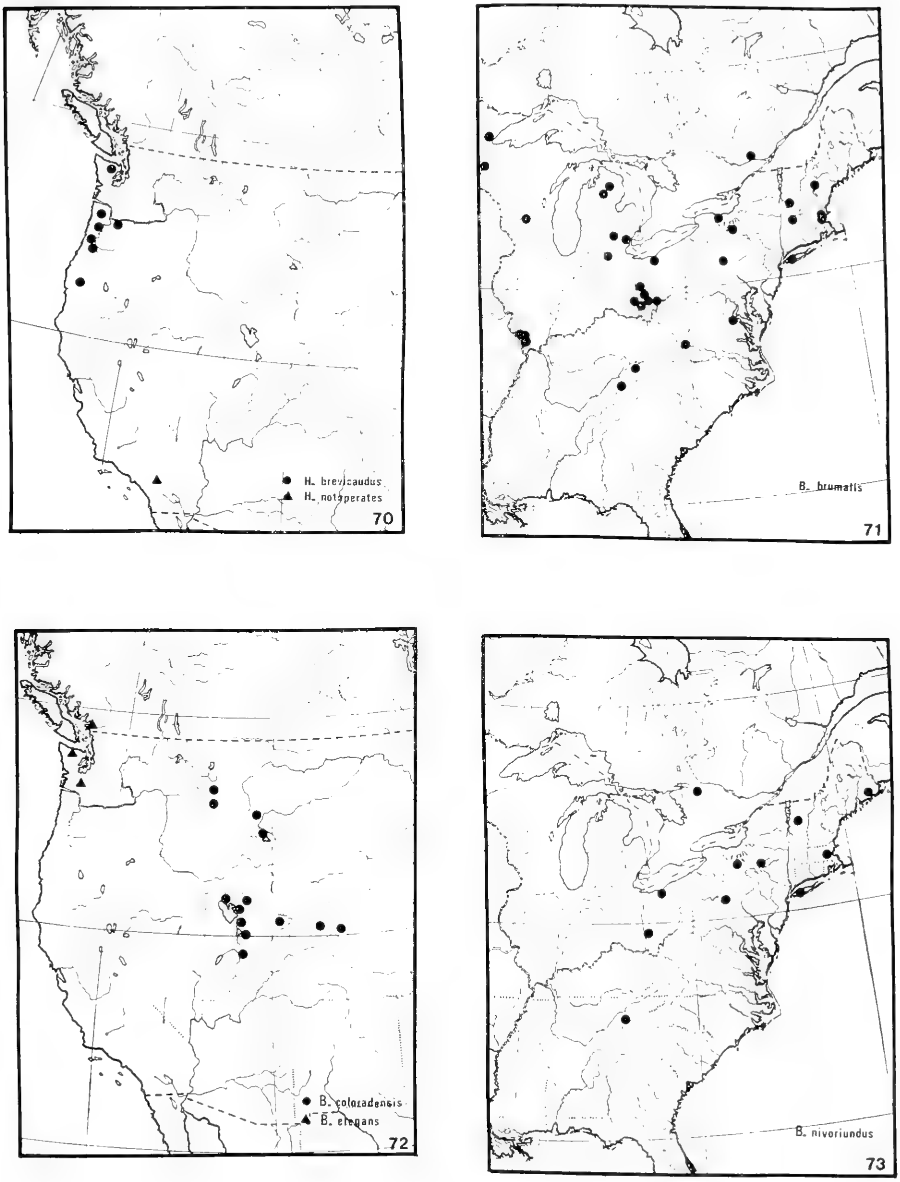
Legs: Yellowish-brown to dark brown with darker colored spines; usually with dark brown apical femoral spine. Tibial spurs light brown.

Male wings: Yellowish-brown to dark brown and abruptly narrowed at midlength; 15 to 23 inner and 7 to 13 outer forewing spines; usually no hindwing spines.

Female forewing: Light to dark brown, oval, with many small setae but no large bristles at apical margin; covering hindwing.

Male abdomen: Dark brown to black. No tergal ridges on second and third segments. Eighth tergum and sternum fused; ninth tergum and sternum not fused. Ninth tergum with large hood, extending to lateral margins of denticular areas; median septum long, thin, with some setae in tergal pockets; smaller setae on dorsal surface of hood. Denticles about 26 in number, of equal size. Dististyle with many small spines arranged from below basal lobe to base of dististylar claw; basal lobe blunt tipped, separated from base of dististyle by cleft. Ninth sternum reaching to bases of dististyles, its apex smoothly rounded to bluntly squared to shallowly depressed medially.

Female abdomen: Dark brown to black; ninth and tenth segments yellowish-brown



Figures 70-73. Fig. 70, distribution of *Hesperoboreus brevicaudus* and *H. notoperates*. Fig. 71, distribution of *Boreus brumalis*. Fig. 72, distribution of *Boreus coloradensis* and *B. elegans*. Fig. 73, distribution of *Boreus nivoriundus*.

to dark brown. Ratio of length of ovipositor to rostrum = 1.10 to 1.30. Cerci light brown to dark brown, evenly tapering to apex.

Body length: Male, 3.6 to 5.0 mm., in alcohol; female, 5.4 to 6.5 mm., in alcohol.

Intraspecific variation: This widespread western species shows considerable variation in coloration, size, number of antennal segments, and male wing spines. Some males from Alberta have very small spines on the hindwings. One color variety is rusty brown. Unfortunately, the type series of *californicus* consists of such specimens. Other specimens with the more usual dark body with light appendages were used by Carpenter (1935) as basis for *B. californicus fuscus.* As noted in the section on coloration, this species generally develops the dark pigmentation in some body parts more slowly than in others. Thus, specimens with yellowish legs will have darker legs later in the season. Rusty red specimens have been found at localities having also darker and lighter specimens. For these reasons, I feel that subspecific rank for any color variants of *californicus* is unjustified.

Most specimens of *californicus* have an apical femoral spine on all legs, but in the northern parts of the range it may be lacking from some legs, and in Arizona and California it is lacking altogether. Eye color, as used by Carpenter (1931) in his key to females, varies depending on the method of preservation.

B. californicus has been collected (Fig. 74) from ARIZONA: Coconino Co., 15 mi. S. of Flagstaff; CALIFORNIA: Mariposa, Co., Yosemite National Park; Inyo Co., 4 mi. N. of Schulman Grove; Sierra Co., Hobart Mills (Lattin, 1956); Lassen Co., Susanville; Modoc Co., Ft. Bidwell and Goose Lake; NEVADA: Nye Co., Kawick Mt. (Lattin, 1956, as *B. unicolor*); Washoe Co., Reno (Carpenter, 1935); OREGON; Umatilla Co., Fly Creek Valley; WASHINGTON: Whitman Co., Pullman area; Spokane Co., Spokane; Pierce Co., near Deer Creek; IDAHO: Latah Co., Moscow area; Idaho Co., Papoose Creek; MONTANA: Ravalli Co., Hamilton area; Missoula Co., Missoula area; Flathead Co., Daphnia Pond; Mineral Co., St. Regis; Lewis & Clark Co., Helena; Lake Co., Lion Creek; Powell Co., Pass Creek; BRITISH COLUMBIA: Ashnola River Valley; Kaslo; Terrace; Salmon Arm; ALBERTA: Banff; Jasper National Park.

This species has been collected from 4 Nov. to 26 April from the semiarid western mountains of central Arizona to northern British Columbia. Specimens have been found from 4000 to 10,300 feet (1220 to 3142 m.).

B. unicolor was originally described as being similar to *californicus,* but with a dark ovipositor. Dark specimens appear structurally identical to lighter specimens of *californicus. B. unicolor* is also similar to *coloradensis,* but the latter species does not have apical femoral spines. G. W. Byers examined the two syntypes of *unicolor* and noted spines on both hind femora. Thus, *B. unicolor* is regarded as a junior synonym of *californicus.*

B. isolatus was described as being similar to *californicus,* but with a deeply notched ninth sternum in males. While studying the holotype (and only known specimen) of *isolatus,* G. W. Byers noted that the notched ninth sternum was asymmetrical. It appeared that apical setae were adhered together with foreign material. After cleaning, the apex of the ninth sternum was found to be smoothly rounded, as in *californicus.* Accordingly, *isolatus* is also placed as a junior synonym of *californicus.*

B. californicus is a member of the group with fused eighth sternum and tergum, and no tergal ridges on second and third abdominal segments of males. It can be separated from other species in this group by characters of the ninth tergal hood, including a long, narrow septum bearing sparse setae that do not obscure the interior of the tergal pockets. *B. californicus* is most often confused with *coloradensis,* which is found farther east, and which has a broader tergal septum, and never has apical femoral spines.

Boreus coloradensis Byers

Boreus coloradensis Byers, 1955, Occ. Pap. Mus. Zool., Michigan Univ. No. 562, Figs. 1-5.

Holotype male and allotype female in the University of Colorado Museum, Boulder, Colorado.

Present description based on 123 males, 132 females.

Head: Dark brown to black, shading to slightly lighter brown on rostrum. Occiput finely reticulate, with few setae. Median ocellus present. Antenna dark brown to black, with 20 to 22 flagellomeres. Numerous setae on anterior surface of rostrum near antennal bases, also on posterior surface, but sparse elsewhere on rostrum. Ratio of length of maxillo-labial complex to rostrum = .86.

Thorax: Pronotum dark brown to black, with an indistinct transverse ridge near mid-length; no bristles. Meso- and metanotum dark brown to black, without bristles. Many small setae covering thorax.

Legs: Dark brown to black with numerous pale setae and dark spines. No apical femoral spines. Tibial spurs light brown.

Male wings: Light brown to black, abruptly narrowed near mid-length, with 19 to 22 inner and 8 to 13 outer forewing spines; no hindwing spines.

Female forewing: Dark brown to black, oval, covering hindwing.

Male abdomen: Dark brown to glossy black. No tergal ridges on second and third segments. Eighth tergum and sternum fused. Ninth tergum and sternum not fused. Ninth tergum with large hood extending to lateral margins of denticular areas; median septum long, wide, with thin crest and less densely sclerotized region between crest and pockets; numerous long setae not obscuring interior of hood, and smaller setae on dorsal surface of hood. Ninth tergal apex with 22 denticles of equal size. Dististyle with many small denticles arranged from below basal lobe to base of dististylar claw; basal lobe blunt tipped, separated by cleft from base of dististyle. Ninth sternum reaching bases of dististyles, smoothly rounded to bluntly squared to shallowly depressed apically.

Female abdomen: Mostly dark brown to glossy black; ninth and tenth segments light brown. Ratio of length of ovipositor to rostrum = 1.30 to 1.43. Cerci dark brown to black, evenly tapering to apex.

Body length: Male, 2.5 to 3.0 mm., pinned (holotype 2.5 mm.), 3.2 to 4.9 mm., in alcohol; female, 4.5 to 5.0 mm., pinned (allotype, 4.5 mm.), 4.3 to 5.4 mm., in alcohol.

Intraspecific variations: The only variation noted in this species was a slightly lighter brown coloration in specimens preserved in alcohol, some variation in the apex of the ninth sternum (see Byers, 1955, for discussion), and differences in number of antennal flagellomeres, wing spines, and other minor numerical differences. There appears to be no geographical or elevational pattern to this variation.

Holotype, allotype, and all paratypes from 12 to 20 miles west of Boulder, Boulder Co., COLORADO. Other specimens (Fig. 72) have been collected at COLORADO: Routt Co., Steamboat Springs; UTAH: Cache Co., Logan area (Blacksmith Fork Canyon, Green Canyon, Logan Canyon); Utah Co., Rock Canyon; Uinta Co., Split Mountain Gorge; Weber Co., Ogden Canyon; Sampete Co., Maple Canyon; Box Elder Co., Promontory; Salt Lake Co., Mill Creek Canyon; WYOMING: Yellowstone National Park (Carpenter, 1935, as *unicolor*); MONTANA: Gallatin Co., Bozeman; Missoula Co., Missoula; Ravalli Co., Hamilton area (Boulder Creek, Gird's Creek, Skalkaho Creek).

In Colorado this species has been collected only high in the Rocky Mountains. Near Boulder it has been taken from 7000 to 12,000 feet (2135 to 3660 m.), and at Steamboat Springs from 7000 to 10,000 feet (2135 to 3050 m.). In Utah *B. coloradensis* can be found at lower elevations from 4700 to 6550 feet (1434 to 1998 m.).

B. coloradensis appears to be tolerant of arid conditions. In the Bitterroot Valley near Hamilton, Montana, this species is only collected on the dry eastern side of the valley. It has been collected on snow in sagebrush desert at Promontory, Utah. However, it has also been collected in thick carpets of moss only a few feet from the bank of Blacksmith Fork near Logan, Utah, obviously a very humid habitat.

Specimens of this species were collected from 1 Oct. to 27 May in Utah, Montana, Wyoming, and western Colorado, and from 31 March to 24 April in central Colorado.

B. coloradensis is a member of the *californicus* group, having fused eighth tergum and sternum and no tergal ridges on second and third abdominal segments of males. *B. coloradensis* has a long median septum of the hood, unlike *B. intermedius,* and fewer long hood setae than *B. borealis. B. coloradensis* is most often confused with *californicus,* but the latter species has a narrow median septum on the ninth tergum. Byers (1955) mentioned that *coloradensis* could be separated from *unicolor* (a synonym of *californicus*) by the latter species having shorter male forewings, indistinct pronotal ridge, blunter denticles on the ninth tergum, and narrower septum on the ninth tergum. I can see only the last of these character states. Differences between the two species are so minor that perhaps specific rank for *coloradensis* is not warranted. However, consistent lack of the apical femoral spine and the broader hood septum in *coloradensis* make me think this is a valid species.

Boreus elegans Carpenter

Boreus elegans Carpenter, 1935, Psyche 42:119, 122, Figs. 8, 12.

Holotype, male, in California Academy of Science, San Francisco.

Present description based on 7 males, 13 females in alcohol.

Head: Rusty brown. Occiput finely reticulated, with no setae. Median ocellus present. Antenna light brown basally, becoming dark brown toward apex, with 20 to 22 flagellomeres. Anterior surface of rostrum with few setae; posterior surface of rostrum with fine setae and numerous stouter setae. Ratio of length of maxillolabial complex to rostrum = .77.

Thorax: Pronotum rusty brown with indistinct transverse ridge near mid-length; anterior and posterior margins with four to six bristles each. Two bristles each on meso- and metanotum. Small setae covering thorax.

Legs: Light brown, with numerous dark brown spines, setae, and apical femoral spine. Tibial spurs light brown.

Male wings: Light brown, tapering evenly to apex, with 16 inner and 16 outer forewing spines, 12 hindwing spines.

Female forewing: Rusty brown, oval, covering hindwing.

Male abdomen: Rusty brown oval, covering hindwing.

Male abdomen: Rusty brown except yellowish-brown on basistyles and dististyles. No tergal ridges on second and third segments. No fusion of eighth tergum and sternum or ninth tergum and sternum. Ninth tergum with hood only reaching mesal margins of denticular areas. About 75 denticles on either side of median cleft. Dististyle with about 30 denticles arranged from below basal lobe to near base of dististylar claw. Ninth sternum broadly rounded apically, reaching bases of dististyles.

Female abdomen: Rusty brown. Ratio of length of ovipositor to rostrum = 1.15. Cerci rusty brown, evenly tapering to apex.

Body length: Male, 4.0 to 4.6 mm., in alcohol (holotype and paratype 3.5 to 3.8

mm., pinned); female, 6.0 to 7.4 mm., in alcohol.

Intraspecific variation: This species shows the usual variation in number of antennal flagellomeres.

Holotype and paratype males, Vancouver, BRITISH COLUMBIA, Dec. 1930, H. E. Hinton. Other specimens (Fig. 72) from WASHINGTON: Cowlitz Co., Seaquest State Park, 29 Dec. 1971, N. D. Penny, 4 females; Clallam Co., 1 mi. E. of Lake Crescent, 30 Dec. 1971, N. D. Penny, 7 males, 9 females.

This species was appropriately named, for it is truly the most elegant boreid known. In color it differs from all other boreids except the reddish color variety of *californicus*. *B. elegans* is the largest boread species and can be seen and recognized on winter snow a considerable distance away. It lives in the warm-winter, maritime climate of western North America where rainfall is abundant and temperatures seldom are below —13° C. (see ecology section on temperature). All three collections of this species were below 1,600 feet (488 m.) elevation.

B. elegans is in the *nivoriundus* subgroup of the nivoriundus group, having bristles on the pronotum and the apex of the male ninth sternum rounded. It can be separated from the only other member of this subgroup, *nivoriundus,* by its large size, more reddish coloration, and more numerous stout setae on the back of the rostrum.

Boreus intermedius Lloyd

Boreus intermedius Lloyd, 1934, Pan-Pacific Entomol. 10:119, Fig. 2.

Holotype male and allotype female, catalogued 7454 and 7453, respectively, were deposited in the Thomas Burke Memorial Washington State Museum, Seattle, but the curator has been unable to locate them for me. Specimens used in this description, from the Museum of Comparative Zoology, Harvard University, were collected from the same locality by the same collector exactly one year later than the type specimens.

Present description based on 1 male in alcohol, 2 females pinned.

Head: Black shading to yellowish-brown on rostrum. Occiput finely reticulated, with a few setae near margins of compound eyes. Median ocellus present. Antenna light brown shading to dark brown toward apex, with 18 to 19 flagellomeres. Numerous setae on anterior surface of rostrum near antennal bases, also on posterior surface, but sparse elsewhere on rostrum. Ratio of length of maxillo-labial complex to rostrum = .91.

Thorax: Dark brown on nota, becoming yellowish-brown on pleural and sternal regions. Pronotum with indistinct ridge at mid-length; no bristles. Meso- and metanotum without bristles. Small white setae dense over entire thorax.

Legs: Yellowish-brown with stout setae and apical femoral spine dark brown; finer setae and tibial spurs yellowish.

Male wings: Yellowish-brown, abruptly narrowed at mid-length; with 33 inner and 10 outer forewing spines, no hindwing spines.

Female forewing: Yellowish-brown, oval, covering hindwing.

Male abdomen: Segments 1 through 8 dark brown; segment 9, basistyles and dististyles yellowish-brown. No tergal ridges on second and third segments. Eighth tergum and sternum fused. Ninth tergum and sternum not fused. Ninth tergum with large hood, extending laterally to lateral margins of denticular areas. Median septum of hood short, with thin crest and extensive sclerotized area between crest and pockets. Caudal medial cleft of ninth tergum large, between ventral fork of medial septum. About 75 denticles on either side of medial septum. Dististyle with many small denticles arranged from below basal lobe to base of dististylar claw. Apex of ninth sternum truncate medially, reaching bases of dististyles.

FEMALE ABDOMEN: First 7 segments black, last 3 visible segments yellowish-brown. Ratio of length of ovipositor to rostrum = 1.14. Cerci yellowish-brown, evenly tapering to apex.

BODY LENGTH: Male, 5.0 mm., in alcohol (holotype 3.5 mm., pinned); female, 4.5 to 4.6 mm., pinned (allotype 4.5 mm., pinned).

INTRASPECIFIC VARIATION: The specimens I examined agree with Lloyd's original description, except the ovipositor of the allotype was described as being twice as long as rostrum (as compared to 1.14).

Holotype male and allotype female from between Kennicott (spelling corrected) and McCarthy, ALASKA, 15 April 1934, Wilbur Lloyd (Lloyd, 1934). Other specimens (Fig. 80) are from Kennicott, ALASKA, 15 April 1935, Lloyd, 1 male, 2 females, in Museum of Comparative Zoology, and Carpenter (1936) mentioned specimens collected at McCarthy, ALASKA, 29 April 1935, 1 male, 2 females.

Kennicott (61°29′ N, 142°54′ W) and McCarthy (61°26′ N, 142°55′ W) are located about four miles apart at the base of Kennicott Glacier, near Fireweed Mountain in the Wrangell Range. Elevation at Kennicott is 2,000 feet (610 m.), at McCarthy 1,400 feet (427 m.).

Males of *B. intermedius* can be separated from other members of the *californicus* group by the septum of the ninth tergal hood, which is short and deeply divided ventrally.

Boreus nivoriundus Fitch

Boreus nivoriundus Fitch, 1847, Amer. J. Agr. Sci. 5:277.

Male and female syntypes in Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts. The male bears the labels "8088," "Hagen," "B. nivoriundus ♂ Fitch" (green), "Type, 11117" red), and "*Boreus nivoriundus* Fitch." It is hereby designated lectotype.

Present description based on 76 males, 80 females.

HEAD: Dark brown shading to lighter brown on rostrum. Occiput finely reticulate, with a few setae. Median ocellus present. Antenna light brown basally, becoming dark brown toward apex, with 20 flagellomeres. Numerous small setae on anterior surface of rostrum near antennal bases, but sparse elsewhere. Posterior surface of rostrum with a few fine setae ventrally and more stout setae dorsally. Ratio of length of maxillo-labial complex to rostrum = .90.

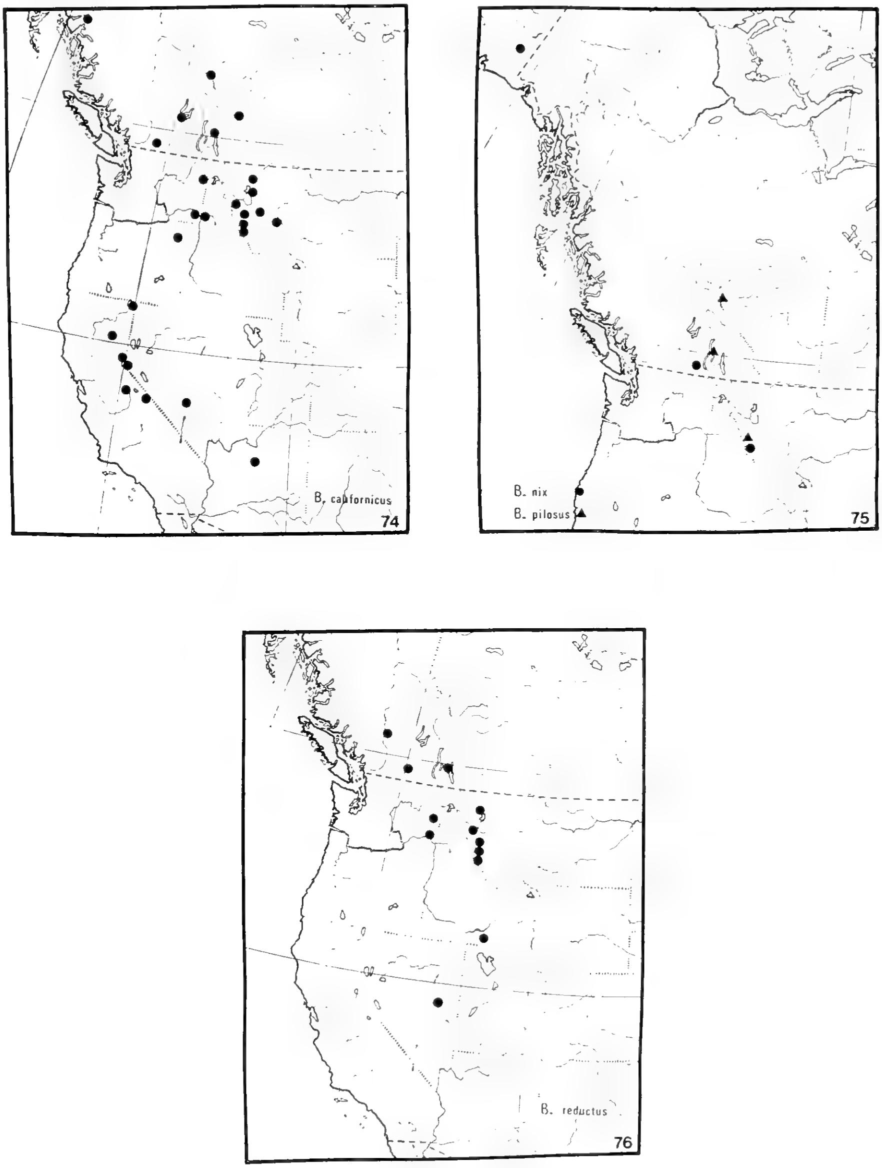
THORAX: Dark brown. Pronotum with no transverse ridge at mid-length; anterior and posterior margins with 4 to 6 bristles. Meso- and metanota occasionally with 2 dark bristles each. Small setae covering thorax.

LEGS: Dark brown, with dark brown apical femoral spine. Setae dark brown and light brown. Tibial spurs yellowish-brown.

MALE WINGS: Light brown, evenly tapered to apex, with 16 to 18 inner and 14 outer forewing spines, 16 hindwing spines.

FEMALE FOREWING: Light brown, oval, covering hindwing.

MALE ABDOMEN: Dark brown except light brown on last two abdominal segments. No tergal ridges on second and third segments. No fusion of eighth tergum and sternum or ninth tergum and sternum. Ninth tergum with small hood extending laterally only to mid-width of denticular areas. No median septum below hood. Medial cleft between areas of about 50 denticles each. Denticles becoming smaller toward hood. Dististyle with about 20 denticles arranged from below basal lobe to base of dististylar claw. Ninth sternum



Figures 74-76. Fig. 74, distribution of *Boreus californicus*. Fig. 75, distribution of *Boreus nix* and *B. pilosus*. Fig. 76, distribution of *Boreus reductus*.

broadly rounded apically, reaching bases of diststyles.

Female abdomen: Dark brown. Ratio of length of ovipositor to rostrum = 1.30. Cerci dark brown, evenly tapering to apex.

Body length: Male, 4.9 to 5.4 mm., in alcohol, 2.3 to 3.6 mm., pinned; female, 4.9 to 5.8 mm., in alcohol, 3.5 to 4.4 mm., pinned.

Intraspecific variation: The coloration and number of thoracic bristles vary.

This species has been collected (Fig. 73) from OHIO: Fairfield Co., Lancaster area; Hocking Co., "Neotoma"; Medina

Co., Hinckley Reservation; NEW YORK: Nassau Co., Sea Cliff; Chenango Co., Bainbridge; Tompkins Co., Ithaca; MASSACHUSETTS: Worcester Co., Spencer; Suffolk Co., Roxbury; NEW HAMPSHIRE: Carroll Co., Jackson (Dohanian, 1915); VERMONT: Chittenden Co., 3 mi. N. of Bolton; MAINE: Hancock Co., Ellsworth; and TENNESSEE: Sevier Co., Newfound Gap (Cole, 1938); and Campbell Co., LaFollette (Goslin, 1950).

B. nivoriundus has been collected from 19 Nov. to 28 March. Apparently E. S. Thomas collected 2 females from Hocking Co., Ohio, on 15 Aug. 1935. The date of these specimens, along with two specimens of *B. brumalis* collected at the same place on the same date by the same collector, is unusual. Only in the Bering Sea area have other specimens of Nearctic *Boreus* been collected at this time of year. Localities for *B. nivoriundus* range in elevation from sea level to about 5000 ft. (1500 m.).

B. nivoriundus can be separated from all other species of *Boreus,* except *elegans,* by the combination of pronotal bristles and rounded ninth sternum of males. *B. nivoriundus* can be separated from the western *elegans* by the former species' smaller size, fewer stout rostral setae, and smaller denticles near the hood.

Boreus nix Carpenter

Boreus nix Carpenter, 1935, Psyche 42: 114, Fig. 7.

Boreus gracilis Carpenter, 1935, Psyche 42:118. New synonymy.

Holotype male and allotype female of *nix* (no. 22359) in Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts. Holotype female of *gracilis* (no. 7452) cannot be located at the Burke Memorial Washington State Museum, Seattle. One paratype female (no. 22361) in Museum of Comparative Zoology, Harvard University.

Present description based on 12 males, 9 females.

Head: Dark brown shading to lighter brown on rostrum. Occiput finely reticulate, with several long setae. Median ocellus present. Antenna brown, with 21 to 22 flagellomeres. Anterior and posterior surfaces with a few long setae, mainly below antennal bases. Ratio of length of maxillo-labial complex to rostrum = .88.

Thorax: Dark brown. Pronotum with indistinct transverse ridge at mid-length; anterior and posterior margins with 4 to 6 bristles. Meso- and metanotum occasionally with 2 bristles each. Long white setae covering thorax.

Legs: Dark brown to black with numerous dark setae and long white setae. Apical femoral spine dark brown. Tibial spurs light brown.

Male wings: Dark brown, abruptly narrowed at mid-length, with 16 inner and 15 outer forewing spines, 10 to 11 hindwing spines.

Female forewing: Dark brown, oval; covering hindwing.

Male abdomen: Dark brown to black with long white setae on all segments, giving this species a frosted appearance. No tergal ridges on second and third segments. No fusion of eighth tergum and sternum or ninth tergum and sternum. Ninth tergum with hood extending laterally to mid-width of denticular areas (Fig. 45); no median septum; medial cleft between areas of denticles; about 33 denticles on each side. Dististyle with about 20 small denticles arranged from below basal lobe almost to base of dististylar claw. Ninth sternum deeply notched apically; reaching bases of dististyles.

Female abdomen: Dark brown to black. Long white setae on all segments. Ratio of length of ovipositor to rostrum = 1.39. Cerci dark brown, evenly tapering to apex.

Body length: Male, 4.3 to 4.5 mm., in alcohol, 2.4 to 4.1 mm., pinned; female, 4.8 mm., in alcohol, 3.3 to 4.5 mm., pinned.

Intraspecific variation: The length of the setae varies somewhat, but is always longer than in other species, except *pilosus*.

Holotype male and allotype female from MONTANA: Ravalli Co., Gird's Creek, 2 Nov. 1934, W. L. Jellison. In addition, there have been 9 other males and 4 other females collected by C. B. Phillip and W. L. Jellison around Hamilton, Montana. Other localities (Fig. 75) are BRITISH COLUMBIA: Ashnola River Valley, 23 Nov. 1963, P. R. Grant, 2 males; ALASKA: between Kennicott and McCarthy, 15 April 1934, W. L. Lloyd, 3 males, 6 females (Carpenter, 1936, as *gracilis*).

Gird's Creek is about 5 miles straight east of Hamilton, Montana. The creek is on the dry eastern side of the Bitterroot River Valley, and is relatively inaccessible. However, this is the only locality where this species has been consistently collected.

B. nix has been collected from 2 Nov. to 11 Feb. in Montana and southern British Columbia, while Alaskan specimens were collected from mid- to late-April. The climate and evaluation of the Alaskan localities were discussed under *B. intermedius*. The dry, hilly area east of Hamilton, Montana, seems to be considerably different from the glacial lowland of Alaska, but differences in climate may be modified by different emergence dates.

When Carpenter (1936) discussed *B. gracilis,* he mentioned that this species differed from *nix* only in having male wings which were not abruptly narrowed at mid-length. However, in observing the series he used in describing the male, I noted that these specimens do have such abruptly narrowed wings. As there are no other differences, I consider *gracilis* as a junior synonym of *nix*.

This species is a member of the *brumalis* subgroup of the *nivoriundus* group, having bristles on the pronotum and a notched male ninth sternum. The long pilosity of the body separates this species from all others except *pilosus*. Males of *pilosus* have only about 19 denticles in each tergal area, while males of *nix* have about 33.

Boreus pilosus Carpenter

Boreus pilosus Carpenter, 1935, Psyche 42:114-115, Fig. 10.

Holotype male and allotype female (no. 22360) in Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

Present description based on 7 males, 9 females.

Head: Dark brown shading to light brown on tip of rostrum. Occiput finely reticulate, with a few whitish setae. Median ocellus present. Antenna brown, with 18 to 20 flagellomeres. Anterior and posterior surfaces of rostrum with long, whitish setae, numerous near antennal bases, sparse over rest of rostrum. Ratio of length of maxillo-labial complex to rostrum = .80.

Thorax: Dark brown. Pronotum with indistinct transverse ridge at mid-length. Anterior and posterior margins of pronotum with 2 to 6 yellowish-brown bristles. Meso- and metanotum occasionally with 2 bristles each. Small setae covering thorax.

Legs: Yellowish-brown with numerous dark brown and long, white setae. Apical femoral spine present, dark brown. Tibial spurs light brown.

Male wing: Yellowish-brown, abruptly narrowed at mid-length, with 19 to 22 inner and 16 to 19 outer forewing spines, 9 to 15 hindwing spines.

Female forewing: Yellowish-brown, oval; covering hindwing.

Male abdomen: Dark brown except yellowish-brown on ninth segment, basistyles, and dististyles. Sclerites with many long, white setae. No tergal ridges on second and third segments. No fusion of eighth tergum and sternum or ninth tergum and sternum. Ninth tergum with hood extending laterally to mid-width of denticular areas; no median septum in hood. Denticles somewhat scattered, only 19 on each side. Dististyle with 17 denticles arranged from below basal lobe to base of dististylar claw. Ninth sternum deeply notched apically, extending to bases of dististyles.

FEMALE ABDOMEN: Dark brown, except for rusty brown ovipositor and cerci. Ratio of length of ovipositor to rostrum = 1.09. Cerci evenly tapering to apex.

BODY LENGTH: Male, 2.6 to 2.9 mm., pinned, 3.0 to 4.0 mm., in alcohol; female, 4.1 to 4.6 mm., pinned, 5.2 mm., in alcohol.

INTRASPECIFIC VARIATION: There is considerable variation in number of antennal segments and male wing spines. Sometimes prothoracic bristles are rubbed off, giving this species the apearance of a combination of characters unlike any group.

Holotype, allotype, and 11 paratypes from BRITISH COLUMBIA: Kaslo, Dec. 1932. Other collections (Fig. 75) are from ALBERTA: Jasper National Park, 2-4 Oct. 1964, 6200 feet, 1 male, 1 female; MONTANA: Missouri Co., 26 Feb. 1957, H. R. Dodge, 2 males; Missouri Co., Grant Creek, 11 April 1972, R. A. Haick, 1 male; Missoula Co., Elk Creek, 4000 feet, 22 Jan. 1972, R. A. Haick, 1 female.

George Ball (personal communication) states that the Alberta specimens were collected in "an alpine meadow on a snow-covered, windblown, northeast-facing slope of Mount Edith Cavell, at 6200 feet." These specimens were collected in association with *B. californicus,* as have been all other known specimens of *B. pilosus.*

B. pilosus has been collected from 4000 to 6200 feet (1220 to 1891 m.) between 4 Oct. and 11 April.

This species is part of the *brumalis* subgroup of the *nivoriundus* group, having thoracic bristles and a deeply notched male sternum. It can be separated from the eastern *brumalis* by the long pilosity, and from the western *nix* by its lighter coloration and by having fewer ninth tergal denticles in males.

Boreus reductus Carpenter

Boreus reductus Carpenter, 1933, Can. Entomol. 65:94-95, Fig. 1A.

Holotype male and allotype female in Canada Department of Agriculture collection, Ottawa.

Present description based on 25 males, 24 females.

HEAD: Dark brown. Occiput finely reticulate, with numerous setal pits. Median ocellus absent. Antennae dark brown; 17 to 18 flagellomeres. Rostrum with many long setae near antennal bases, few setae over remainder of rostrum. Ratio of length of maxillo-labial complex to rostrum = .90.

THORAX: Dark brown. Pronotum with indistinct transverse ridge at mid-length; no bristles present. No bristles on meso- and metanotum.

LEGS: Dark brown with numerous light-colored and dark setae. No apical femoral spine. Tibial spurs light brown.

MALE WINGS: Dark brown, abruptly narrowed at mid-length, with 19 inner and 16 to 19 outer forewing spines, three hindwing spines.

FEMALE WINGS: Dark brown; reduced to small vestiges; forewing not overlapping hindwing; with short, whitish setae.

MALE ABDOMEN: Dark brown throughout. No tergal ridges on second and third segments. No fusion of eighth tergum and sternum or ninth tergum and sternum. Ninth tergal hood extending laterally to mid-width of denticular areas. Hood projecting dorso-caudally as a medial point (Fig. 47). Denticular areas large, with about 20 denticles on each side, forming a continuous area when medial cleft is not opened by internal pressure. Dististyle with about 13 denticles arranged from basal lobe to dististylar claw. Cleft between blunt-tipped basal lobe and rest of dististyle. Ninth sternum narrowed sharply at mid-length, smoothly rounded at apex, not reaching bases of dististyles.

FEMALE ABDOMEN: Dark brown. Ratio of length of ovipositor to rostrum = 1.10. Cerci dark brown, evenly tapering to apex. Internal sclerotized plate of eighth segment shaped like oval disc with two ventral funnels.

BODY LENGTH: Male, 1.9 to 2.4 mm., pinned, 3.3 to 3.9 mm., in alcohol; female, 2.8 to 3.1 mm., pinned, 4.8 mm., in alcohol.

INTRASPECIFIC VARIATION: Only variation noted is in number of antennal segments and male wing spines.

Holotype and allotype from BRITISH COLUMBIA: Kaslo, 29 Dec. 1906, J. W. Cockle. In addition, there is one other female with the same data, but no type label, in the Museum of Comparative Zoology. Other specimens (Fig. 76) are from BRITISH COLUMBIA: Lillooet, Jan. 1917, A. W. A. Phair, 1 male, 2 females; Ashnola River Valley, 23 Nov. 1963, P. R. Grant, 1 female; MONTANA: Ravalli Co., Hamilton area, from 27 Nov. to 31 Jan., W. L. Jellison, 15 males, 7 females; Missoula Co., from 6 Feb. to 11 March, John Chapman, D. S. Potter, and R. A. Haick, 6 males, 7 females; Mineral Co., St. Regis, 28 Dec. 1957, H. R. Dodge, 1 male, 6 females; Flathead Co., near Strick, 11 March 1961, W. L. Jellison, 1 male; WASHINGTON: Spokane Co., Spokane, 28 Dec. 1942, H. W. Prescott, many specimens; Whitman Co., 8 mi. W. of Colton, 18 Feb. 1972, W. J. Turner and J. Brunner, 2 males, 8 larvae; IDAHO: Oneida Co., 5 mi. SW. of Juniper, 22 Nov. 1969, George Knowlton, 1 female; NEVADA: White Pine Co., T18N, R54E, 1 Jan. 1971, Chambers and Nelson, 2 females.

This species has been taken in the arid Great Basin and mountainous regions of western North America, frequently in association with *B. californicus*. Specimens from Whitman Co., Washington were collected by Berlese funnel from *Selaginella* sp., a club moss.

B. reductus is unusual in many ways, and should not be confused with any other North American species of *Boreus*. Females of this species alone have forewings which do not overlap the hindwings. This is the only species for which an internal sclerotized plate is known in females. Males have no pronotal bristles and unfused eighth tergum and sternum—a combination unique among North American species. The *B. reductus* group is the only group of *Boreus* with no median ocellus. The ninth tergal hood is distinctive in having a medial point.

The nearest relatives of this species are found in the Old World, from the Crimea to the Pacific Ocean. Whether *B. reductus* is an early relic of this group in the Nearctic Region, or has more recently moved back into this region, cannot be determined at this time.

KEY TO MALES OF PALEARCTIC *Boreus*

1. Bristles present on margins of pronotum .... *beybienkoi*
   No bristles present on pronotum 2
2. Transverse ridge on second abdominal tergum 3
   No transverse ridge on second abdominal tergum 6
3. Ridge on second abdominal tergum divided medially .... *kratochvili*
   Ridge not divided medially 4
4. Occiput smooth .... *hyemalis*
   Occiput rugulose 5
5. Transverse ridge on third abdominal tergum .... *westwoodi*
   Tubercle on third abdominal tergum .... *lokayi*
6. Tergal hood present on ninth abdominal segment 7
   No tergal hood on ninth abdominal segment .... *chadzhigireji*
7. Symmetrical points on either side of midline of margin of hood .... *vlasovi*

Medial point on margin of ninth tergal hood 8

8. Medial point of tergal hood acute .... *semenovi*

Medial point of tergal hood smoothly rounded apically .... *orientalis*

No males are known for *sjoestedti* and *navasi.*

Key to Females of Palearctic *Boreus*

1. Bristles present on margins of pronotum .... *beybienkoi*

No bristles present on pronotum 2

2. Forewings not covering hindwings 3

Forewings covering hindwings 4

3. Forewings similar in shape to hindwings .... *navasi*

Forewings longer and broader than hindwings .... *chadzhigireji*

4. Cerci evenly tapering to a point 5

Cerci narrowing abruptly at mid-length .... *vlasovi*

5. Known distribution—Europe 6

Known distribution—eastern Asia 8

6. Occiput smooth .... *hyemalis*

Occiput finely reticulated 7

7. Known distribution—mainly northern Europe .... *westwoodi*

Known distribution—the Balkan Peninsula .... *lokayi*

8. Known distribution—Kamtchatka Peninsula .... *sjoestedti*

Known distribution—Asian continent proper .... *semenovi and orientalis*

No females are known for *kratochvili.*

SPECIES DESCRIPTIONS

Boreus beybienkoi Tarbinsky

Boreus bey-bienkoi Tarbinsky, 1962, Sbornik Entomologicheskikh Rabot. Akademiia Nauk Kirgizsk 1:134-135.

Holotype, allotype, and all paratypes in Tarbinsky's collection.

The following is a translation by Mr. Christopher Starr of Tarbinsky's original description:

"Males smaller than females. Body short. Length of body 2.75 mm. Color of body black, short with metallic bronze. Pleura of thorax (episterna and epimera) and coxae of middle and hind legs dull. Entire body covered by short white setae. An especially heavy pubescence visible on abdomen, front coxae and base of rostrum. Abdomen wide. Legs long, forelegs shorter than middle legs, middle legs shorter than hind legs, hind legs more than twice as long as body. To transverse ridges. Antennae 21-segmented. Basal segment of antennae wide, second segment thick and round-oblong, apical segments almost twice as short as segments placed closer to base. Two pairs of wings. Forewings not bent hook-like, held straight along body. Setae along edges of forewings somewhat bent, and at ends directed toward wingtip. Forewings comparatively narrow at base, 0.25 mm; length of wing, including terminal spine 1.45 mm; terminal spine 0.2 mm. Length of wing almost six times greater than width at base. Forewings long (relative to length of body), with terminal spines, reaching to sixth abdominal segment. Along front and hind edge wings are covered by long spines, the longest of them shorter than terminal spine, placed at tip of wing. In middle part of wing all spines comparatively equal in length; shorter ones placed nearer to base of wing, but longer ones near tip of wing. Spines placed along front edge of wing began somewhat nearer to base of wing than spines along hind edge of wing. All spines evenly spaced. On dorsal surface of wings close to base up to 3 long bristles; entire wings covered by sparse but clearly visible hairs. Bases of wings brown, remaining parts black. Second pair of wings even more modified and in this species very thin, long and toward tip strongly curved in pincer-like form. Width of wing at base 0.15 mm.; length 1.05 mm. When extended, small spines visible from below in middle part of hindwings, but on inner edge in curved part of wing a fringe of very small setae. Hindwings brown. Pronotum short; along front edge of it 4 bristles placed in pairs, also some bristles on hind legs.

"No tergal ridges on dorsal side of second and third terga. Ninth tergum short; on top a comparatively deep and broad cavity. Caudal apex of tergal hood rounded off, blunt, and densely covered with short, thick, blunt setae on each side. Above base of cavity, covering it (when examined from above), rises up a small, triangular plate which fuses at its base with middle of tergum. Ninth sternum (subgenital plate) with detached apical part and obtuse engraving along apical edge. Lateral edges of sternum with visible cavities. In its total form ninth sternum similar to that of *B. chadzhigireji* Plig., differing from it by wider apical part and cavity along front edge. Length of ninth sternum along mid-line 0.65 mm. Gonocoxites massive, with wide tips, their bases with rather long end; diststyles with wide base, their width being from claw on inner side to lower edge of base. Apical part of diststyles terminates in massive and comparatively short claw. Cavity between base of apical claw and claw on inner side of diststyles is uniformly deep; edge of cavity covered with short, easily visible denticles. Claw on inner side of diststyles blunt with shovel-shaped broadened upper part.

"Females larger than males. Length of body, including ovipositor, 3.16 to 3.6 mm. Eighth tergum very large, one side making blunt angle with rounded tip. Ninth segment comparatively short and wide. Tenth segment short and thick; when examined from above greatest width in middle, visibly narrowed toward tip and base. Twelfth segment wide at base with detached, bluntly cut off tip. Valves of ovipositor (eighth segment) with wide base. Distal ends of valves separate near small angle, but at base of them small cavity visible. From below, distal end of valves covered with strong, short spines, tips of which are directed toward base of valves.

"Examined material: northern slope of Kirghiz Ala-Tau range (Fig. 78), low hills-foothills (the massif Paspeldik); 9 Dec. 1957, 2 males; 5 Jan. 1958, 16 males, 12 females; 4 Feb. 1960, 45 males, 40 females. Author's collections."

This species can be separated from all other Palearctic boreids by the presence of spines on the pronotum. For this reason *B. beybienkoi* apparently is a member of the *nivoriundus* group. The description indicates that the male ninth sternum (hypandrium) and uncurved wings are markedly different from those of other species, and may also be diagnostic characters. However, further description and illustration of these structures is needed for clarity.

Boreus chadzhigireji Pliginsky

Boreus chadzhi-gireji Pliginsky, 1914, Revue Russe d'Entomologie 14:366-367, figs. 9-13.

The two female types from Sevastopol and Simferol, and 1 male, 2 females from Eupatoria, all in Pliginsky's private collection have probably been lost (Martynova, 1954). Four males and 12 females from Eupatoria are in the collection of the Zoological Museum, Academy of Science, Leningrad.

Following is Esben-Petersen's (1921) translation of the original Russian description, followed by my translation of the German summary:

"Female shining; dark greenish metallic coloured or partly purplish shining. Rostrum yellowish-brown, darker at the tip. Palpi blackish. Eyes elliptical, yellowish. Head between the eyes evenly punctuate. Antennae 19-jointed, blackish; 1st joint large and robust; 2nd globular, half as broad as 1st, and twice as long as broad; 3rd joint small, cylindrical, half as broad as 2nd, and twice as long as broad; 4th joint longer than 3rd; 5th-10th long, cylindrical. 11th-18th cylindrical, somewhat longer than broad; 19th joint elliptical; all the joints clothed with very short blackish and whitish hairs. Prothorax as long as broad, narrowed in front, and finely rugosed transversely. Mesothorax as broad as hind margin of prothorax, with parallel lateral margins and somewhat incised posterior margin. Metathorax broad, with a semi-lunar incision posteriorly and with a transversely placed groove in its centre. Wings yellowish; forewings oblong and punctuate; hindwings have the shape of small narrow plates. Abdomen evenly clothed with short whitish hairs, transversely rugose. Ovipositor almost straight. Legs slender, yellowish, whitish haired; tarsi somewhat darker.

"Length: 3 mm.; breadth: 0.75 mm.

"Male. The male only differs from that of *B. navasi* in possessing 19-jointed antennae.

"The female of this species is separated from the other species of the genus by a completely straight ovipositor and through the appearance of the forewings, which are strongly elongate and comparatively large. The male is distinguished from *B. navasi* only by its 19-segmented antennae.

"The area around Sevastopol and Simferopol, 2 females in my collection; Eupatoria, 5 males and 14 females in the collection of the Zoological Museum of the Academy of Science and in my collection."

In addition to this description, further characters can be mentioned (Martynova, 1954). In the male, the eighth tergum and sternum are not fused, the ninth tergum and sternum are fused, and the ninth sternum does not taper evenly to the apex, but narrows rather abruptly at mid-length, as in *reductus*, ending in a square-tipped apex. The female tenth tergum is relatively short, but no ovipositor-to-rostrum ratio is available. There are no caudal extensions of the female tenth segment below the cerci, and cerci narrow rather sharply, as in *vlasovi*. Spines are present only on the apical one-third of the hypovalves.

Pliginsky made no mention of abdominal tergal ridges, and Martynova stated that they were almost absent. Because this species appears to be a part of the *reductus* group, having fused ninth tergum and sternum, I am inclined to think that it has no tergal ridges.

From Martynova's illustration it appears that males of *B. chadzhigireji* have no tergal hood. However, the absence of pronotal bristles, fusion of ninth tergum and sternum, and shortening of female forewings are traits which I feel are derived, and evolved after development of the tergal hood. Therefore, Martynova's illustration is probably incomplete; I suspect that this species does have a tergal hood that extends to the middle of the denticular areas.

The three localities of Sevastopol (44° 36′ N, 33°32′ E), Simferopol (44° 57′ N, 34°06′ E), and Eupatoria (Yeupatoriya) (45°12′ N, 33°22′ E) are all located near the southern and western coast of the Crimean Peninsula of the U.S.S.R. in an outlying range of the Caucasus Mountains (Fig. 78).

Martynova (loc. cit.) recorded the dates of collection of the type material from Eupatoria as 10 July 1905 and 18 Nov. 1905—3 Jan. 1906. The July record seems unusual, and perhaps was misread or misprinted, although there have also been reports of collections of *B. brumalis, hyemalis,* and *nivoriundus* from mid-summer.

Females of *B. chadzhigireji* are unusual in not having oval forewings covering the hindwings like most boreids, nor forewings reduced to small vestiges like *reductus* and *navasi,* but rather intermediate forewings that are small enough not to cover hindwings, but large enough to form an elongate wing pad. Males may be identified by the sharply narrowing ninth sternum.

Boreus hyemalis (Linnaeus)

Panorpa hyemalis Linnaeus, 1767, Systema Naturae 1:915. 12th edition.

Gryllus proboscideus Panzer, 1796, Faunae insectorum Germanicae initia 27:18.

Bittacus hiemalis (Linnaeus) Latreille, 1805, Histoire Naturelle générale et particulière des Crustacés et des Insectes 13:20.

Boreus hyemalis (Linnaeus) Latreille, 1816, Nouveau Dictionnaire d'Histoire Naturelle 4:152-153.

Boreus hiemalis (Linnaeus) Latreille, 1817, Le Regne Animal 3:433-434.

Ateleptera hiemalis (Linnaeus) Dalman. Analecta Entomologica p. 34. (1823)

Boreus gigas Brauer, 1876, Festschrift der K. K. zool.—bot. Gesellschaft in Wien, pp. 263-300. Nomen nudum.

Whereabouts of type specimens unknown.

Present description based on 8 males, 8 females in alcohol.

HEAD: Dark brown shading to yellowish-brown on rostrum. Occiput smooth with numerous small setae. Median ocellus present, light brown. Antenna light brown basally, dark brown apically, with 20 to 21 flagellomeres. Many light setae on rostrum close to antennal bases, few setae over rest of rostrum. Ratio of length of maxillolabial complex to rostrum = .89.

THORAX: Dark brown. Indistinct transverse ridge on pronotum at mid-length; no pronotal bristles.

LEGS: Yellowish-brown with dark brown setae. Apical femoral spine present. Tibial spurs light brown.

MALE WINGS: Light brown, abruptly narrowed at mid-length, with 22 inner and 8 to 10 outer forewing spines, no hindwing spines.

FEMALE FOREWING: Yellowish-brown, oval; covering hindwing.

MALE ABDOMEN: Dark brown except yellowish-brown on ninth abdominal segment, basistyles, and dististyles. Transverse ridge on second tergum tilted anteriorly. Lateral margin of ridge with dorsal lobes. Tergal ridge of third segment reduced to rugulose area or smaller ridge with dorso-lateral lobes. Eighth tergum and sternum fused. Ninth tergum and sternum not fused. Large hood of ninth tergum extending laterally to lateral edges of denticular areas. Median septum of hood long, narrow. About 20 denticles on each side of septum very sharply tipped, more like spines. About 17 spines along anterior margin of dististyle from below basal lobe to base of dististylar claw; basal lobe sharp-tipped with cleft between lobe and rest of dististyle. Ninth sternum smoothly rounded at apex, reaching bases of dististyles.

FEMALE ABDOMEN: Dark brown except yellowish-brown on last 4 visible segments. Ratio of length of ovipositor to rostrum = 1.14. Cerci yellowish-brown, evenly tapering to apex.

BODY LENGTH: Male, 2.7 to 3.5 mm., in alcohol; female, 3.8 to 4.5 mm., in alcohol.

INTERSPECIFIC VARIATION: I have seen some German specimens with light brown coloration. The most important variation is in the shape of the ridges of the second and third abdominal terga, which sometimes have no lobes. The shape of the ridges has been used to distinguish species of the *hyemalis* group.

B. hyemalis has been collected from many localities (Fig. 81) in: Austria, Belgium, Czechoslovakia, Denmark, France, Germany, Great Britain, Italy, the Netherlands, Norway, Poland, Rumania, Sweden, and Switzerland.

Specimens have been collected from 7 Sept. to 13 April in Norway. The adult emergence period appears to be shorter than that farther south. One Dutch specimen was supposedly collected on 22 June.

This species has been collected at 1400 m. in Norway to 2000 m. in the Alps of southern France and northern Italy to 2500 m. in the French Pyrenees, but also has been collected near sea level of the Netherlands and Belgium.

B. hyemalis is the typical member of the *hyemalis* group, having abdominal tergal ridges in the male. Of the other species in this group, *B. kratochvili* has a forked ridge on the second abdominal tergum, *westwoodi* has a ridge on the third abdominal tergum with no lateral lobes, and *lokayi* has a tubercle in place of the tergal ridge on the third abdominal tergum. Because of the variation noted in the ridge of the third abdominal tergum of *B. hyemalis,* this character may be unreliable in taxonomy. Meinander (1962) and others have noted that *hyemalis* has a smooth occiput with scattered setal pits, while *westwoodi* and *lokayi* have a rugulose occiput. In the admittedly inadequate amount of material I studied, the third abdominal tergum was variable and differences in smoothness of the occiput hard to detect. It is my impression that with further study of a larger number of specimens, *B. kratochvili, lokayi,* and *westwoodi* will be synonymized.

Boreus kratochvili Mayer

Boreus kratochvili Mayer, 1938, Entomologicke listy 1:132, Figs. 3, 6, 9, 12, 15, 18, 24.

Location of type specimens unknown.

The following is my translation of the summary of Mayer's (1938) original description:

"Large like *Boreus hyemalis* (male 2.5-3.5 mm.).

"Body pitch black with metallic blue reflections. Rostrum, antennae, palpi, second and third thoracic segments, legs, wings, and genital appendages brown (like *Boreus hyemalis* L.).

"Head: Surface very weakly wrinkled (high magnification!), without large pits. Antennae: male with 25 segments; the 2 basal segments and the whole distal half dark. The first antennal segment is stout, somewhat smaller on the distal end. The second segment is broader in the middle than at the base and at the distal end; maximal breadth to length 1:1.5. Third and fourth antennal segments very short, the fifth through twelfth elongate to the distal end. From the thirteenth segment on, they are shortened again.

"The second pair of mandibles brown, like *Boreus hyemalis.* Lacinia has on the base only nine, stout, dark brown bristles that sit on wider rings. On the distal end of the lacinia is a brush of long, whitish hairs.

"The first thoracic segment is very dark, almost black, clearly cross-furrowed. The underside of the forewing has two rows of stouter, short, nearly black bristles; the outer row consists of 11 (5+1+1+3+1) bristles. On the end the first pair of wings terminates in a long, black spine.

"The second abdominal tergum bears before the hind margin a stout, somewhat foreward-bent ridge, that terminates on both sides in sharp points, but in the middle is cut strongly in V-shape. For this reason the male of this species is conspicuously distinguished from the other males of this genus. On the third tergum is a much smaller ridge, that resembles the form of a single specimen of *Boreus hyemalis;* on the upper margin it is again pointed and weakly squared on the side.

"The subgenital plate brown, like *Boreus hyemalis;* base to height 1:43:1, the end (from only 2 males) appears to be somewhat rounded.

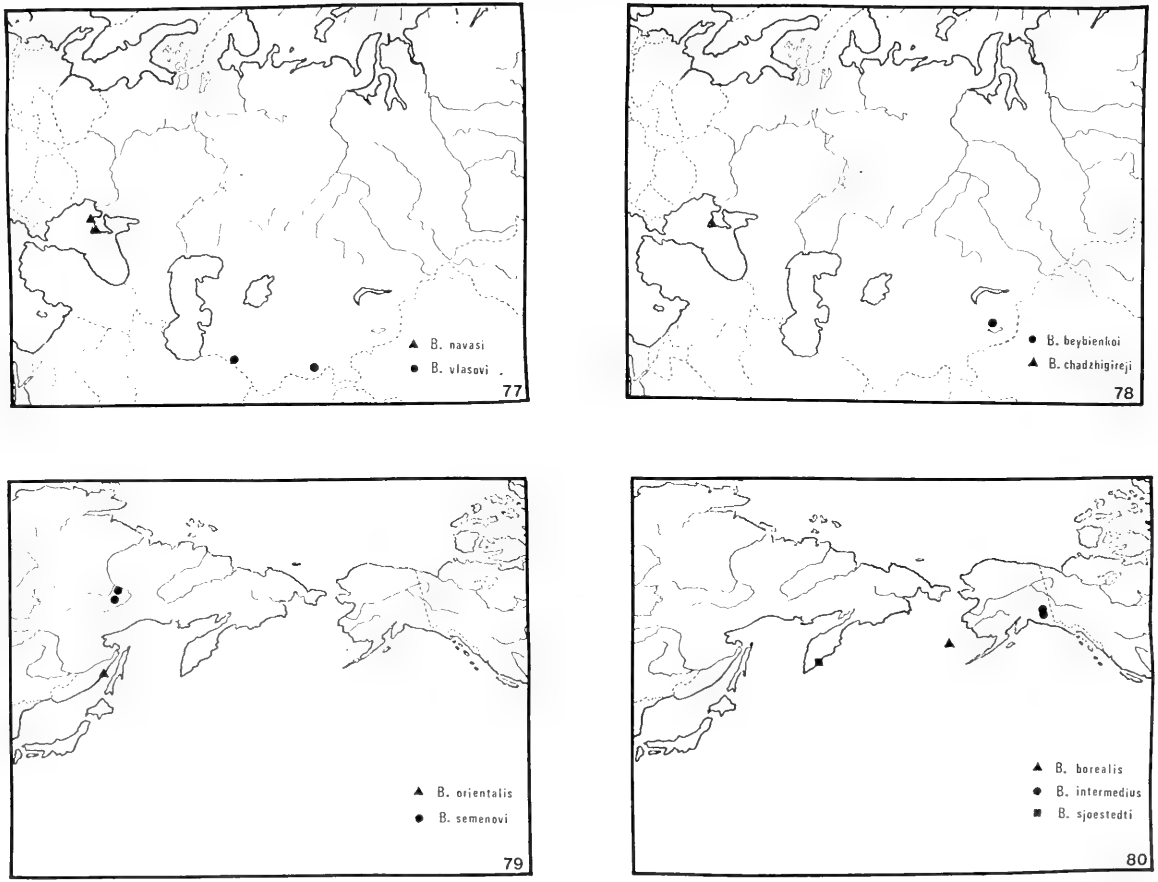
"The genital appendages are stout, two-branched; the upper branch is bent-hook-shaped and the second shortened; both are dark brown.

"The tongue-shaped extension of the ninth episclerite brown, strongly chitinized, filled with long bristles, ending in a rather high, colorless, compact cone. Base to height 1.8:1.

"Female unknown.

"This species has until now only been collected from three localities in the vicinity of Brno together with *Boreus hyemalis* L."

Little is known about this species. Lestage (1941) illustrated the second abdomi-



FIGURES 77-80. Fig. 77, distribution of *Boreus navasi* and *B. vlasovi*. Fig. 78, distribution of *Boreus beybienkoi* and *B. chadzhigireji*. Fig. 79, distribution of *Boreus orientalis* and *B. semenovi*. Fig. 80, distribution of *Boreus borealis*, *B. intermedius*, and *B. sjoestedti*.

nal tergum of the male as having a bipartite ridge, which would indicate that *kratochvili* is a member of the *hyemalis* group. This character state also distinguishes it from all other members of the group.

This species has been collected only in association with *hyemalis,* and therefore its validity comes into question. Although the ridge of the third abdominal tergum of *hyemalis* varies considerably, the ridge of the second abdominal tergum appears to be fairly constant.

No females are known, but this is not surprising because females of the *hyemalis* group are difficult to distinguish morphologically.

The only known specimens of *kratochvili* (3 males) were collected near Brno, Czechoslovakia (49°12′ N, 16°40′ E) (Fig. 82).

Boreus lokayi Klapálek

Boreus lokayi Klapálek, 1901, Rozpravy Ceská Akademie císare Frantiska Josefa pro Védy, slovesnost, a Umeni, Prague 10(21):1-19.

Location of type specimens unknown.

Present description based on 2 males, 1 female, pinned.

Head: Occiput dark brown, finely reticulated. Median ocellus present. Rostrum light brown basally, shading to yellowish-brown distally. Antenna light brown basally, dark brown distally, with 19 flagellomeres. Numerous setae below antennal bases, few setae on anterior and posterior surfaces of rostrum. Ratio of length of maxillo-labial complex to rostrum = .90.

Thorax: Light brown. Pronotum with indistinct transverse ridge at mid-length and no bristles along anterior and posterior margins. Meso- and metanota without bristles.

Legs: Yellowish-brown, with numerous setae and apical femoral spine. Tibial spurs light brown.

Male wings: Yellowish-brown, abruptly narrowed at mid-length, with about 25 inner and 8 to 10 outer forewing spines; 18 very small hindwing spines.

Female forewing: Yellowish-brown, oval; covering hindwing.

Male abdomen: Shiny dark brown except light brown on basistyles and yellowish-brown on dististyles. Ridge of second abdominal tergum large, with acute dorsolateral lobes, occasionally with two such lobes. Ridge of third abdominal tergum smaller than second, with a medial peak. Peak varies from indistinct to quite prominent tubercle. Eighth tergum and sternum fused. Ninth tergum and sternum unfused. Ninth tergum with large hood extending laterally to lateral margins of denticular areas. Medial septum narrow, short. About 35 acutely-tipped denticles on either side of mid-line. About 23 denticles arranged from near base of each dististyle to near base of dististyle to near base of dististylar claw. Ninth sternum broadly rounded apically, reaching bases of dististyles.

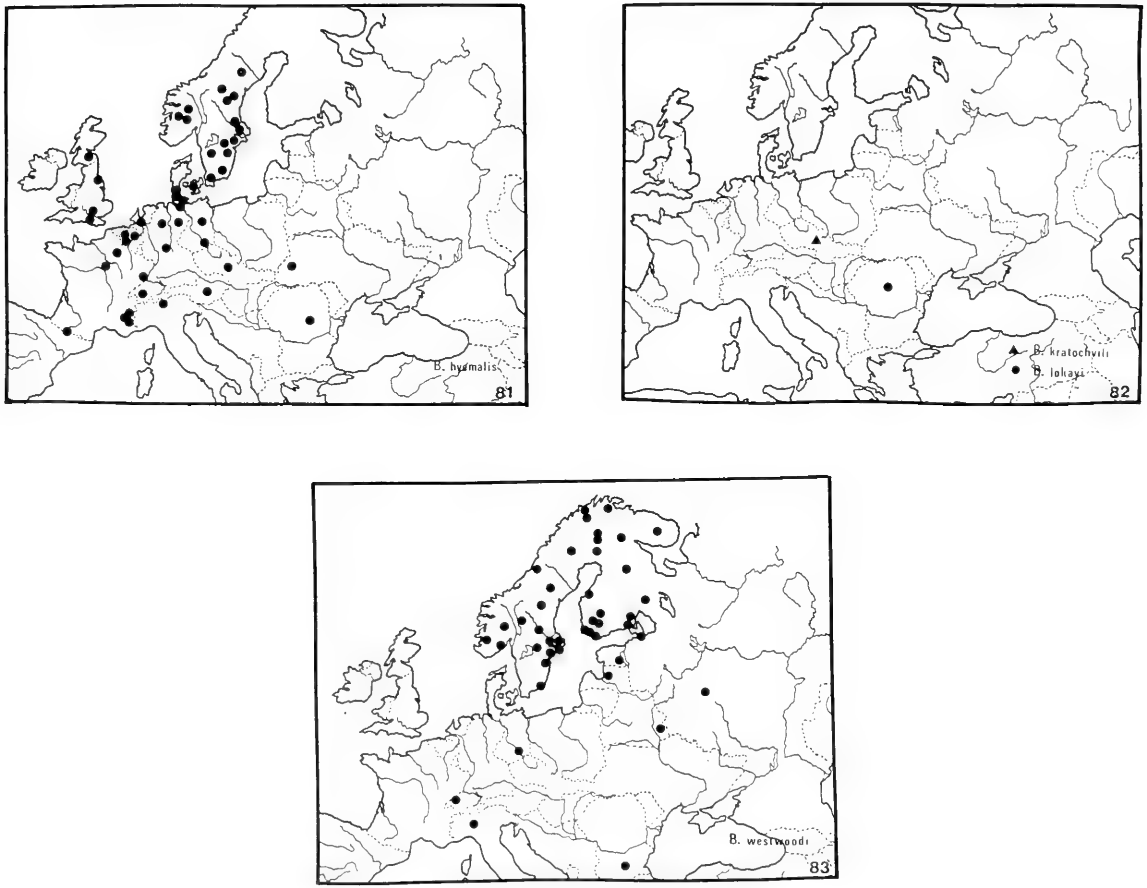
Female abdomen: Light brown. Ratio of length of ovipositor to rostrum = .66. Cerci light brown, evenly tapering to apex.

Body length: Male, about 3.2 to 3.9 mm., pinned; female, 4.1 mm., pinned.

Intraspecific variation: Even on opposite sides of the same ridge of the second abdominal tergum, the shapes differ from one to two acute lobes. The third tergum is peaked medially, but may or may not have a transverse ridge.

All three present specimens from Bucsecs, Transylvania (now Romania) (no date label). All known specimens of *B. lokayi* are from Bucsecs (Fig. 82) (see Cooper, 1972:280).

This species is very similar, if not identical, to *B. hyemalis.* However, I have not seen enough variation in the second and third tergal ridges of *B. hyemalis* to warrant synonymy at this time.



Figures 81-83. Fig. 81, distribution of *Boreus hyemalis*. Fig. 82, distribution of *Boreus kratochvili* and *B. lokayi*. Fig. 83, distribution of *B. westwoodi*.

Boreus navasi Pliginsky

Boreus navasi Pliginsky, 1914, Revue Russe d'Entomologie 14:364-366, Figs. 1-8.

Boreus aktijari Pliginsky, 1914, Revue Russe d'Entomologie 14:367, Fig. 14. New synonymy.

Syntypes (3 males, 1 female) of *navasi* and holotype female of *aktijari* in Pliginsky's private collection. According to Martynova (1954) these type specimens have not been preserved. They are the only known specimens.

I repeat here the translation of the original Russian description of *navasi* appearing in Esben-Petersen (1921), followed by my translation of the German summary.

"Dark-green, almost black, metallic shining. Rostrum yellowish, darker towards apex. First joint of palpi brownish yellow, the remainder blackish. Eyes elliptical, yellowish. Antennae 20-segmented, blackish and clothed with whitish hairs; basal joint robust, as long as broad; second joint somewhat longer than broad; third joint oblong, half as broad as second; 4th-8th cylindrical, twice as long as broad; 9th-11th somewhat stouter and shorter than 8th; 11th-19th somewhat longer than broad; 20th joint elliptical. Prothorax narrowed in front, blackish and coarsely striated transversely; in the male sex the hind part of prothorax is brownish yellow. Mesothorax broad, trapezoidal, punctuated and not so coarsely striated transversely as the prothorax; in the centre a transversely placed groove. Metathorax broader and shorter than the mesothorax, with a transversely placed groove in its centre and with a deep semi-lunar incision posteriorly. Abdomen black, greenish metallic shining and finely rugosed transversely; in the male sex the abdomen is clothed with short white hairs; in the female sex it is naked. Legs tiny, yellowish; tarsi blackish.

"Male. Wings yellowish, reaching the third abdominal segment. Forewing curved, darker at apex, shining, punctate, and finely rugose and haired dorsally; coarsely haired ventrally. Hindwings narrower and shorter than forewings; densely haired ventrally. Hindwings narrower and shorter than forewings; densely haired ventrally. Tip of the wings with a claw-like prolongation. No elevations on second and third abdominal segments. Subgenital plate brownish yellow, very thin, punctuated downwardly and finely haired. The plate narrowly incised laterally.

"Length: 2.5 mm.; breadth: 1 mm.

"Female. Forewings very small; hindwings have the shape of very small and narrow plates. All the wings yellowish coloured. Ovipositor blackish, curved.

"Length including the ovipositor: 3 mm.; breadth: 0.75 mm.

"The female of this species is differentiated from all presently known species by the tiny forewings and through the appearance of the ovipositor which is bent under at a nearly straight angle.

"The area around Sevastopol (Fig. 77), 20 Dec. 1913, 3 males and 1 female in my collection."

Mountains near Sevastopol (44°36′ N, 33°32′ E) are a part of the Caucasus Range in the Crimea of southern U.S.S.R.

Pliginsky separated *aktijari* from *navasi* on the basis of *aktijari's* 19-segmented antennae, rounded female forewings, lack of fine abdominal striations, and angle of depression of the cerci. *B. reductus* has antennae which vary from 19 to 20 segments, and Cooper (1974) has found antennal segments to vary from 18 to 20 in *H. notoperates,* pointing out the questionableness of making distinctions on this basis. Fine abdominal striations and depression of the cerci, which Pliginsky identifies as the ovipositor, are not useful taxonomic characters due to variation in both. As can be seen in Pliginsky's Figures 6 and 14, the shape of the female forewings is almost identical. In addition, both nominal species have been collected only in the vicinity of Sevastopol. Because there are no type specimens, and because of lack of useful distinguishing character states, any future collections could be placed in either species with equal facility. Therefore, I feel that *aktijari* is a junior synonym of *navasi*.

The original description is very poor, but if other specimens are collected, the females should be immediately recognized by the low number of antennal segments and very reduced wings, as in *reductus* of North America.

Boreus orientalis Martynova

Boreus orientalis Martynova, 1954, Trudy Zoologicheskii institut, Akademia nauk S.S.S.R., Moscow 15:65, Figs. 6, 11, 15, 20, 24, 27.

Types in the collection of the Zoological Museum, Academy of Science, Leningrad.

The following is a translation by Christopher Starr of Martynova's original description:

"Male. Front wing a little shorter than in *B. semenovi* Plig., but with base of same width; length of wing, including terminal spine, 1.4 mm.; along front edge of wing, spines begin a little closer to base and end a little closer to tip than along hind edge of wing; spines uniformly spaced. No tergal ridges on dorsal side of second and third terga. Ninth tergum almost trapezoidal; at base almost same width as at tip; tip truncated, as in *B. semenovi* Plig., divided into two blades, forming somewhat shorter slit; base of slit placed in depression, over which is small hood, as in *B. semenovi* Plig., but of somewhat different form; base of hood without cavity, projection on distal side of it very gently sloping and cavities not as deep; ninth sternum (subgenital plate) very short, almost one-third the length in *B. semenovi* Plig., with very deep and wide cavity along top edge; gonocoxite with shorter and blunter base than in *B. semenovi* Plig., also with wedge-shaped, but shorter distal end and with less massive claw on inner side of dististyles.

"Female. Eighth tergum in form resembles eighth tergum of *B. semenovi* Plig., but outer corner of lateral line of it placed lower, therefore not in form of isosceles triangle; front edge of eighth sternum at base forms large projection, then sharply narrows and remains uniform width to the end; valves of ovipositor separate gradually, forming cavity; ninth segment of almost same form as in *B. semenovi* Plig.; tenth segment not as long, with deep cavity on dorsal side of distal end; this cavity in form similar to that of *B. westwoodi* Hag., but longer than latter; valves of ovipositor and first segment terminate at same level; twelfth segment in *B. semenovi* Plig. and *B. orientalis* sp. n. alike, but in *B. orientalis* lower side with two shallow cavities.

"Examined material: Sovetskaya Harbor, Maritime Provinces (Fig. 79), 29 VIII-1 IX 1908, 1 male, 1 female (types), on outdoor woodpile (ZIN collection).

"Both east-Siberian species closely related, though also quite sharply different, one from the other."

There is no twelfth segment in female *Boreus;* Martynova was probably referring to the cerci.

The tergal hood has a medial point, which is not as acute as in *B. semenovi*. The male ninth sternum appears to be extremely short, perhaps being broken off.

Martynova's Figure 6 shows the male *B. orientalis* with fused eighth tergum and sternum, and ninth tergum and sternum. Because fusion of the ninth tergum and sternum and presence of a medial point on the tergal hood are only known in the *reductus* group, the eighth tergum and sternum are likely unfused.

If *B. orientalis* has unfused eighth tergum and sternum, it is in the *reductus* group, and can be separated from other eastern Asiatic species by the less acute angle of the medial point of the hood. At this time the female cannot be definitely separated from *B. semenovi* and *sjoestedti.*

Sovetskaya Harbor (48°58′ N, 140°18′ E) is in the Tatarskiy Proliv between the Sea of Japan and the Sea of Okhotsk.

Boreus semenovi Pliginsky

Boreus semenovi Pliginsky, 1930, Revue Russe d'Entomologie 24: 230-231.

Holotype male in collection of Academy of Sciences Museum, Leningrad.

I present here my translation of Lestage's (1941) French translation of Pliginsky's original Russian description of *B. semenovi.*

"Male. Black with slight purplish reflections. Head metallic green, smooth above, save some points between the eyes. Frons smooth. Eyes large, elliptical. Rostrum and palps yellow-brown. Antennae brown-black, with 24 segments.

"Wings I yellow, sclerotized, punctuated, wrinkled, with little black spines on the borders, enlarged basally, narrowed at the apex, which terminates in a point, triangular seen from above, gradually narrowed, without lateral sinuousity, covered with a yellow pubescence directed backwards.

"Wings II forming yellow, narrow lances.

"Abdomen laterally reddish; terga smooth and without ridges; sides near the edges with dark hairs; sterna covered with whitish hairs.

"Ninth sternum very convex, conical, tapered caudally, its extremity slightly notched. Apex of gonopods acuminate and black. Femur I relatively thin. All legs clear brown.

"Length: 4 mm.

"Distribution. Russia, Aian-Nelkansk Expedition, 62nd kilometer."

Illustrations from Martynova (1954) give additional information about this species. Male with 10 inner and 14 outer forewing spines. Male eighth tergum and sternum unfused, ninth tergum and sternum fused. Ninth tergum with hood extending laterally to middles of denticular areas. Margin of tergal hood produced into a caudally directed, medial projection. Female eighth sternum with spines on apical one-third of hypovalves. Tenth segment long, but ratio of length of ovipositor to rostrum not available. Tenth segment may have short caudal extensions below cerci. Cerci tapering evenly to apex.

The holotype was collected in U.S.S.R.: Yakut S.S.R., Jakoti, on 20. IV. 1903. The specimen was collected by the Aian-Nelkansk Expedition on the slopes of the Oijski Mountain Range between the Lena and Aldan Rivers. Neither the locality nor the mountain range can be found on available maps. However, the collection was probably made somewhere along the track that leads from Ayan (56°27′ N, 138°10′ E) to Nel'kan (57°40′ N, 136°13′ E) to Yakutsk (62°00′ N, 129°40′ E).

One other collection of 7 males, 1 female was made in 1926 at the confluence of the Tumpsu and Aldan Rivers (Fig. 79), Yakut S.S.R. The Tumpsu River cannot be located on available maps either.

This species appears to belong to the *reductus* group, and males can be separated from other Asiatic members of this group by the medial projection of the hood, as in the North American *reductus.* Females cannot be distinguished at this time.

Boreus sjoestedti Navás

Boreus sjöstedti Navás, 1925, Arkiv för Zoologi 18B(2):3-4, Fig. 2.

Holotype female in Naturhistoriska Riksmuseet, Stockholm, Sweden.

Present description based on original description and unpublished notes on the type specimen by George W. Byers.

Head: Black shading to brown on rostrum. Occiput with fine surface sculpturing and setal pits. Antenna brown, with 18 flagellomeres. Rostrum with many whitish setae at antennal bases, few setae elsewhere on rostrum. Ratio of length of maxillo-labial complex to rostrum = .81.

THORAX: Black. Pronotum with indistinct transverse ridge at mid-length, anterior and posterior margins without bristles, finely striated.

LEGS: Brownish.

FEMALE FOREWING: Brownish, oval; covering hindwing.

FEMALE ABDOMEN: Shiny black with short setae along caudal margins of terga and over all of sterna. Ratio of length of ovipositor to rostrum = 1.14.

BODY LENGTH: Female, 4.9 mm., pinned.

Holotype female (and only known specimen) from Achomten Bay (Bukhta Akhomten: 52°26′ N, 158°30′ E3, Kamtchatka Peninsula, U.S.S.R.

This specimen was collected on 12 June 1925 by R. Malaise. Although this summer collection date seems late, specimens of *borealis* from the Bering Sea area have been collected at a similar date, and there are a few scattered collections of other species at this time of year.

Achomten Bay is a small, uninhabited inlet in Kamtchatka (Fig. 80), 42 miles south of Petropavlovsk, with 7000-foot-high Sopka Mutnaya volcano of the Kamchatka-Kuril Range rising steeply to the west.

This female specimen is very similar to other eastern Asiatic and Alaskan specimens of other species, allowing no easy differentiation. Navás gave no useful characters for separating this from other species. However, since this is the only species described within a radius of 820 miles, it may well be a valid species and more male specimens from the Kamtchatka Peninsula may give us additional characters for this species. Martynova (1954) did not include this species in her monograph of Boreidae of the U.S.S.R.

Boreus vlasovi Martynova

Boreus vlasovi Martynova, 1954, Trudy Zoologicheskii institut, Akademiia nauk S.S.S.R., Moscow 15:61-62, Figs. 4, 9, 13, 18, 22, 26.

Whereabouts of type specimens unknown.

Present description based on 7 males, 2 females in alcohol.

HEAD: Dark brown. Occiput rugulose with many white setae. Median ocellus absent. Antenna dark brown, with 16 to 17 flagellomeres. Many long setae near antennal bases of rostrum; few setae over rest of rostrum. Ratio of length of maxillo-labial complex to rostrum = 1.00.

THORAX: Dark brown. No transverse ridge at mid-length or marginal bristles on pronotum.

LEGS: Dark brown with light-colored and dark brown setae. Apical femoral spine absent. Tibial spurs dark brown.

MALE WINGS: Light brown, abruptly narrowed at mid-length, with 15 inner and 11 to 12 outer forewing spines, 3 to 4 hindwing spines.

FEMALE FOREWING: Light brown, oval, short, reaching only middle of metanotum, barely covering hindwing vestiges, with many whitish setae.

MALE ABDOMEN: Dark brown throughout. No tergal ridges on second and third segments. No fusion of eighth tergum and sternum, but ninth tergum and sternum fused in many cases. Ninth tergum with hood extending laterally to middles of denticular areas. Margin of hood produced caudally on either side of mid-line. Small median septum of hood present. About 20 denticles on each side. Dististyle with about 15 denticles arranged from below basal lobe to base of dististylar claw; basal lobe blunt-tipped, with cleft between it and rest of dististyle. Ninth sternum smoothly rounded apically, reaching bases of dististyles.

Female abdomen: Dark brown. Ratio of length of ovipositor to rostrum = .93. Cerci dark brown, not evenly tapering to point, but sharply pointed at apex; fused.

Body length: Male, 2.3 to 4.1 mm., in alcohol; female, 3.6 to 4.0 mm., in alcohol.

Intraspecific variation: One male was noted to have two spines at apex of ninth sternum; normally this species has no spines on ninth sternum. The sharp projections of the caudal margin of the female eighth tergum, illustrated in Martynova's (1954) Figure 18, were not noted in specimens examined. Fusion of ninth tergum and sternum is complete in only about half the available specimens. (cf. Cooper, 1973).

Collections of this species are from (Fig. 77) Turkmen S.S.R., Ashkabad (37° 57′ N, 58°23′ E), 3 Jan. to 20 Feb. 1932, and 1935, 148 males and females; Tadzhik S.S.R., 30 km N of Stalinabad (Dushanbe), 1100 m (38°33′ N, 68°48′ E), 10 to 12 March 1943, 3 males, 3 females; and Turkmen S.S.R., Askhabad, Dec. 1955, 7 males, 2 females. There is 1 male in the Deutsches Entomologisches Institut, Berlin, which I did not examine.

This species is a member of the *reductus* group having no thoracic spines and unfused eighth tergum and sternum. Although other Asiatic species are poorly known, this species probably can be differentiated by the two caudal projections of the lip of the hood in males, and the sharply narrowed cerci in females.

Boreus westwoodi Hagen

Boreus westwoodi Hagen, 1866, Entomol. Monthly Mag. 3:132.

Boreus tarnanii Navás, 1911, Revue Russe d'Entomologie 11:277-278, Fig. 1.

Boreus boldyrevi Navás, 1911, Revue Russe d'Entomologie 11:278, Fig. 2.

Location of all type specimens unknown.

In the original description, Hagen gave no information on type locality, although he listed the distribution as Germany, Finland, and England. As currently delimited, *B. westwoodi* is a northern and alpine species, not found in England, as MacLachlan (1869) pointed out. However, since the types cannot be located, it is impossible to say whether the current *B. westwoodi* is the same one that Hagen envisioned, or even if it is a valid species.

Navás (1911) mentioned no repository of types of *boldyrevi* and *tarnaii* and they, too, cannot be located. However, the type localities are listed as "Russie, environs de Moscou" and "Pologne de la Russie: Novaja-Alexandria," respectively. Martynova (1954) considered both *boldyrevi* and *tarnanii* as synonyms of *westwoodi*, which is commonly collected in the vicinity of Moscow.

Present description based on 18 males, 14 females, pinned.

Head: Occiput black with fine reticulations. Rostrum yellowish-brown; fine setae on caudal surface, no stout setae. Median ocellus present between antennal lobes. Antenna light brown basally, becoming dark brown apically; with 21 to 23 flagellomeres. Ratio of length of maxillolabial complex to rostrum = .85.

Thorax: Dark brown. Indistinct transverse ridge at mid-length of pronotum; no pronotal bristles.

Legs: Yellowish. Apical femoral spine present, dark brown. Tibial spurs light brown.

Male wings: Yellowish-brown. Forewing abruptly narrowed at mid-length, with 26 to 29 inner and 6 to 9 outer forewing spines. Hindwing with ventral fringe of setae, no spines.

Female forewing: Yellowish, oval, covering hindwing.

Male abdomen: Dark brown, except yellowish-brown dististyles. Transverse ridge of second tergum with large dorso-lateral lobes. Ridge of third abdominal tergum prominent, without dorso-lateral lobes. Eighth tergum and sternum fused. Ninth tergum and sternum not fused. Ninth tergum with large hood extending laterally to lateral margins of denticular areas. Medial septum short, thin. Only about 16 sharp-tipped denticles on each side. Ninth sternum smoothly rounded apically, reaching bases of dististyles. Denticles on dististyle arranged from below basal lobe to base of dististylar claw. Cleft between basal lobe and rest of dististyle.

Female abdomen: Segments 1 to 8 dark brown, segments 9-10 and cerci yellowish-brown Ratio of length of ovipositor to rostrum = 1.41. Cerci evenly tapered to apex.

Body length: Male, 3.0 to 3.5 mm., pinned; female, 4.0 to 4.5 mm., pinned.

Intraspecific variation: There is some variation in number of antennal segments and male wing spines. Lestage (1941) inindicated variation in the male ridge of the third abdominal tergum.

Svensson (1972) listed the distribution of *westwoodi* as the following (Fig. 83): Bulgaria, Czechoslovakia, East Balticum, Finland, Germany, Italy, Norway, Poland, Sweden, Switzerland, and U.S.S.R.

This species has been frequently collected from November to April, with a few scattered records from June, September, and October.

B. westwoodi is a member of the *hyemalis* group, having tergal ridges. It can be separated from *hyemalis* by the fine reticulations on the occiput, from *kratochvili* by the unipartite second tergal ridge with dorso-lateral lobes, and from *lokayi* by the ridged third tergum (no tubercle).

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THE UNIVERSITY OF KANSAS
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COMPARATIVE ANATOMY OF CAECILIAN ANTERIOR VERTEBRAE

By

EDWARD H. TAYLOR

Vol. 51, No. 6, pp. 219-231 June 24, 1977

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Comparative Anatomy of Caecilian Anterior Vertebrae

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ABSTRACT

The limbless caecelian amphibians have vertebral adaptations for their burrowing habit and mode of life that suggest an evolutionary change of certain thoracic vertebrae to assist motile, cervical functions, despite retention of rudimentary ribs on them. The changes appear related to distinct stresses placed on the vertebrae by movements necessary to burrowing. Also, the changes are distinct enough to be taxonomically useful for potential distinction of genera and/or species in the several families of caecelians.

INTRODUCTION

All caecilians differ from other amphibians in lacking an appendicular skeleton. Thus, without this, we lack the usual criteria for classifying the vertebrae. It is generally agreed that there is but a single cervical vertebra, the atlas, in amphibians. Yet, in caecilians the anterior four or five vertebrae function together in critical pivoting movements of the cranium. These retain free ribs, but although loss or fusion are commonly accepted as prerequisite of cervical vertebrae, that criterion is not infallible, as for example in lizards and crocodilians wherein all vertebrae anterior to the first bearing a rib articulated with the sternum are accepted as cervicals despite the fact that one or more posterior cervicals bear free ribs. A more realistic criterion for cervicals in limbless tetrapods lacking a sternum is a functional one, wherein the most anterior trunk vertebrae that serve importantly in pivotal movements of the cranium are accepted as cervicals. Therefore, in this study all of the anterior four or five trunk vertebrae are regarded as cervicals.

In the evolution of animals, changes that occur in body characteristics are the result of a cause; otherwise we would have miracles! Usually, regions having the greatest stresses (as for example the pelvic region in frogs) tend to change most extensively, to varying degree. In burrowing forms lacking limbs, the head-and-neck region evidently is just such a region of stress. For example, should an animal such as a skink find it difficult to compete with other animals for accustomed food, it either becomes extinct or acquires an ability to augment the food supply from another source. A source often sought by such types of animals, is within a few inches of the accustomed habitat, but involves burrowing in the earth, where insects, insect larvae, worms, etc. are usually available. Animals adapting for exploitation of such food resources find limbs and digits actually a hindrance, particularly if the adaptation leads to the use of burrows for permanent habitat. Thus, in a number of cases, we find the digits are discarded one by one and finally the entire limb may be lost.

Animals having run the full gamut of such burrowing adaptation, with complete loss of limbs, of necessity will be forced to use the head or neck for burrowing if it continues its course of adaptation to that way of life. Perhaps at this point, most snake phylogenies parted company with other invaders of the burrowing adaptive zone, failing to evolve the subsequently essential perfections that more successful burrowers, such as the Scolecophidia, caecilians and amphisbaenids, have devised.

The present study is an attempt to determine whether support for this hypothesis may be evident in modifications, if any, that may have taken place in the anterior vertebrae of caecilians.

Unfortunately, a limited number of species has been available for examination. Thus, the number of samples I have used is far too small to justify generalizations about consistency of structure in orders or families or perhaps even in genera. However, one may reasonably presume that the differences pointed out are obvious from the illustrations and would be evident in other examples of comparable size and age.

I am not alone in considering generic and specific differences to exist in the contours of vertebrae. Recently, a single, small, broken vertebra found in Brasil served as the type for a new species and genus of fossil caecilians and led the describers to postulate a closer relationship with an African genus than with other American genera.

Such photographs as I have were prepared several years ago; but I was unable to obtain as much material for making skeletons as I desired and I withheld publication until now, hoping to acquire a more adequate representation of species.

ACKNOWLEDGMENTS

The following abbreviations are used: AMNH—American Museum of Natural History, New York, New York; ANSP—Academy of Natural Sciences, Philadelphia, Pennsylvania; DSBM—Division of Systematic Biology, Stanford University, California; EHT-HMS—Edward Taylor-Hobart M. Smith, Lawrence, Kansas; MCZ—Museum of Comparative Zoology, Harvard University; UIM—University of Illinois Museum of Natural History, Urbana, Illinois.

DESCRIPTIONS OF CERVICAL VERTEBRAE

Family Scolecomorphidae

Scolecomorphus kirkii Boulenger (Fig. 1). Upper portion of the first (atlas) vertebra very much longer than the ventral portion. No dorsal ridges evident on the vertebrae; ridges on ventral surfaces strongly marked, widening posteriorly, closely held by the anterior processes which are curved slightly inwardly.

Family Typhlonectidae

Typhlonectes natans (Fischer in Peters) (Fig. 2). Total length of atlas much greater than median ventral length. Dorsal

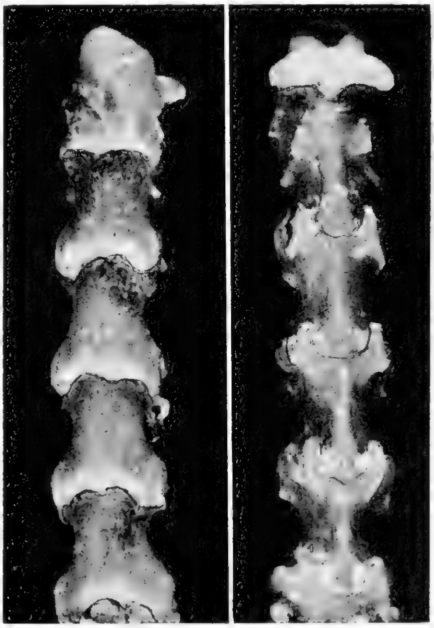

Fig. 1. *Scolecomorphus kirkii* Boulenger. MCZ 27106, Cholo Mountains, Malawi, Africa, "elev. 3600 ft." (see Table 4, U. Kan. Sci. Bull., vol. 48, p. 602). A, Dorsal view of 5 cervical vertebrae. B, Ventral view of same.

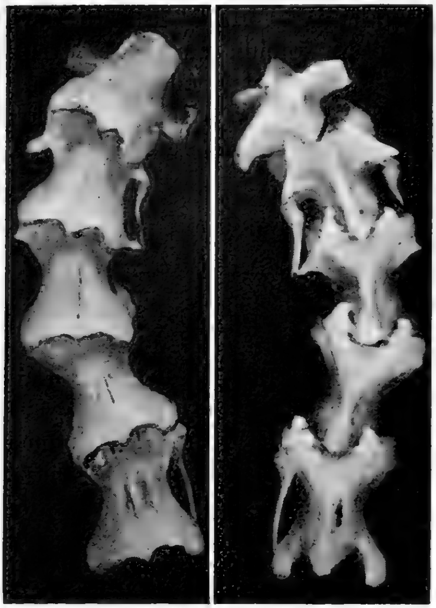

FIG. 2. *Typhlonectes natans* (Fischer in Peters). MCZ 24524, Río Magdalena, Cucutá, Colombia, South America. A, Dorsal view of 5 cervical vertebrae. B, Ventral view of same.

ridges not or scarcely indicated, but the third and fourth vertebrae each with weak, paramedian dorsal grooves, the fifth vertebra with two stronger parallel dorsal grooves. On the ventral surface the ventral ridge is somewhat curving or saddle-shaped. The fifth has a deep groove on each side of the ventral ridge. Ribs still remain on the second and fifth vertebrae. The anterior processes of the ventral part of each vertebra are moderately close to the preceding vertebra, and tend to curve in slightly.

FAMILY ICHTHYOPHIIDAE

Ichthyophis kohtaoensis Taylor (Fig. 3A, B; Fig. 4B, C). In Fig. 3, length of dorsal part of atlas 27 mm; length of ventral portion of axis 15 mm. Dorsal ridges very strong on second to fifth vertebrae; anterior processes of third vertebra grasping the ventral ridge of the preceding vertebra, those on the following two vertebrae curving inward around the posteriorly widened part of the ventral ridge of preceding vertebrae.

In Fig. 4, in ventral view, the processes directed forward on vertebrae four and five widely separated. A ventral ridge barely indicated on the fourth vertebra. In dorsal view, only a vague suggestion of a dorsal ridge. Four have ribs attached.

Ichthyophis beddomei Peters (Fig. 3C, D). Length of dorsal part of atlas much longer than ventral portion. The paired ventral processes extending forward from the third to the fifth vertebrae are nearly parallel, rather than curving inward. No dorsal ridges; strong ventral ridges, their posterior terminal portions widened. Two ribs attached.

Ichthyophis mindanaoensis Taylor (Fig. 4A). A dorsal view of four vertebrae, the posterior three with a very low dorsal ridge.

Caudacaecilia larutensis Taylor (Fig. 5A, B). Dorsal length of axis only a little longer than ventral length. A vague suggestion of dorsal ridges on vertebrae; well-defined ventral ridges widening posteriorly. Processes on rib attachment somewhat elongated anteriorly.

Caudacaecilia nigroflava Taylor (Fig. 5C, D). Dorsal length of axis only two or three mm greater than ventral length. Anteriorly directed ventral processes parallel.

FAMILY CAECILIIDAE

Oscaecilia bassleri (Dunn) (Fig. 6A, B). On five anterior vertebrae, the dorsal ridge is only vaguely indicated. Ventral ridge on vertebrae 2 and 4 relatively very narrow throughout most of its length, widening suddenly posteriorly. A pair of small projections from the forwardly directed processes seemingly serve as braces. They are directed inwardly and somewhat backward.

Oscaecilia ochrocephala (Cope) (Fig. 6C, D). Five anterior vertebrae with well-defined dorsal ridges. In ventral view, the

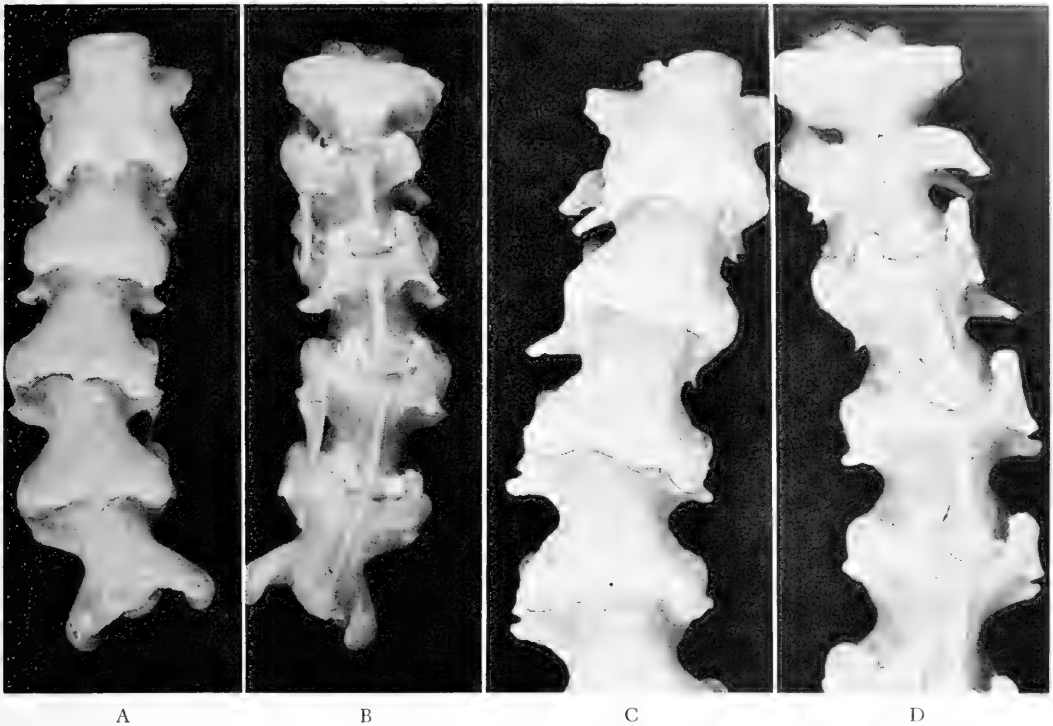

FIG. 3. A-B, *Ichthyophis kohtaoensis* Taylor. EHT-HMS 3935, 10 miles N Chiang Dao, northern Thailand. A, Dorsal view of 5 cervical vertebrae. B, Ventral view of same. C-D, *Ichthyophis beddomei* Peters. EHT-HMS 3186, Kotegehar, India. C, Dorsal view of 4 cervical vertebrae. D, Ventral view of same.

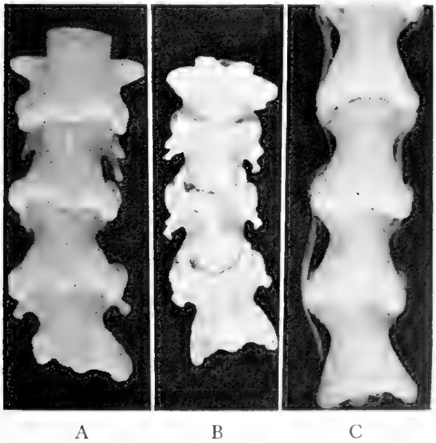

FIG. 4. A, *Ichthyophis mindanaoensis* Taylor. DSBM 20926, 11 km SE Buena Suerte, on side of Dapitán Peak, Mindanao, "elev. 3700 ft." Dorsal view of cervical vertebrae. B, *Ichthyophis kohtaoensis* Taylor. EHT-HMS 1838, Dansai Province, Thailand. Four cervical vertebrae, ventral view. C, *Ichthyophis kohtaoensis* Taylor. DSBM 25496, Kerala Forest, India. Body vertebrae, from near middle of body, dorsal view.

processes enclosing the preceding vertebra much thickened, slightly curving in. The ventral ridge sharply defined and strongly widened posteriorly, somewhat pointed terminally. The differences between the dorsal and ventral views of these two presumed species of the same genus is remarkably great.

Caecilia albiventris Daudin (Fig. 7A, B). Five anterior vertebrae, all except atlas with a well-defined narrow dorsal ridge. A well-defined ventral ridge on all but axis, all widening posteriorly. The vertebrae of *albiventris* are relatively narrower than most vertebrae of *Caecilia*. The forwardly-directed ventral processes are nearly parallel and lack small, inwardly-directed processes.

Caecilia degenerata Dunn (Fig. 7C, D). Four anterior vertebrae, the second and third each with a vague, dorsal ridge

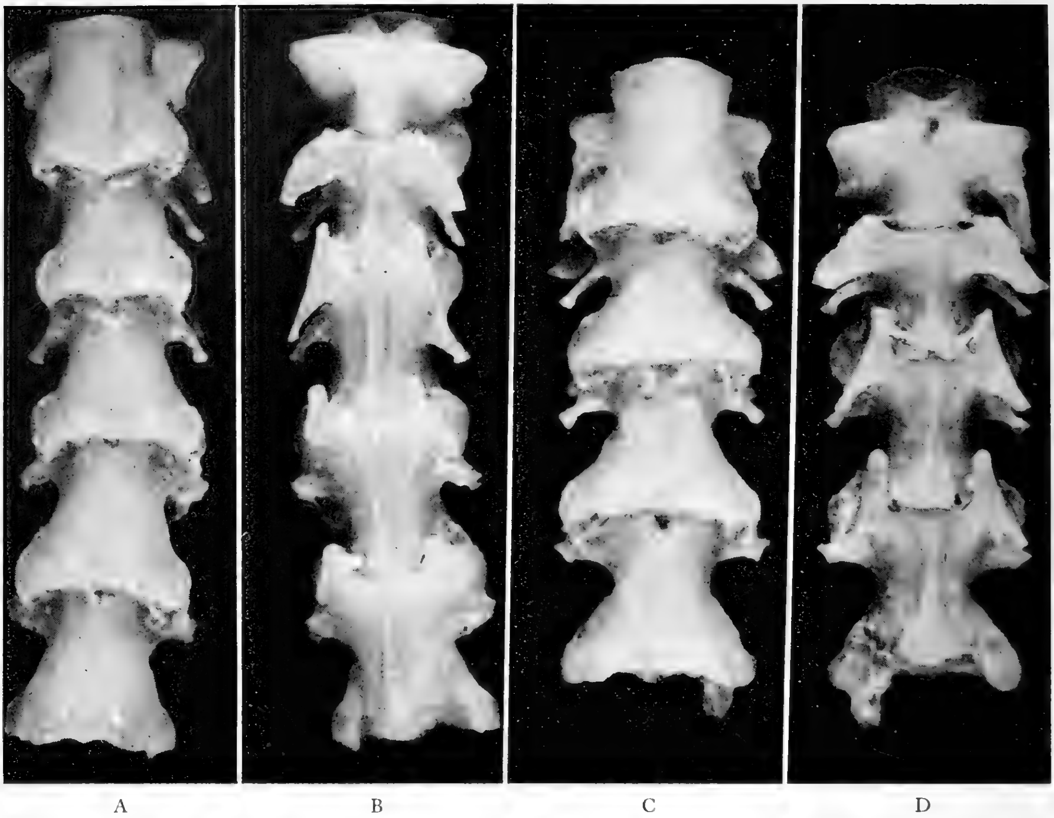

FIG. 5. A-B, *Caudacaecilia larutensis* (Taylor). EHT-HMS 3359, Maxwell Hill, Larut Hills, Perak, Malaya (topotype, within ½ mile of type-locality). A, Dorsal view of 4 cervical vertebrae. B, Ventral view of same. C-D, *Caudacaecilia nigroflava* (Taylor). EHT-HMS 8375, Bukit Lagong Forest Reserve, Selangor, Malaya. C, Dorsal view of 5 cervical vertebrae. D, Ventral view of same.

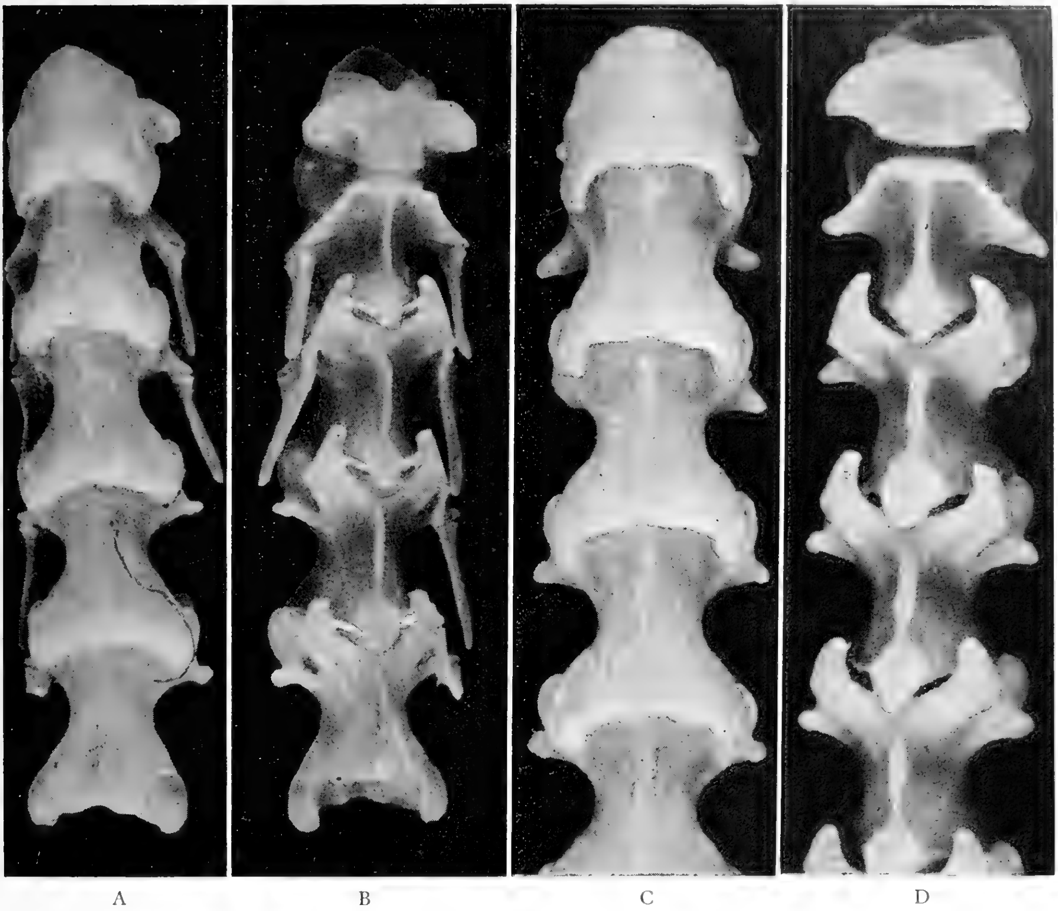

FIG. 6. A-B, *Oscaecilia bassleri* (Dunn). EHT-HMS 4675, "Ecuador." A, Five cervical vertebrae, dorsal view. B, Ventral view of same. C-D, *Oscaecilia ochrocephala* (Cope). UIM 41092, Gatún, Canal Zone, Panamá. C, Five cervical vertebrae, dorsal view. D, Ventral view of same.

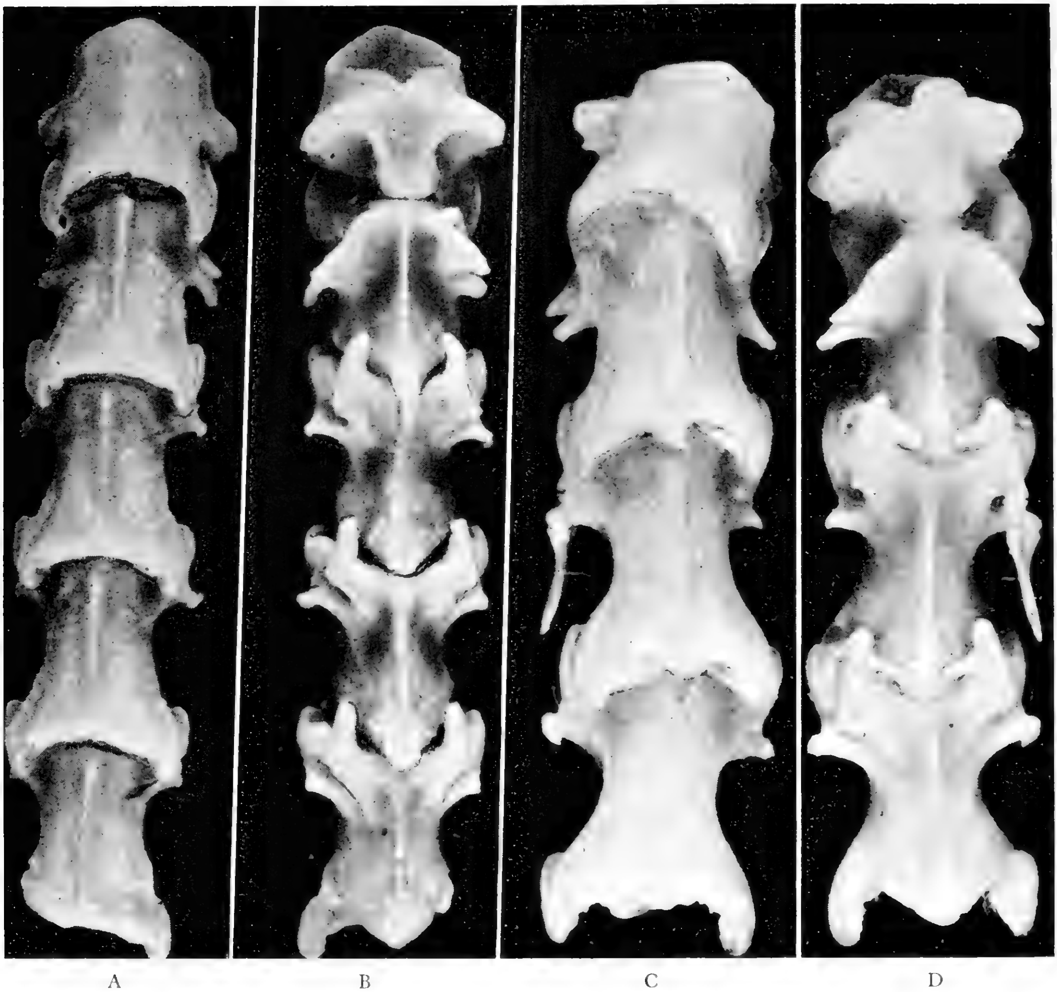

FIG. 7. A-B, *Caecilia albiventris* Daudin. AMNH 49960, "Bogotá" Colombia, S.A. A, Cervical vertebrae, dorsal view. B, Ventral view of same. C-D, *Caecilia degenerata* Dunn. AMNH 23354, "Colombia, S.A." C, Cervical vertebrae, dorsal view. D, Ventral view of same.

extending to posterior border of the vertebra. In ventral view, with very narrow, clearly-defined ridges widening slightly posteriorly. The forward processes of third and fourth each with a small branch pointing inward and somewhat backward.

Caecilia occidentalis Taylor (Fig. 8A, B). Four anterior vertebrae relatively broad, with slight median ridges on last three. In ventral view, the last three with low ridges; forwardly-projecting processes widely separated, nearly parallel.

Caecilia disossea Taylor (Fig. 8C). Ventral view of the first five vertebrae with last four showing a narrow, sharply-defined ventral ridge that curves down and widens a little posteriorly. The ventral processes directed forward, rounded at tips, not parallel, lacking any internal directed branches.

Caecilia orientalis Taylor (Fig. 8D). A vague, dorsal ridge indicated on posterior three of the four anterior vertebrae. In ventral view, with three, sharply-defined ventral ridges tending to narrow mesially and widen slightly at posterior end. Proc-

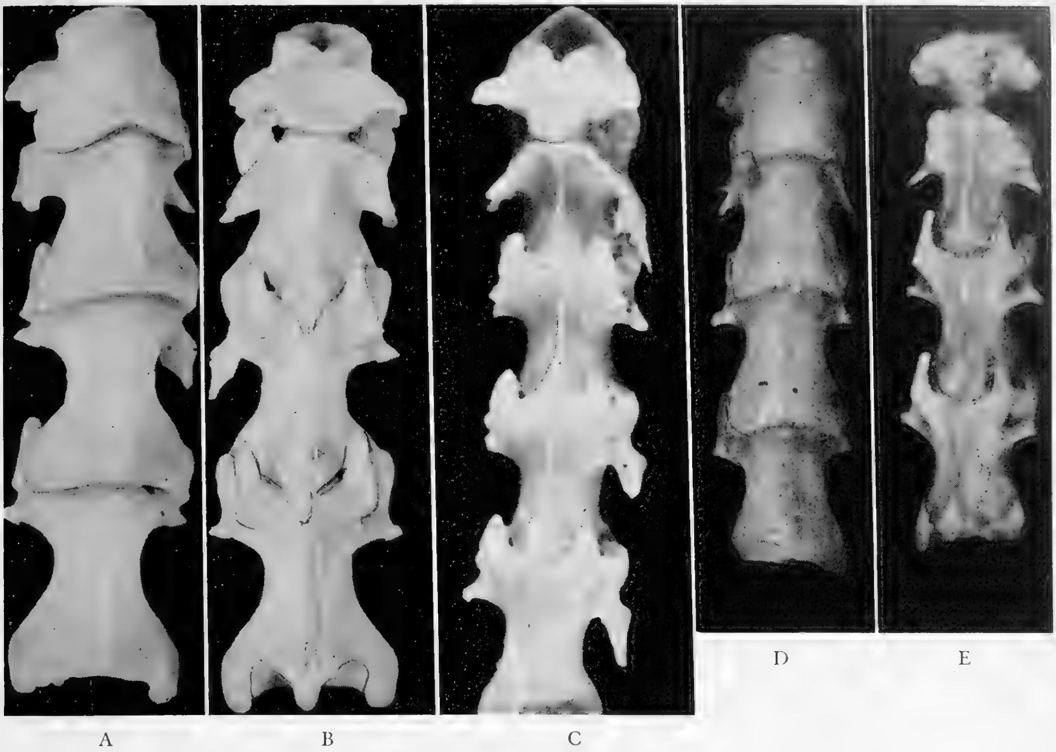

FIG. 8. A-B, *Caecilia occidentalis* Taylor. ANSP 25568, Popayán, Cauca, Colombia, S.A. A, Cervical vertebrae, dorsal view. B, Ventral view of same. C, *Caecilia disossea* Taylor. EHT-HMS 1808, Alto Curaray, Napo Pastaza, Ecuador, S.A. Four cervical vertebrae, ventral view. D-E, *Caecilia orientalis* Taylor. EHT-HMS 4677, "Ecuador," S.A. D, Four cervical vertebrae, dorsal view. E, Ventral view of same.

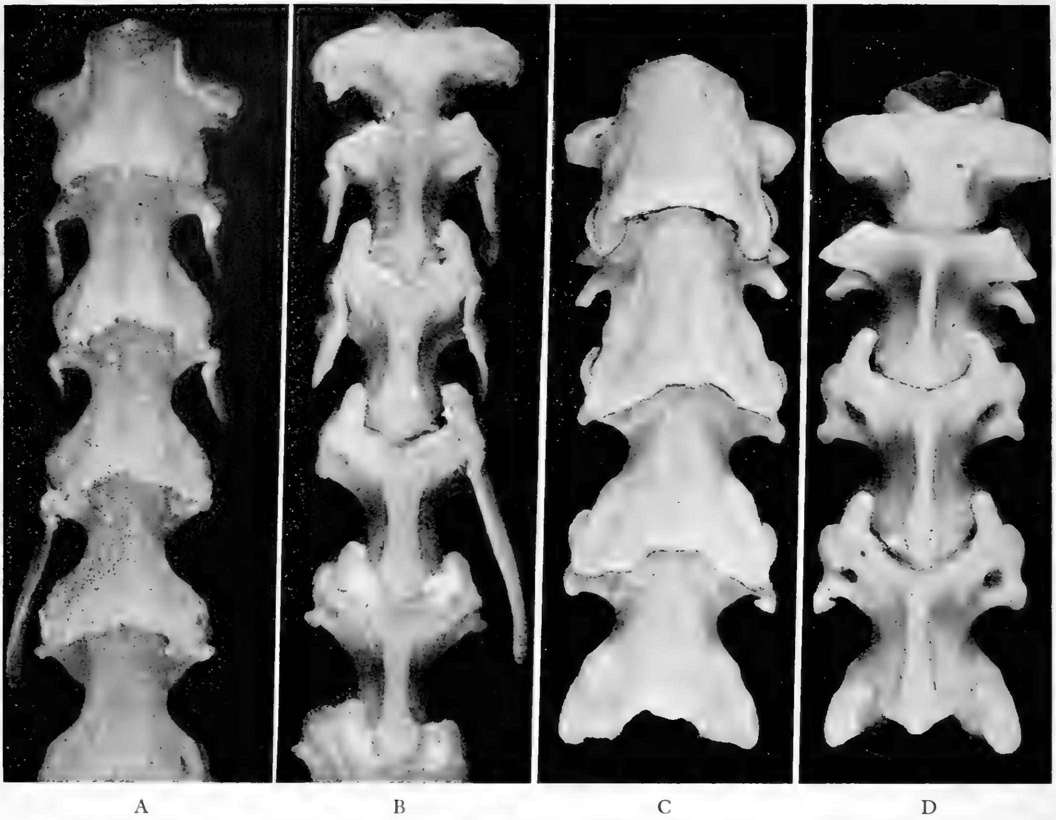

FIG. 9. A-B, *Gymnopis multiplicata* Peters. EHT-HMS 4702, Rancho San Bosco, Tilarán, Guanacaste Province, Costa Rica. A, Five cervical vertebrae, dorsal view. B, Ventral view of same. C-D, *Dermophis mexicanus* Duméril and Bibron. UIM 66889, Chiapas, Mexico. C, Four cervical vertebrae, dorsal view. D, Ventral view of same.

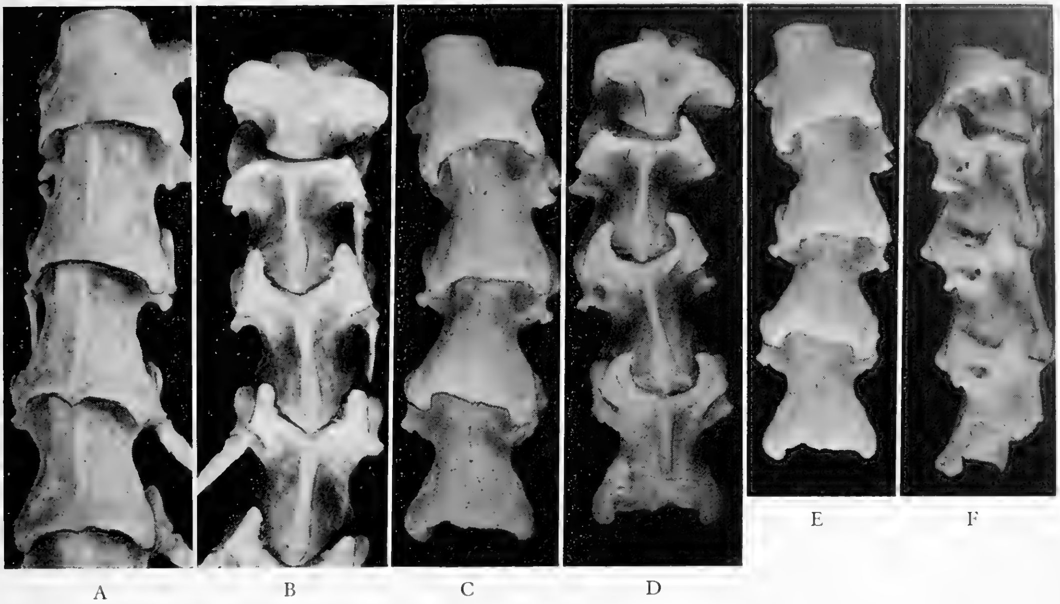

Fig. 10. A-B, *Siphonops paulensis* Boettger. AMNH 23433, "Brasil." A, Four cervical vertebrae, dorsal view. B, Ventral view of same. C-F, *Siphonops annulatus* (Mikan). UIM 56668, Limón Cocha, Ecuador, S.A. C, Four cervical vertebrae, dorsal view. D, Ventral view of the same. E, Four cervical vertebrae, dorsal view. F, Lateral view of same.

esses relatively slender, nearly parallel and rather widely separated.

Gymnopis multiplicata Peters (Fig. 9A, B). Five anterior vertebrae, in dorsal view with practically no traces of ridges. In ventral view, with a relatively broad ventral ridge, a widening posteriorly, the forward-directed processes heavy, somewhat blunted at their tips, not exactly parallel. The third has a pair of small branches from the forward projecting processes.

Dermophis mexicanus Duméril and Bibron (Fig. 9C, D). Four anterior vertebrae showing dimly a median ridge on last three. The lower lateral parts of the vertebrae show a more or less distinct elevation. In ventral view, the last three with sharply defined ventral ridges widening but slightly posteriorly. Forwardly directed processes curving inwardly somewhat.

Siphonops paulensis Boettger (Fig. 10A, B). Four anterior vertebrae, with distinct ridges the greater part of dorsal length. Sharply defined ventral ridges widening very slightly posteriorly; processes at terminal forward part, parallel.

Siphonops annulatus (Mikan) (Fig. 10C, D). Four anterior dorsal vertebrae with a very narrow dorsal ridge scarcely discernible. In ventral view, strong but rather narrow median ridge, widening posteriorly somewhat, the processes directed forward and curving inwardly as if grasping. In lateral view, foramina for blood vessels and nerves evident.

Geotrypetes seraphini seraphini (A. Duméril) (Fig. 11A, B). Atlas smaller than usual. The third and fourth anterior dorsal vertebrae are elongated more than in most forms. In ventral view, anterior border of second vertebra circular rather than angular. Third and fourth vertebrae elongate, the processes nearly parallel, the ventral ridge prominent for most of length. Median ventral length of axis very short.

Schistometopum gregorii (Boulenger) (Fig. 11C, D). Four anterior vertebrae, the last three with a low dorsal ridge. In ventral view, the lower part of the atlas longer than in *G. seraphini*. The frontal

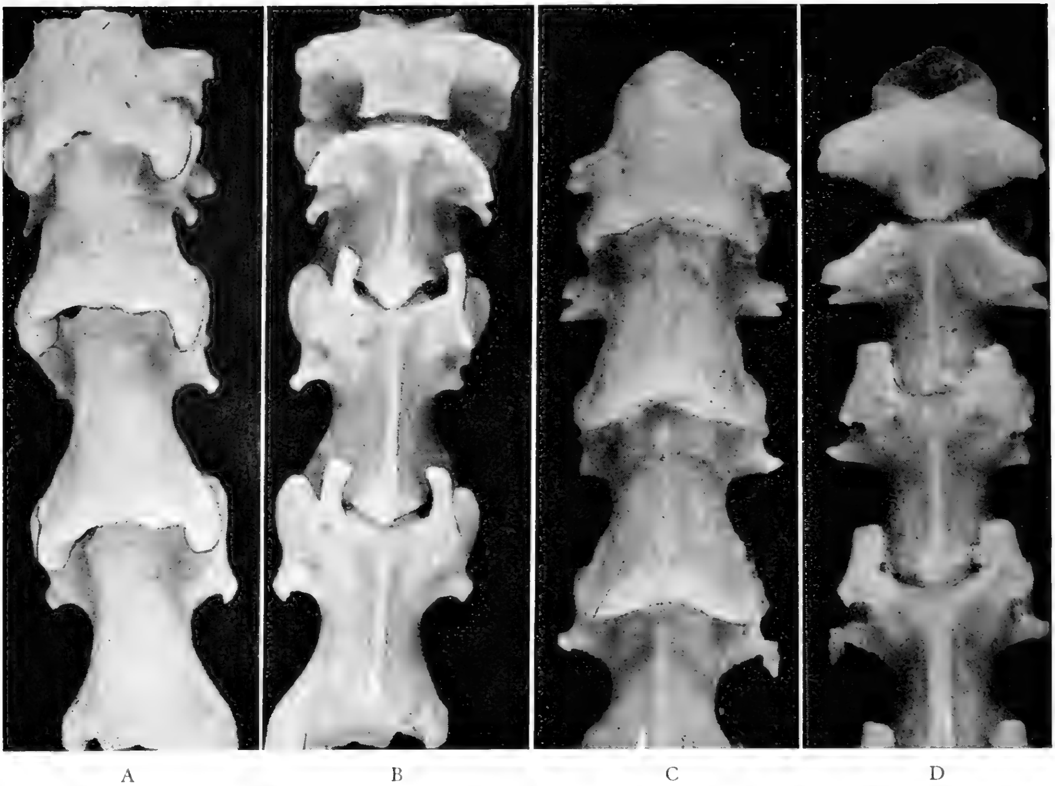

Fig. 11. A-B, *Geotrypetes s. seraphini* (A. Duméril). MCZ 3424, Metet, Cameroons, Africa. A, Four cervical vertebrae, dorsal view. B, Ventral view of same. C-D, *Schistometopum gregorii* (Boulenger), MCZ 20146, Lake Peccatoni, Kenya, Africa. C, Four cervical vertebrae, dorsal view. D, Ventral view of same.

border of the second ventral is strictly angular. The forward-directed processes are much thickened, nearly parallel and not terminally rounded; well-developed ventral ridges.

Hypogeophis r. rostratus (Cuvier) (Fig. 12A, B). Four anterior vertebrae, without trace of dorsal ridges. In ventral view, each with a median ridge, at least on last half of ventral surface, widening posteriorly. The second is angular anteriorly, the posterior part of ridge closely bordered by nearly parallel forward projections; following vertebrae with processes longer and merging, extending outward somewhat.

Uraeotyphlus oxyurus Duméril and Bibron (Fig. 12C, D). Four anterior vertebrae, the posterior ones with a vague dorsal ridge. In ventral view, with a thin, slightly developed ventral ridge, widening posteriorly, and curving down slightly posteriorly. Forward-directed processes widely separated, nearly parallel anteriorly.

Grandisonia alternans Stejneger (Fig. 13). Five anterior vertebrae, not or only vaguely suggesting dorsal ridges on four posterior ones. Most ribs retained. In ventral view, each with a strongly-defined ventral ridge becoming widened at the posterior terminal, almost as if formed by two branches. Forward processes tending to curve inwardly.

Gegeneophis ramaswamii Taylor (Fig. 14A, B). Four anterior vertebrae, the third and fourth showing vague dorsal ridges. In ventral view, posterior vertebrae with moderately well-defined ventral ridges, the

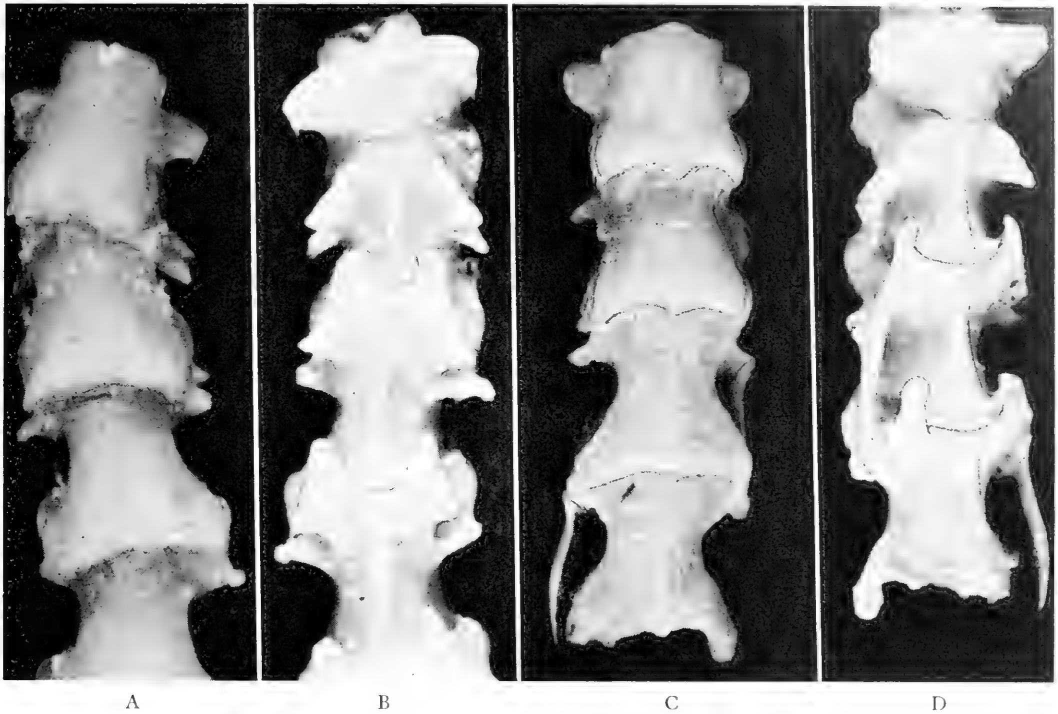

FIG. 12. A-B, *Hypogeophis r. rostratus* (Cuvier). MCZ 48935, St. Anne Island, Mahe Coast, Seychelles Islands. A, Cervical vertebrae, dorsal view. B, Ventral view of same. C-D, *Uraeotyphlus oxyurus* Duméril and Bibron. MCZ 9484, Taliparabambia, Travancore, India. C, Four cervical vertebrae, dorsal view. D, Ventral view of same.

FIG. 13. *Grandisonia alternans* Stejneger. EHT-HMS 4647 (formerly MCZ 15638), Mahe, Seychelles Islands. A, Five cervical vertebrae, dorsal view. B, Ventral view of same.

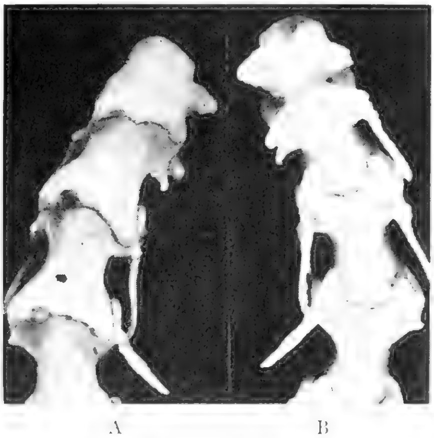

FIG. 14. *Gegeneophis ramaswamii* Taylor. EHT-HMS no no., no locality. A, Four cervical vertebrae, dorsal view. B, Ventral view of same.

terminal part of forward processes nearly parallel.

THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

GEOGRAPHICAL VARIATION IN NESTING BIOLOGY AND SOCIAL ORGANIZATION OF *HALICTUS LIGATUS*

By

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Geographical Variation in Nesting Biology and Social Organization of *Halictus ligatus*

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ABSTRACT

The halictid bee *Halictus ligatus* ranges from southern Canada to Colombia and Trinidad. In cool, temperate regions it develops small, summer, eusocial colonies similar to those of many halictids and consisting of a queen and several workers which are usually unmated and which lay few if any eggs. These colonies collapse in late summer or autumn, when the old queen and workers die; only new young queens survive the winter. In the tropics and probably also in Florida and elsewhere in the warm temperate regions, while such eusocial colonies may occur as an ontogenetic stage, the colonies become larger and presumably consist of daughters or more remote descendants of the foundress. They are active through all or most of the year and all adult females appear capable of surviving unfavorable seasons. While some of the bees are old foragers, unmated, with slender ovaries, i.e., workers, over half are mated, egg-laying foragers. Most of the eggs are laid by such foragers and in most colonies in these warmer regions there is no evidence of nonforaging reproductives, i.e., queens. The social structure in the tropics does not correspond to any of the named types of social organizations.

There is a continuum in size with no bimodality from the smallest to the largest females. In temperate regions large individuals are produced primarily in late summer and are the young gynes which will overwinter. In the tropics, large individuals are produced at all seasons when there is reproduction. At least some large individuals are produced in large cells with elongate food masses.

Other geographically-varying, biological features are as follows: From Florida southward, males seem to be produced in any months when females are produced. In cool temperate regions, perhaps with the exception of the northernmost population studied (Ontario), males are produced principally in late summer; early summer progeny are nearly all females. Northern populations usually make shallow nests which are often aggregated. From Kansas, southward, nests are commonly deep and rarely aggregated. Nest guarding is common in cool, temperate regions, rare in the tropics.

INTRODUCTION

This paper is an account of the nesting and social biology of a sweat bee, *Halictus ligatus* (Family Halictidae). In most parts of its range this species is common and is presumably a major pollinator, especially of many Compositae. It is important, therefore, that its biology be known, to serve as a basis for its possible future management. The objectives of this study are to make biological information available for this species, to describe a novel type of social organization found in its tropical populations, and to elucidate the geographical variation in social behavior found in this species.

Halictus ligatus is one of the most widespread bees, ranging from southern Canada to northern South America (Fig. 1). At least a little information on nests in burrows in the ground; it falls in the subgenus *Halictus*, but is a distinctive form not closely related to any other species.

The subgenus *Halictus* is largely restricted to temperate regions and has its center of abundance and diversity in Eurasia. *H. ligatus* is the only species of the subgenus occurring in the American tropics and it does not range south of northern South America. For these reasons it seems likely that this species is a recent invader of tropical climates and that attributes of populations in temperate North America are primitive, relative to those of tropical populations. This view is supported by the fact that the social organization in cool temperate areas is similar to that of various other well known halictid bees such as *Lasioglossum imitatum* and *L. zephyrum*. In contrast, the social organization of *H. ligatus* in the tropics is in some features unique among known insects and thus differs considerably from its relatives, including northern populations of the same species.

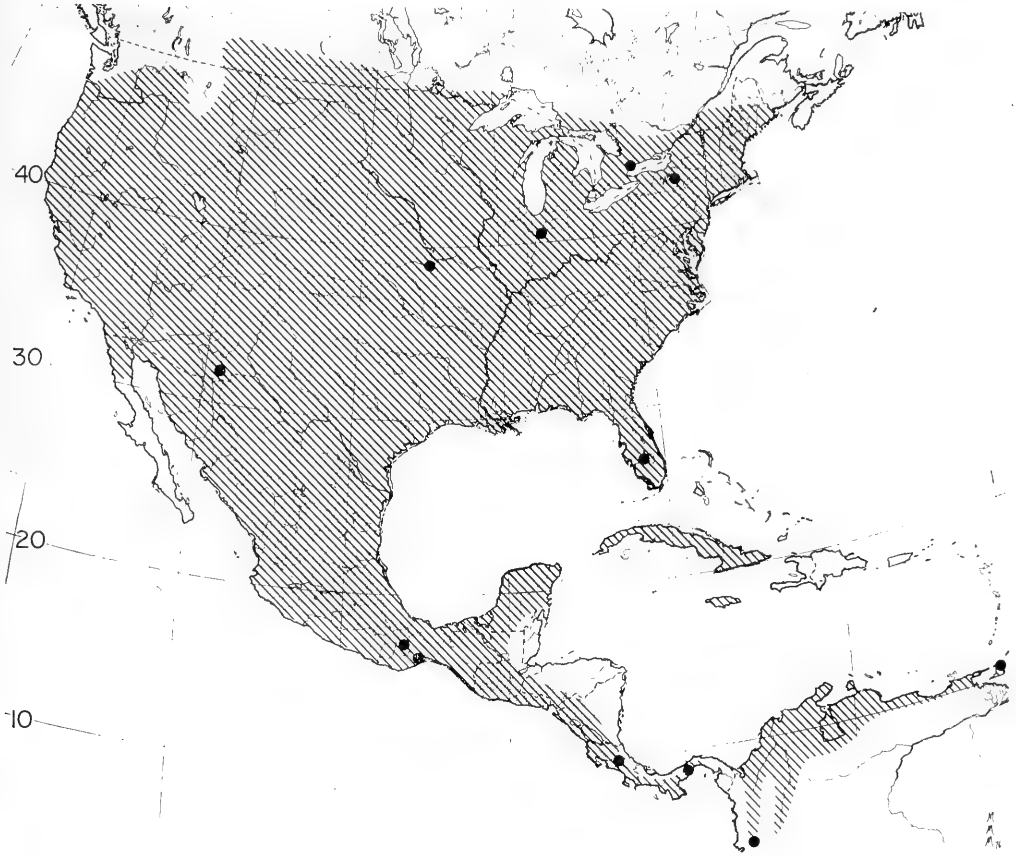

FIG. 1. Distribution of *Halictus ligatus* with dots indicating the localities where field observations have been made. Areas within the general range where the species does not occur, such as high mountains and deserts, are not indicated.

and seasonal cycles is available from diverse localities, indicated by dots on the map. It is a primitively-social species, usually living in small colonies of females

Halictus ligatus is probably much more abundant, now, in the formerly wooded parts of its range than in primeval times and may have extended its range substantially. Thus, no early collector is known to have obtained it in Trinidad or in South or Central America. Yet in the present century it is common in those areas.

The life cycle and social organization of the species in the temperate region is reviewed in some detail in part I, below. Our data from tropical America are presented as part II. Part I is the work of the first author and is largely based on the unpublished and published works of others acknowledged therein. Far more than for most papers, we are indebted to the helpfulness and cooperation of these individuals. Part II is a joint work of both authors, based largely on observations made in Trinidad and materials collected there. We are indebted, however, to Drs. M. J. West-Eberhard and W. G. Eberhard for greatly facilitating CDM's brief work in Cali, Colombia.

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measurements of bees by Kenneth W. Richards, James C. Trager, and Robert E. Gorton, as well as aid in statistical work by the last mentioned. We are especially indebted to Drs. George C. Eickwort and Marcia Litte for reading the manuscript, suggesting improvements, and generously providing information from their own observations.

I. TEMPERATE POPULATIONS

Except for the last subsection, this section is based on populations in the cool, temperate part of eastern North America, i.e., latitude 39° and northward and east of the 96th meridian. Information on populations of cool, temperate regions is from several sources. The first important account of the species concerns populations in the vicinity of Lafayette, Indiana; it is by Chandler (1955), who has given us permission to include material from his unpublished work. It contains many important conclusions about the species, but few data are presented. Chandler apparently made few dissections of bees and no examinations of spermathecae. Parts of Chandler's results were published by Roberts (1973), along with some information from Oregon. Additional material on the Indiana population is included in unpublished work by the late Dr. Rodney Kirkton (1963, 1968).

A series of publications by Knerer and co-authors contains information on *H. ligatus* populations near Toronto, Ontario, Canada, and Kirkton (1968) also provides certain information on the same populations. A comprehensive treatment of the Toronto population has not been provided.

Kirkton (1963, 1968) assembled information about caste differences and geographical variation in *H. ligatus*. His information about nests is not only from Indiana and Ontario, but also from Oaxaca, Mexico.

Litte (in press) made a study near Ithaca, New York, which is very important in clarifying observations made at the other sites. She is the first author to provide appropriate statistical data to document her conclusions.

Near Lawrence, Kansas, one of us (CDM) has made observations on nests of *H. ligatus*, some of them together with H. V. Daly, A. Wille, and E. A. Cross. No major study was made, however, for the nests are sparse. A few of the results appeared in Sakagami and Michener, 1962.

From the sources listed above, the following account of nesting behavior of *H. ligatus* in cool, temperate regions has been assembled; authors' names used without dates refer to the sources cited above. Thereafter an account is given of our limited knowledge of the species in warm, temperate regions.

Nest sites: The nests consist of burrows in gently sloping or flat soil, either bare or with short vegetation, exposing considerable soil. In Indiana, Chandler suggests, nests disappeared from an abandoned garden when weeds became too dense. Nest sites are ordinarily exposed to the sun, but a few of the nests studied in Kansas were partially shaded by trees. Soils are varied, from soft, garden loams or mixed sand and clay to firm silt or hard-packed bare clay paths.

There is a strong tendency for nests to be aggregated. Thus, Chandler reports an aggregation of nearly one hundred nests in Indiana, Litte studied three dense aggregations in New York, and Roberts mentions dense aggregations in Oregon. Kirkton believed that aggregations in Indiana and Ontario, usually on dry hilltops, resulted from limited suitable nesting habitats. Litte, however, believes that the aggregations result from bee behavior, not mere limitation of suitable soils. She notes (*in litt.*) that two aggregations contained 295 nests, an average of 15 nests

TABLE 1. Seasonal Data for *Halictus ligatus* in the Cool Temperate Region, Eastern North America.

Location (North Latitude)	and Source	Flight Season	Workers	Males	First Young Gynes	Last Old Queens
N. Dakota (47°)	(Stevens, 1951; Kirkton, 1968)	June 18-late Sept.		Aug. 10-? (peak mid Sept.)		
Ontario (43°40′)	(Knerer and Plateaux-Quénu, 1967a; Kirkton, 1968)	mid May-mid Oct.	late June-early Sept.	late June-early Oct. (peak early Sept.)	mid Aug.	mid July*
New York (42°30′)	(Litte, in press)	May 8 (or 19)†-Sept. 15 (or Oct. 14)	June 21 (or July 11)-?	July 28 (or 31)-?	Aug. 5	Aug. 31
Indiana (40°30′)	(Chandler, 1955)	May 3-Oct. 10	June 26-Aug. 29	July 31-Oct. 12	Aug. 10	Aug. 22
Indiana (40°30′)	(Kirkton, 1968)	late Apr.-mid Oct.		peak mid Aug.		
Kansas (39°)	(Kirkton, 1968)	early Apr.-late Sept.		peak mid Aug.		

* One reported in a nest on August 13 (Knerer and Plateaux-Quénu, 1966).

† G. Eickwort (in litt.) reports flight in the warm April of 1976 as early as April 19, but nesting activity did not begin until June.

per m^2, the mean distance between nearest neighbors being only 14 cm. Solitary nests are also recorded from Indiana, but the large aggregations are striking when compared to sites in Kansas and more southern localities, where nests are usually solitary or in loose groups of only two to ten.

Seasonal activity: Table 1 shows the timing of some major landmarks in the seasonal activity of *H. ligatus* in the northern half of its eastern North American range. The flight season begins with the emergence from the ground of the overwintered gynes and ends with the disappearance into the ground of the new young gynes that will hibernate during the following winter. The column for workers gives the flight season for workers of matrifilial colonies, i.e., daughters of the overwintered gynes which are by now queens. Since workers are short-lived, no one worker lives for the whole period indicated. The first young gynes are the first daughters that will pass the following winter. The last old queens are the last of the overwintered gynes that have lived through the summer as queens. Kirkton's data are based on museum specimens from squares 270 miles on a side, while data presented by Chandler, Litte, and by Knerer and Plateaux-Quénu are presumably from specific nesting sites.

Nest structure and development: Nests in temperate areas have been described by Chandler, Kirkton, Litte, and Roberts. Sakagami and Michener (1962) also gave data on nests.

In spring, overwintered gynes establish nests by making new burrows, appropriating burrows of the same or other species, or remaining in and refurbishing the overwintering burrows, i.e., the nests of the previous summer. A circular tumulus usually develops; it is much larger at the entrances of new burrows than at those of the other nest types. Such tumuli range up to 5 cm in diameter and over 1 cm high. Similar tumuli are found at nest entrances during the summer, whenever the nests are being extended. Tumuli at entrances of certain nests found in Kansas were highly asymmetrical, fan-shaped, because the upper two or three centimeters of the burrow sloped strongly and tumulus material was ejected up the sloping burrow rather than symmetrically around a more or less vertical burrow entrance. The burrow entrance is round; Chandler says it is often slightly smaller in diameter than the rest of the burrow, but contrary to that of most Halictinae, often not constricted. In Kansas, however, measurements show entrance diameters of 3 mm, burrow diameters of 5 mm. The soil particles of the tumulus are usually loose and easily blow or wash away, but walls of packed soil, probably consolidated with the aid of a secretion, sometimes extend from the upper part of the burrow up through the tumulus. In such cases, dispersal of the loose material of a tumulus by wind may leave a fragile turret at the nest entrance. The entrance is plugged with soil at night and in inclement weather; indeed, Litte reports that nests inhabited by a single gyne are open for only about 30 minutes per day, while those with multiple foundresses remain open for about six hours.

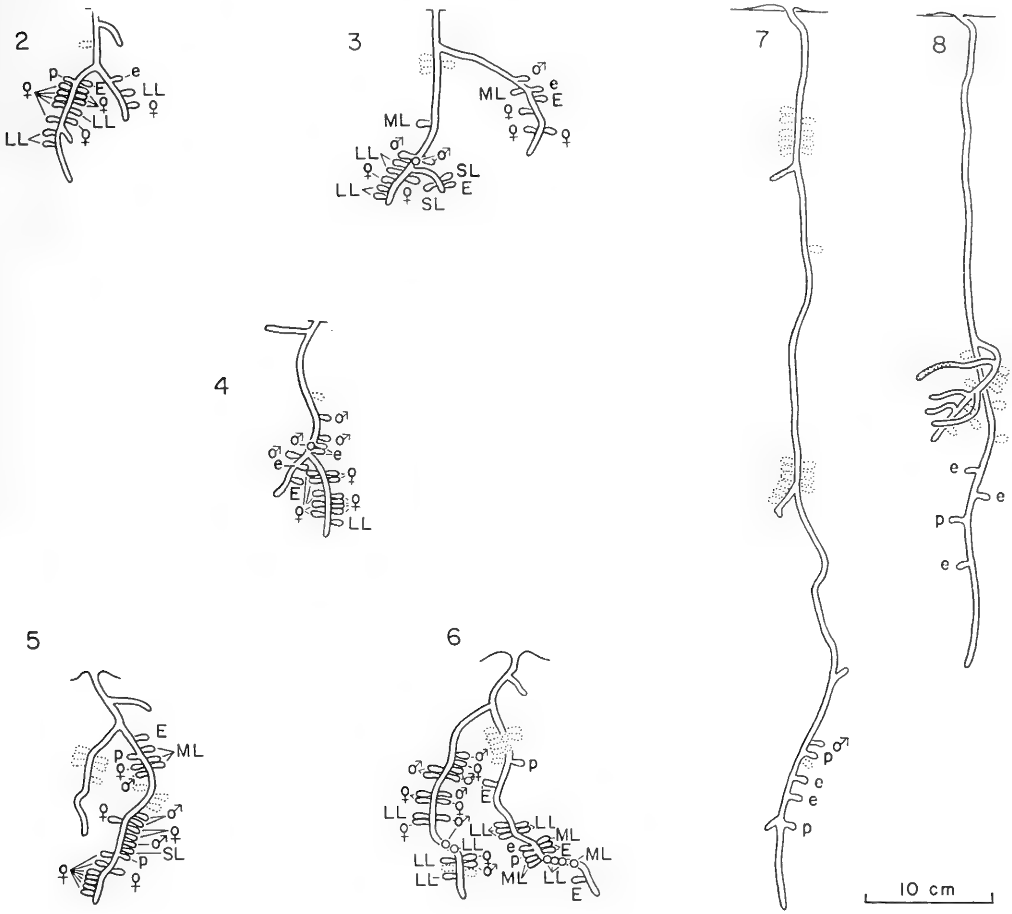
Below the soil surface the burrows commonly slope slightly, or often considerably in the lower parts where cells are excavated. Thus, cells are commonly attached to portions of burrows sloping as much as 45°. Litte, however, found most burrows that she examined to be vertical. Chandler says that the consolidated lining of the burrow often extends downward, so that only the lower extremities lack it.

Chandler reports horizontal, lateral burrows 2.5 to 10 cm below the soil surface, each ending in a roughly excavated enlargement (forage cell), in early spring nests. Other authors do not report such features in burrows of this or other halictids and their construction by this bee requires verification. These laterals and cavities are filled with earth before brood cell construction. The spring nest is therefore an unbranched burrow at the time of cell construction and provisioning; Litte reports the average nest depth at this time to be 15 cm and Kirkton says that brood cells are between 7.5 and 12.5 cm deep. The first completed cell found by Chandler, in different nests in Indiana, occurred from as early as May 15 to as late as June 9.

After a lone overwintered gyne has made and provisioned her brood cells, she closes the nest entrance with earth which fills the upper 3 cm or more of the burrow. She remains in the closed nest until emergence of her first adult workers. In Indiana, Chandler reported that nest closure occurred from June 3 to 14, reopening being on June 26 to 28, or even later. Litte found, however, that nests occupied by two or more overwintered bees do not have a distinct, inactive period between spring and summer phases, such colonies remaining more or less continuously active.

With emergence of daughters, extension of the burrow is begun and this commonly involves branching of the burrow. New cells are mostly along the branches. The maximum number of branches is six. As shown in Figures 2-6, there is often no deep, "main" burrow; below about the level of the bottom of the spring nest or somewhat deeper, branching occurs without a recognizable main axis. Some deep nests in Kansas are still unbranched in August, however (Figs. 7, 8). Perhaps lack of branches characterizes nests in dry soils where great depth is necessary to attain needed humidity.

In Indiana, the cells in summer were less than 25 cm deep, an unsuitable layer of soil being at that depth (Chandler, in Roberts). Such shallow nests, however, appear normal in Indiana, New York, and Ontario. Kirkton says summer nests are 15-30 cm deep, uncommonly in dry summers 45 cm deep, while Litte reports average summer depth as only 18 cm, the cells obviously being even shallower. In a moist region such as the northeastern United States, the cells are probably consistently shallow. As in other halictids, they are deeper when the soil is dry than when it is wet, for they must be con-



FIGS. 2-4. Nests from Lafayette, Indiana, June, July 27, and August 13, 1963, respectively; contained three, seven, and eight adult females, respectively (after Kirkton). For explanation of symbols see Figures 15-17.

FIGS. 5-6. Nests from Toronto, Ontario, August 11 and 27, respectively; contained ten and fourteen adult females, respectively (after Kirkton). For explanation of symbols see Figures 15-17.

FIGS. 7-8. Nests from Lawrence, Kansas, August 29 and 22, 1953, respectively. Each contained four adult females. For explanation of symbols see Figures 15-17.

structed where the soil is moist enough to be workable. Therefore, as summer passes, particularly in dry years, the cells are constructed progressively more deeply.

In Kansas, nests are extended to depths of at least 70 cm in the dry summer months (Sakagami and Michener, 1962). On the basis of few excavated nests, spring cells seem to be at the same depths as in Ontario and Indiana, but in July and August, cells are constructed at depths of 40-65 cm.

Brood cells are of the usual shape for Halictini—horizontal to sloping slightly downward, scattered along the burrows, much as in such *Lasioglossum* as *L. (Dialictus) imitatum* or *versatum* (Michener and Wille, 1961; Michener, 1966). Except for the short necks, they are lined with wax-like material; also, as in most other Halictini.

Worker-producing cells are 9-11 mm long, 5-7 mm in diameter, with the neck joining them to the burrow 1-3 mm long

(Chandler). Chandler reports that in the spring a queen constructs two cells and lines each, then provisions one, then the other. Then she constructs and provisions each subsequent cell before beginning with the next. It seems unlikely that this is a consistent pattern.

As soon as a cell is completed and provisioned and an egg laid in it, it is closed with earth which is so smoothed at the surface of the burrow that the location of the cell is not visible from the burrow. There is no evidence that the cells are opened again until emergence of the adult, although inspection of the young as in *Lasioglossum zephyrum* and other species of *Dialictus* (Michener, 1974, p. 67) may well occur.

Soon after a bee emerges from its cell, the cell is filled with earth. Re-use of old cells has not been recorded and presumably does not occur although new cells may be made in the same vicinity. Chandler notes that cells in which mold develops are somehow recognized in spite of the closed entrances and are packed with soil, a process which pushes moldy material into a mass at the far end of the cell and apparently inhibits fungal proliferation. (Similar behavior is known in *Nomia*; see Batra and Bohart, 1969.)

A lone gyne makes up to six (Chandler) or seven (Litte) cells before closing her nest and awaiting emergence of the first workers. Chandler noted that during one spring in Indiana most gynes made only three cells each, a few up to five; another year when spring weather was better, most nests contained four to six cells before being closed. Litte noted even greater differences between years in New York, mean production being 1.9 *vs.* 4.0 daughters in two different spring seasons. She found nests with two founders sometimes producing more workers, up to 14.

After emergence of the first daughters, cell construction and provisioning go on continuously through the summer. In mid-September, one of Chandler's nests in Indiana contained 40 cells, including the old, earth-filled ones, and a few other old cells may have been missed in opening the nest. This was the maximum size observed in Chandler's Indiana study. On August 27, a nest illustrated by Kirkton from Indiana contained 50 cells, 12 of them earth filled. These authors give no numerical data but their illustrations suggest that nests often have 15 to 30 cells (including earth filled ones) in August and early September. Litte gives the maximum cell number found among nests in New York as 32 with means of only 10.1 and 6.8 in two different years; these figures do not include old earth-filled cells and thus exclude spring production of daughters.

Although cells in the gyne nests in the spring are constructed in progressive sequence, the shallowest first and subsequent ones progressively deeper, locations of summer cells are often irregular or even retrogressive, so that young of different ages are intermixed.

Cells from which males emerge are similar to those that produce workers, possibly slightly larger in average size; Chandler gives their diameters as 6 to 7 mm, lengths 10 to 11.5 mm. Queen-producing cells, however, are markedly larger according to Chandler, having diameters of 5 to 9 mm ($\bar{X} = 6.5$) and lengths 12 to 17 mm ($\bar{X} = 14$). Reproductives of both sexes are produced from cells irregularly interspersed among worker cells, according to Chandler.

Provisions, as in most other Halictinae, form a smooth, firm, flattened ball on the top of which, in a weak longitudinal depression, a curved egg is laid with its long axis parallel to the long axis of the cell and only its two ends touching the food-mass. Pollen-balls in worker and male-producing cells are reported by Chandler to be about 3 mm wide, 4 mm long and 2 mm deep, but his photographs, in agreement with our Kansas data, show lengths and widths more nearly equal, the ball being nearly circular as seen from above (see Fig. 9). The pollen-masses in queen-producing cells, however, are not only larger but also elongate, 3.5 mm wide and 5 to 9 mm long (Fig. 9), according to Chandler's text and photographs. No other author reports such a modified cell size and pollen mass shape for queen production in *H. ligatus*, but the parallel with the Damitas population of *Lasioglossum (Dialictus) umbripenne* is obvious (Wille and Orozco, 1970). Two pollen masses from a nest in Florida (see below) were large and elongate, however, while another from a different nest was round (G. C. and K. R. Eickwort, unpublished).

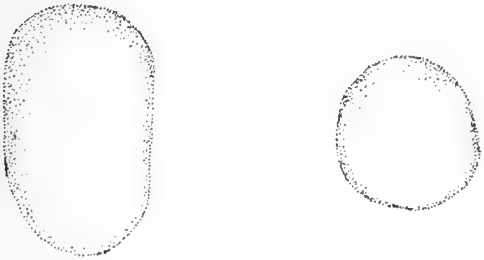


Fig. 9. Pollen-masses from cells from Indiana, traced from photographs by Chandler (1955). Mass from queen producing cell at left, from worker cell at right.

The social life cycle: For a short time after nests are first opened in the spring, Chandler, in Indiana, noted that the one to several gynes in a nest come and go, feeding at flowers. It was at this season that he reported construction of the "foraging cells" to which the gynes retreated when disturbed and at night. He reports that brood cell construction does not occur until the foundresses disperse, leaving only one in the parental nest as well as in each new nest. Litte's data from New York appear to support such dispersal, for she found more bees in the early spring nests than later, when brood was being reared, but in different years she found 25 and 32 percent of the nests during brood rearing with two or more bees. Knerer and Plateaux-Quénu (1966) report that in Ontario 60 percent of the spring nests contain more than one (2-7) female. These foundresses, according to the same authors, are not always overwintering groups of sisters, but may contain individuals from other nests. The largest female of a group becomes the queen, the others have less ovarian development and become, in effect, workers or auxiliaries. Litte reached similar conclusions, although in three of eleven two-foundress New York nests, the two females had similar ovarian development. Kansas data on these matters are meager. Of six spring nests found in different places and different years, only one contained two females in mid-May when cells were being provisioned in it.

At least in one nest studied by Knerer and Plateaux-Quénu (1966), a marked auxiliary survived and before dying foraged in early July along with the new workers, thus making an easy transition from a spring, semisocial colony of overwintered mated gynes to the summer, matrifilial, or eusocial colony with a queen and unmated workers. Litte also found in four nests that auxiliaries retained their behavioral roles for at least several days after daughters had emerged and started to forage and two nests opened in August each contained two large, worn, inseminated, foundress-type bees, presumably overwintered gynes; one in each nest had smaller ovaries and was presumably an auxiliary.

In Indiana (Chandler) and New York (Litte) the first brood of offspring, appearing in late June, consists of workers, there being no males until late July. In Ontario, however, according to Knerer and Plateaux-Quénu (1967a), some males are produced in late June, along with the first workers. Under laboratory conditions, the same authors (1967b) found that the monogynous colonies produce principally males, the polygynous colonies, workers.

According to Chandler, male production increases as the season advances, 50 to 75 percent of the cells containing male pupae in the period June 30 to August 14, after which the percentage of male pupae decreases. Adult males leave the nests permanently soon after emergence from the cells. As many as 12 males were found developing in a single nest.

In Indiana (Chandler), New York (Litte), and Ontario (Knerer and Atwood, 1967; Knerer and Plateaux-Quénu, 1967a) worker production continues through much of the summer, the last, newly-constructed worker cells being found about August 1 and the last, active, adult workers on August 29 in Indiana. The length of life of adult workers is so short that colonies never become large. Both Chandler and Litte found that the maximum number of adult workers in a nest at any one time was nine or ten; Litte reports average colony sizes (adult females, including queens) in August of two different years as 4.3 and 3.4 (N = 25 and 28, respectively). Chandler says that 18 to 20 workers in total may be produced by a colony, but presumably less than half of them are usually living adults at any one time. Litte found lower productivity, a maximum for both sexes of 20, with means of only 8.3 and 4.8 in different years. The greatest number of developing workers found in cells of one nest at one time by Chandler was seven.

Overwintered queens may survive through much of the summer (see Table 1, last column). Knerer and Plateaux-Quénu (1966) report excavating a functional, overwintered queen from her nest as late as August 13, although in Ontario most apparently die in July (Knerer and Plateaux-Quénu, 1967a). Litte also indicates considerable mortality of queens during the summer in New York, for 14.3 and 43.8 percent of the nests in July and August, respectively, lacked overwintered queens. Chandler (1955 and in Roberts, 1973) emphasizes (apparently on the basis of few observations) that if a queen dies, her full function is not taken over by one of the workers, presumably because they are unmated. Instead, they construct some cells, produce male offspring, and the colony dies. This corresponds to the late production of males in Indiana; they were first seen on July 31. Possibly in Ontario, where males develop as early as late June, young females in an orphaned colony may mate, producing replacement queens, and the colony may thus continue more or less normal development. In view of the numbers of colonies reported by Litte to lack overwintered queens, it seems clear that in New York also, replacement queens can be produced. Litte cites two nests in which young were being produced in the absence of overwintered queens. She says, however, that even when the overwintered queens are absent, very few daughters attain fully queenlike ovarian development.

Young gynes first appeared as adults in mid-August, both in Indiana and Ontario. The large brood cells were first constructed in Indiana about July 20 while the last were constructed about August 27. This seems to be slightly later than male cell construction (July 10 to August 22). In New York, Litte found a probable young gyne in a nest on August 5. The number of young gynes produced by colonies in Indiana ranged from 2 to 15, with up to 8 developing in cells of one nest at a time.

The prevalence of gyne and male brood in late summer, failure to produce worker cells in August, and failure of young gynes to contribute to the work of the colony, result in a diminution of nesting (i.e., cell construction and provisioning) activities during August. After the end of that month, the nests are occupied only by young gynes.

Caste differences: There are striking differences in average size between castes, as shown by the following measurements (mm) of head widths and forewing lengths:

Chandler (Indiana)

Workers:
head widths—2.04-2.68 ($\bar{X}=2.34$, $N=51$)
wing length—4.33-5.82 ($\bar{X}=5.14$, $N=50$)
Gynes:
head widths—2.42-3.19 ($\bar{X}=2.68$, $N=48$)
wing length—4.93-6.79 ($\bar{X}=5.88$, $N=48$)

Litte (New York)

Workers:
head widths—2.1-2.7 ($\bar{X}=2.49$, $SE=0.13$, $N=76$)
wing length—5.0-5.9 ($\bar{X}=5.50$, $N=76$)
Gynes:
head widths—2.4-3.4 ($\bar{X}=2.91$, $SE=0.19$, $N=84$)
wing length—5.3-7.4 ($\bar{X}=6.30$; $N=84$)

Chandler does not indicate the seasons when his samples was taken; Litte's were taken in June and July (daughters), May and June (gynes). The implication of Chandler's work is that there is a recognizable switch from worker production to production of reproductives and that most females can be recognized as to caste by size. Heads of queens seem disproportionately large. In Chandler's data one can see that minimal head width of gynes is larger than mean head width of workers, but minimal wing length of gynes is less than mean wing length of workers. There was probably better differentiation of castes by head width than by wing length.

Examining colonies separately, Chandler and Litte both say that the largest worker is consistently smaller than its own queen. Chandler gives data from eight colonies to demonstrate this. (In one case the wing length of a worker exceeds that of the queen, but other measurements were smaller than those of the queen.)

Knerer and Atwood (1966), in Ontario, found differences in mean size between castes similar to those described by Chandler and Litte, on the basis of measurements of 162 queens and 137 workers. They give no statistical treatment nor data on seasons of capture, but state that workers become progressively larger during the summer and that there is no abrupt change in size of food masses as production changes from workers to young gynes. Litte implies the same, although she is careful not to jump to the conclusions that the words "workers" and "gynes" imply. She does describe the increasing size of daughters as the summer advances. Probably, there is a continuum from small females (workers) produced early in summer to large females (gynes) produced late.

Kirkton, by means of smoothed curves rather than data, showed bimodality in head width measurements of females throughout the range of the species. He gives no statistical evidence for bimodality, nor do other authors.

To gain further insight into seasonal size variation, head widths of 206 females collected on flowers in the eastern third of Kansas were measured. There is no evidence of bimodality in the whole set of data or for any month. Bees taken in Spring (May) and Autumn (September to November) were lumped as presumed gynes, while each summer month was examined separately, with the following results (mm):

Spring, Autumn (gynes),
1.61-2.94 ($\bar{X}=2.58$, $SE=.023$, $N=68$)
June, 2.23-3.06 ($\bar{X}=2.58$, $SE=.026$, $N=39$)
July, 1.99-2.92 ($\bar{X}=2.53$, $SE=.017$, $N=72$)
August, 2.12-2.67 ($\bar{X}=2.41$, $SE=.027$, $N=27$)

Analysis of variance showed significant heterogeneity among these four means ($P << .001$). A student-Neuman-Keuls test showed the August mean to be significantly smaller than the others ($P << .01$), but no significant differences appear among the other three means. Figure 10 is a histogram showing the frequencies of the various size classes. The relatively large size of the July bees and small size of August bees is a surprise, since one would expect July bees to be mostly workers and August bees to be partly

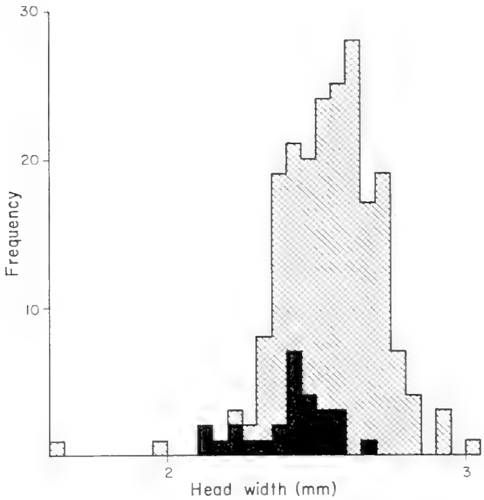


Fig. 10. Histogram showing frequencies of head width classes of females from the eastern third of Kansas. Black represents bees taken in August.

young gynes. Apparently the foraging bees in August, however, are mostly workers, perhaps having matured in July. Samples taken from nests, like those of the authors mentioned above, would probably have been influenced by gynes in August and smaller bees in July. Indeed, there may well be a mixture of castes in our August sample, for the mean head width of the gynes (2.58 mm) is only 7 percent greater than the mean for August bees, compared to 14.5 and 16.9 percent difference in head widths between gynes and daughter workers in Chandler's and Litte's nest populations.

The Kansas data suggest a longer season of activity than in the northeastern localities, with gynes not common away from their nests until September. Perhaps in an area with a long summer season, such as Kansas, the daughter bees on flowers in July, largely reared in June, are larger than the bees produced in midsummer. This is suggestive of the seasonal size variation found in *Lasioglossum zephyrum* (Batra, 1966; Kamm, 1974) and is in contrast to areas with short summers where the first daughters produced are perhaps smallest in mean size.

Gynes live as adults for about a year—August or September of one year to July or August of the next. Workers probably survive as adults for only about three weeks, according to estimates by Chandler; Litte observed marked workers for up to 36 days with a mean of 21 (N = 46). (Males are estimated by Chandler to survive for two to two and one half months.) Gynes hibernate, but workers do not even live until the advent of cold weather. When nesting alone, gynes commonly go through a quiescent period after provisioning their spring nests; workers are not known to have quiescent periods. After a gyne has reared her first brood of workers, she leaves the nest only occasionally and never brings back pollen for cell provisioning. Chandler reports that even if all workers are removed, such a queen does not revert to cell construction and provisioning. In the absence of the queen, workers often do not fill vacated cells with earth, construct but little, and spend long periods in the nest between provisioning flights.

In the matrifilial, summer nests in Indiana, according to Chandler, the queen with her large head is the usual guard. In a much more detailed study of division of labor, Litte in New York showed that in seven out of eleven nests the principal guard for a colony was the minimal forager, therefore perhaps the queen. This result seems to corroborate Chandler's general statement. In other cases, however, the principal guard was found to be an uninseminated worker. Guards bite at potential enemies, but if sufficiently stimulated, turn and close the burrow with the dorsum of the abdomen.

Chandler says that the early-spring, polygynic nests are guarded as in summer, but that during the monogynous period of spring cell-construction and provisioning, the nest is often not guarded.

Knerer and Plateaux-Quénu (1966) and Knerer and Atwood (1967), however, say that spring nests are never guarded, even polygynous ones, a surprising observation, since Litte found spring multifoundress nests to be regularly guarded. Chandler also notes that in autumn, after the workers are dead, the gynes in a nest sometimes guard the entrance.

Litte found that in *H. ligatus*, as in *Lasioglossum zephyrum* (Brothers and Michener, 1974), there is a marked tendency for workers to specialize, some being principal foragers, some being principal guards, and some being less active or doing little. Guards in spring nests averaged larger and had more ovarian development than did principal foragers.

Of course, a prime difference between female castes is in ovarian development. Considering this factor, Litte classified females as follows: A, 5-6 ovarioles enlarged; B, 2-4 ovarioles enlarged; C, one considerably or several slightly enlarged ovarioles; D, all ovarioles slender. The symbols + and o are used to indicate presence or absence of sperm cells in the spermatheca.

All young, adult females are class D; if ovarian enlargement occurs, they join other classes. In spring and summer ovoposition periods, egg layers are in classes A+ or B+. In eleven spring nests each with two foundresses, Litte found that the bees ranged from A+ to D+; the foundresses (one from each nest) with most enlarged ovaries had an average ovarian score of 2.6 (A = 3, B = 2, D = 1) while for the other foundresses (workers) the score was 1.7. In three of the nests there was little size difference between ovaries of the two foundresses.

In July and August the ovaries of workers often show some enlargement. Thus, 70 daughters (workers) taken in July and 81 taken in August are distributed as follows in terms of percentages of ovarian classes and fertilization:

	A+	Ao	B+	Bo	C+	Co	D+	Do
July	1.4	4.3	1.4	1.4	0	28.6	2.8	60.0
August	0	3.7	8.6	3.7	0	18.5	8.6	56.8

In New York about 13.7 percent of the daughters (months lumped) have much enlarged ovaries (classes A and B) while a larger number (23.2%), but none of them mated, have limited ovarian enlargement (class C).

Gynes mate readily, but workers are reported by Chandler to be not attractive to males. This presumably is not entirely so, for Litte's data show 5.6 percent of July daughter females and 17.2 percent of August daughter females to be mated.

Overwintering: Mated gynes hibernate in the deeper parts of the nest burrows, presumably in nests in which they matured. Hibernating gynes were found by Chandler at depths of 16-24 cm. The gynes close the burrows behind them with plugs of soil a centimeter or so in length, so that the overwintering cell is a burrow termination or section somewhat longer than the bee. The upper part of the burrow is left open and unattended, but during autumn and winter it is closed by blowing and washing soil.

Warm temperate populations: Few data are available concerning *Halictus ligatus* in the warm temperate areas. Kirkton gives conclusions on the season of activity in all temperate areas, but as they are based on museum specimens, the information may relate to activity of collectors as much as to activity of bees. For the southern half of Florida his maps suggest that the first females appear in late January and that the last females are in the field in late December. It is quite likely that there is no period when flight activity is absent, at least in some years. Mitchell (1960) indicates that there is activity every month and that males were taken on December 18. At the Archbold Biological Station, Lake Placid, Highlands County, Florida, however, Dr. M. Litte (personal communication) found no individuals of either sex on flowers and found no nests from January to late March, 1975. This was a warm but very dry winter.

Nests found in warm temperate areas, like those in Kansas, have mostly been isolated. G. Eickwort (*in litt.*) suggests that humid conditions of soil may be important in determining nest distribution or survival, for the nests he found in Florida at the end of the dry season were either where they received drainage from a shed roof or along the banks of a drainage canal. Also, in southern New Mexico, 51 km south of Animas, near a water hole where the soil was moist, he found a large, dense, nest-aggregation similar to those in the northern part of the range.

Data on two nests from the Archbold Biological Station have kindly been made available by Drs. George C. and Kathleen R. Eickwort. The nests, opened on April 24, 1972, were in sandy soil, nearly vertical, 86 and 170 cm deep, and did not differ in form from other deep nests of the species, such as those from Kansas (Fig. 11). The bees in this region, like those in the tropics, are large and the burrows were 6-9 mm in diameter (mostly 6.5-7). One had a tumulus 7.5 cm in diameter. The two nests contained 16 and 23 cells and 4 and 7 adult females, respectively. One cell and an earth-filled old cell were found at a depth of 21 cm, but otherwise the cells were located from 48 to 160 cm in depth. They contained young of all stages, including male pupae.

The Eickworts' observations verify Chandler's report of some elongate pollen masses, no doubt producing large bees (gynes?). They measured one round pollen mass (5 × 5 mm × 3 mm high) and two elongate ones (9 × 5 mm, 4 mm high).

In each nest the largest bee was mated and had much enlarged ovaries (class A) and in the deeper nest this individual was also much worn. One or two other individuals in each nest also were mated and with enlarged ovaries (our class A or B). The unmated individuals had ovaries of classes B and C, except for one in class D, and were not or were little worn.

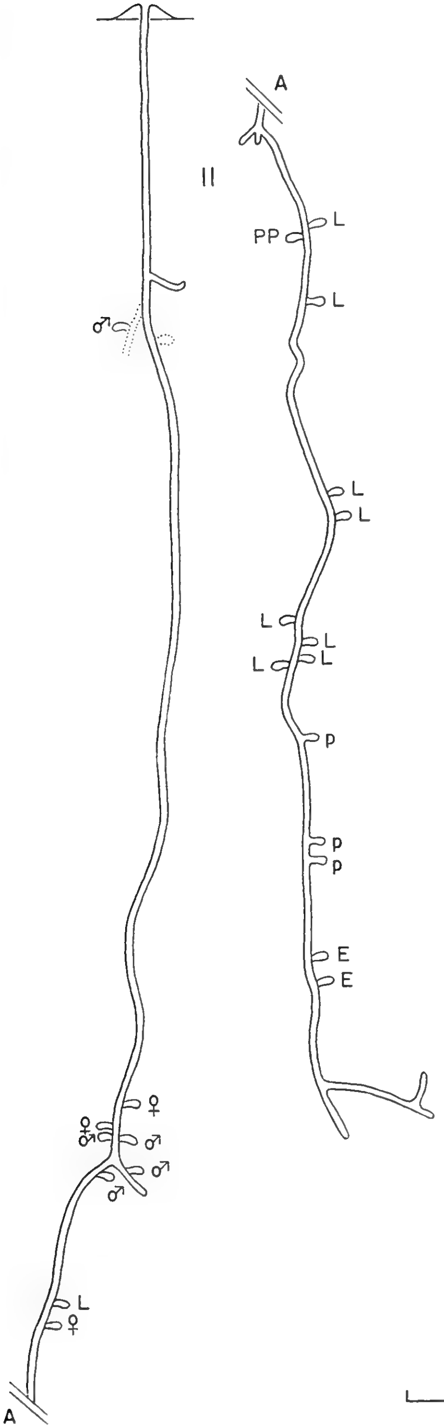
The large number of mated bees with enlarged ovaries is suggestive of the tropical populations. This similarity is strongly supported by 17 females taken on flowers by Dr. G. C. Eickwort at Lake Okeechobee and 23 miles southwest of Clewiston, Florida, April 5 and 11, 1974. All these foragers, which were dissected by Dr. Eickwort, were mated and eight had at least somewhat enlarged ovaries, probably falling in our classes B and C. Of course, these bees could have all been queens, but this was not suggested by their size nor by the populations of the two nests found at the Archbold Biological Station, which is in the same general area.

The only two bees taken in a nest in red volcanic soil 12 miles southwest of Apache, Arizona, August 16, 1972, and dissected by Dr. G. C. Eickwort, were mated, with enlarged ovaries. This nest was only 35 cm deep and contained but one active cell in addition to old, earth-filled cells and a dead female.

From these meagre data, it seems probable that during the long flight seasons in warm temperate areas, colonies like those of the tropics develop.

II. TROPICAL POPULATIONS

Information on tropical populations has been obtained in several areas. The bulk of the data were obtained at Curepe, Trinidad, West Indies (10°40′N) by Bennett and Michener. Limited amounts of information, however, were gathered at Cali, Colombia (3°30′N) and 5 km north of Chame, Panama (8°30′N) by Michener, at Turrialba, Costa Rica (9°40′N) by



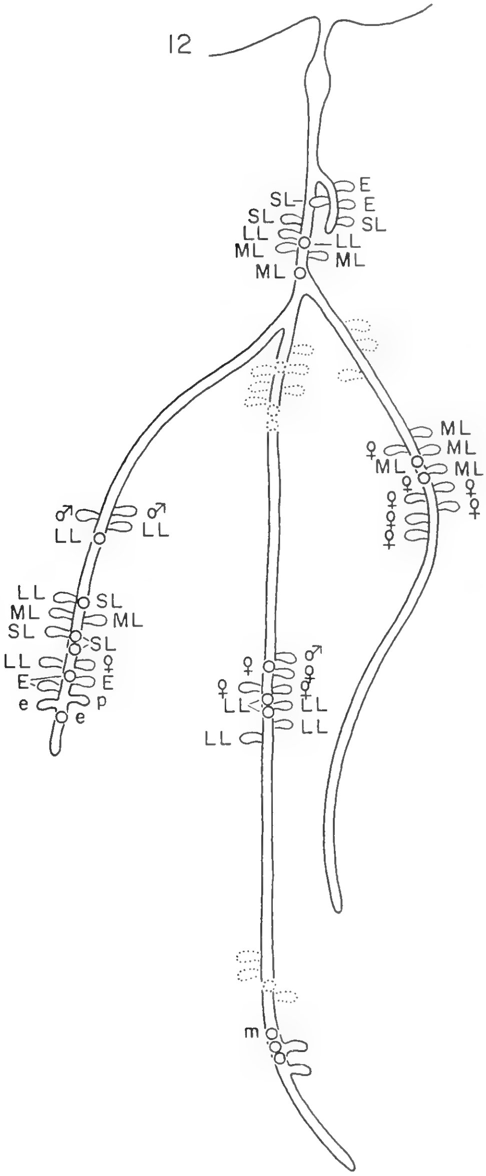


Fig. 11. Nest from Archbold Biological Station, Lake Placid, Florida, April 24, 1974; contained seven adult females (from field notes by G. C. and K. R. Eickwort).

Fig. 12. Nests from Mitla, Oaxaca, Mexico, July 5, 1965; contained eleven adult females (after Kirkton). For explanation of symbols, see Figures 15-17.

Drs. George C. and Kathleen R. Eickwort (unpublished) and 9 km east of Tehuantepec (16°20′N) and at Mitla (16°50′N), both in Oaxaca, Mexico, by Kirkton (1968). The more southern of these sites approximate the southernmost known localities for the species, both in the west (Colombia) and in the east (Trinidad) (Fig. 1).

Methods: To roughly monitor seasonal abundance on flowers and to obtain material for studies of any seasonal changes in bee size, ovarian development, wear, frequency of mating, and the like, "special collections" were made at intervals through three years in the general vicinity of the nesting site at Curepe, Trinidad. They were made by walking in midmorning along roadside patches of *Bidens pilosa*, which fortunately blooms throughout the year, capturing as many *Halictus* as practical in a period of about an hour. For some lots bees that had collected pollen loads on the scopae were kept separate from those that did not have large scopal loads. Except in January, 1972, the special collections were made by FDB.

The nests at Curepe were watched casually over a period of years by FDB. Some of these nests, as well as those at Cali, Colombia, were excavated by CDM, using in general the techniques described by Michener et al. (1955). Burrows, however, were marked by blowing powder from a plastic squeeze bottle into them instead of by pouring in plaster of Paris.

Before opening it, each Trinidad nest was watched for an hour or more and all returning bees captured. Departing bees were allowed to go, but captured on their return. Thus, all individuals active in the field at the time were caught and kept segregated from bees remaining in the nest, which we call "nest bees." Of course, some of these nest bees might well leave the nest at another time. Bees returning with pollen loads were also separated from the rest for study. The expression "bees associated with nests" is used for the nest bees plus foragers taken as they returned to nests, 62 in all. For statistical purposes "foragers" are the bees taken in special collections plus those that were returning to nests, 383 in all.

Bees from the nests as well as from special collections were preserved in Dietrich's (Kahle's) fixative and were measured and dissected later, using the techniques described by Michener et al. (1955). Head-width was used as the measure of size, although forewing-length was also taken. Mandibular wear was coded one (unworn) to five (worn down to subapical mandibular tooth). Alar wear was recorded as the number of nicks in the apical margin of each forewing. An index of wear for each bee was obtained by adding its mandibular code number to the average number of nicks on the two forewings; a freshly emerged bee has an index of wear of 1. Bees were regarded as mated if the spermatheca contained sperm cells; otherwise they were considered unmated. The ovaries of each bee were sketched and maximum ovarial width and length of the longest oocyte were also recorded. Some of the drawings were sent to Dr. Marcia Litte who classified them according to the system summarized in Part I above. Not all ovarioles were visible in the drawings, but she was confident of the categories. We are thus able to use, in addition to the measurements, lettered categories equivalent to hers.

Nest sites: The site in Trinidad, which was active for at least six years, was near houses on a hill just north of Curepe. The nests were in soil consisting of decomposed shale near the surface that could be cut with a knife, the soil being harder and with solid rocky regions at depths of 70 to 90 cm. The site was almost level, covered with coarse vegetation that was usually clipped short. The nests survived a period of two months when the uncut grasses and weeds grew to a height of about 30 cm, but disappeared ultimately, possibly because vegetation was allowed to grow for a longer period. Six nests were found in an area of about one square meter. There were a few scattered nests nearby and there must have been many in the general area, for the bees were common on flowers of *Bidens pilosa* and *Melanthera nivea*, both weedy Compositae. Pollen loads from each plant (distinguishable by color) which were carried into the nests indicated that *Bidens* was more often visited than *Melanthera*. Nests were excavated in late December, 1971, and January, 1972; otherwise the population was kept track of by monthly samples from the *Bidens* flowers. Three isolated nests near Turrialba, Costa Rica, were also in level ground with grasses and herbs.

Near Cali, Colombia, and Chame, Panama, nests were found in the very hard, bare soil of foot paths. The soil surface was flat or gently sloping. Most of the nests were isolated although three were about 20 cm apart. Kirkton's three nests from Oaxaca were all isolated.

At no tropical site have we encountered dense nest-aggregations like those in Indiana, New York, and Ontario. Dr. Alvaro Wille of the Universidad de Costa Rica, however, has told us of a site near San Mateo, Costa Rica, inhabited by a moderately dense aggregation.

Seasonal activity: This section is based entirely on data from Trinidad, although seasonal activity at other tropical locations is presumably similar. Nests excavated in January in Colombia appeared to be in the same condition as those excavated at the same time of year in Trinidad and, in fact, nests excavated in July in Costa Rica and Oaxaca were also similar.

To understand the bee's seasonal activity, it is necessary to have information on the seasonal cycle itself. Weather data are from the University of the West Indies, St. Augustine, about 3 km from the nesting site. Temperatures are warm and rather uniform throughout the year. Monthly mean minima during the years 1972-1975 ranged from 19° to 23° C (67° to 74° F), with a tendency for lower mean minima during the Northern Hempishere winter and spring months. Monthly mean maxima ranged from 29° to 33° C (84° to 91° F), again with a tendency for lower means in the Northern Hemisphere winter and spring months.

Rainfall occurs in every month of the year with a total annual rainfall of 1200 to 1475 mm (48 to 59 inches). The dry season, with 3 to 75 mm (0.12 to 3 inches) of rainfall per month, usually extends from January through May, in some years beginning in December or extending through June. Sometimes (e.g., 1972) January and May are wet so that the dry season is only February through April. The wet season, with a monthly rainfall of about 100 to 300 mm (4 to 12 inches), occupies the rest of the year.

Data on seasonal activity in Trinidad are based largely on the special collections made from flowers at Curepe, but, in part, on dates of capture of specimens in the collection of the Commonwealth Institute of Biological Control in Curepe. These collections were somewhat irregularly distributed, but, over three years, one or more special collection was made or attempted in each month except November.

Halictus ligatus has been taken on flowers at Curepe in every month except May and November. In November, although no special collections were attempted, there is good reason (abundance in late October and early December) to believe that activity continues uninterruptedly. In most months, a special collection, such as is described above, resulted in capture of 25 to 38 female *Halictus*. Three different collections in April, however, produced 5, 1, and 4 bees each. In May, none were taken and in

June only two. The collection of the Commonwealth Institute of Biological Control contains 13 taken in April, none in May and two in June.

From these data, it seems that there is a period at the end of the dry season and perhaps continuing into the beginning of the wet when the species is scarce on flowers. There is no obviously competing flower that might account for its disappearance from *Bidens* at that time. The special collections in April to June were all made or attempted in 1974, a year in which the dry season continued through June, the rainfall that month being only 2.33 inches.

In July, there is the same mixture of fresh and worn bees as in any other month. Thus, if adults of mixed ages become relatively inactive in April to June, they probably emerge and resume work after the rainy season begins. It is possible that after a long dry season the soil is too dry to make cells and the bees become inactive until it is workable again.

Males have been taken at Curepe in January, March, July, August, September and December and probably are active whenever females are to be found.

Large females, suggestive of north temperate gynes, but even larger (workers, also, are larger in the tropics than northern workers), occur in the tropics. As explained later, however, such individuals are not always gynes. In Panama and Oaxaca three such individuals were found, apparently starting new nests, in June and July. By itself, this is not evidence that nest establishment is highly seasonal, but it might occur predominantly at the beginning of the wet season when activity resumes. Colonies in large nests can also be found in July (Costa Rica, Oaxaca), suggesting that they do not break down in the inactive season as do colonies in the cool temperate autumn. The months of capture on flowers of the largest 10 percent of the females taken in Trinidad are January, March, April, August, September, October, December. Thus, large females can probably be found on flowers whenever other females are there. The largest female taken at Curepe, markedly larger than any other, was on flowers in October. Fresh and unworn, it could not have started a nest in June or July.

Nest structure and development: Three apparently new nests, shallow burrows each occupied by one large female with no cells or with a cell or two roughed out, have been found by CDM in Panama in early July and by Kirkton in Oaxaca in June. If new nests are started primarily by large, unworn females, as seems possible in view of the situation in a temperate climate, it may be significant that essentially unworn, large females (head width over 3.5 mm) have been taken in Trinidad in January, March, July, September, and October, four of them in the latter month. New nests were not found in Trinidad, despite a search in December and January and general surveillance throughout various years.

The nests studied in Trinidad and Colombia in December and January are the bases for the following account, with parenthetical comments for other regions. The nests were much larger than those in the northeastern parts of the range. Tumuli of fresh soil up to 9 cm in diameter (Fig. 13) were found, showing extensive

FIG. 13. Nest entrance at Curepe, Trinidad, showing large, fresh tumulus. The numbers represent inches (2.5 cm = 1 inch).

digging in some nests in December and January. Old tumular material, packed and washed by rain and sometimes with grass growing in it, but recognizable by the color of the subsoil, was also evident around many of the nests.

Measurements of entrances and burrows are slightly larger than for those in Kansas, entrances being 3.5 to 5 mm in diameter, burrows 5.5 to 6 mm. Nothing suggestive of a turret was seen at any time, nor were nest-entrances ever seen closed by soil, except sometimes by fresh tumulus material being pushed out. There was no evidence of regular nocturnal closure, as is reported in the north. Although part-time guarding occurred early in the morning, and the sun was often on the nest sites, flights from the nests did not begin until about 9:30 a.m. Rain or threatened rain usually stopped activity in the early afternoon.

While the nests were much deeper than in the north, the number of branches was not greater (Figs. 12, 15-17), the mean for six nests being 4.4 and the maximum being 6. The distribution of earth-filled, abandoned cells showed that there had been other branches at depths from 15 to 60 cm, but they had evidently been filled and abandoned at earlier stages in nest-development. Presumably, the number of branches remains more or less constant, old ones being filled as new ones are made.

The deepest nest (Trinidad) was 97 cm deep, the shallowest (Colombia), 79 cm (Costa Rica, 55 cm). The burrow walls are often lined 0.5 to 1.0 mm thick with soil from deep in the nest (as shown by color), bearing the marks made by tamping with the apex of the abdomen. Chandler's report of a consolidated soil lining is thus verified (as also in Arizona and Florida nests excavated by the Eickworts). The tendency of burrows to slant, often in a single direction, is prominent in Trinidad (and Costa Rica) (Figs. 15-17). The bottoms of some nests in Trinidad were offset 60 cm or more horizontally from the entrance. In Colombia and Oaxaca, the burrows were nearly vertical.

Many earth-filled, old cells, mostly with feces, indicating probable survival and emergence of the occupants, showed that the colonies had been active for considerable periods, months and possibly years, prior to our digging of them. In Trinidad the shallowest earth-filled cells found were 18 cm deep; in Colombia, 15 cm. This may be the depth at which nest foundresses make cells, but, if so, the nests were perhaps established by multiple foundresses, as there were many old cells at these depths.

The uppermost, occupied cells found were 27 cm deep, both in Trinidad and Colombia (9 cm in Costa Rica); the deepest were 95 cm (19 in Costa Rica). They were often intermixed with earth-filled cells and young of different ages were often intermixed. Nonetheless, in general, eggs and younger brood were deeper in the nests than pupae. In six Trinidad nests with a total of 161 occupied cells, 82 percent of the 61 cells less than 70 cm in depth contained pupae and only 7 percent contained eggs or feeding larvae. For the 100 cells over 70 cm deep, the figures are 51 percent for pupae and 37 percent for eggs and feeding larvae.

The tendency of the tropical nests to be very deep, despite humid climate, is interesting, since in Europe and North America (Michener and Wille, 1961) halictid nests are deeper in dry than in humid seasons. Perhaps soil temperature is also important in influencing nest-depth. It is also true that the heat of the tropical sun tends to dry the soil more in a given time than the same period of sunshine in the north. In both Colombia and Trinidad, the surface soil seemed rather dry much of the time in January, despite frequent rains.

All cells (Fig. 14) found in the tropics correspond to Chandler's male-and-work-

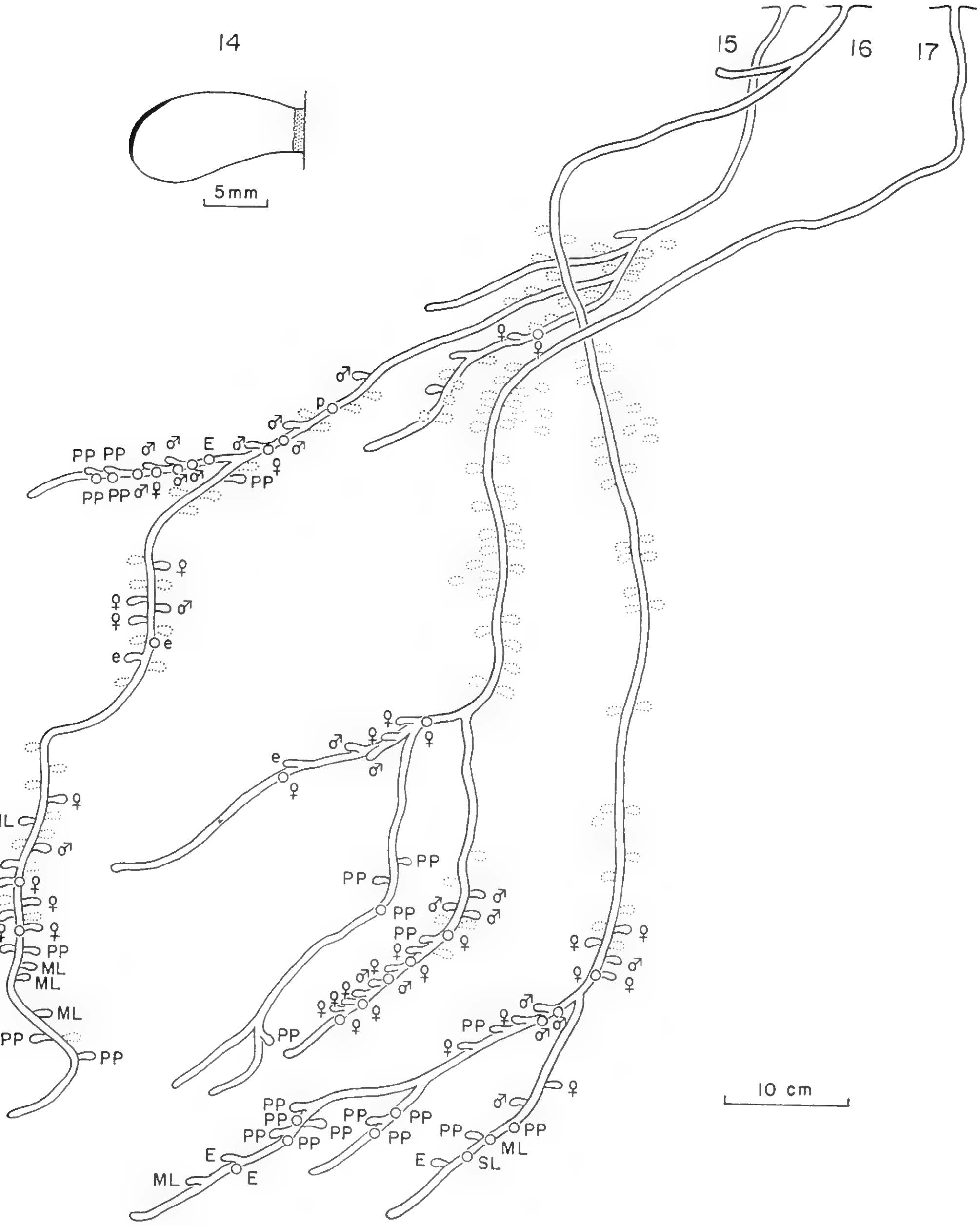


FIG. 14. Cell from Curepe, Trinidad. Black represents larval feces.

FIGS. 15-17. Nests from Curepe, Trinidad, December, 1971, and January, 1972; contained 14, 16, and 12 adult females, respectively. The symbols used in these and other illustrations of nests are as follows: Dotted cell = earth-filled, abandoned cell; m = moldy; P = pollen in open cell, being provisioned; e = empty, adult recently emerged; E = egg; SL = small larva; ML = medium-sized larva; PP = large larva, usually prepupa; ♂ ♀ = pupae of the sex indicated.

er-producing cells. The southern bees are somewhat larger, hence measurements are in general a little longer, as follows: Cell length (including the neck) 12 to 20 mm (Chandler's measurements apparently did not include the neck); diameter 6 to 7 mm; diameter of neck 3.5 mm. The cell-closure was usually about 1 mm thick and most cells were 14 to 15 mm long including the neck or closure. Sometimes there was a small irregular hole in the closure. This might result if some of the loose soil fell out, but did not seem to be a result of the investigator's work.

The number of occupied cells per nest from six nests in Trinidad ranged from 18 to 44 ($\bar{X} = 34$) (11 in Costa Rica). Earth-filled cells were at least as numerous and probably more so; counts were difficult to make and were not seriously attempted. This mean is enormously greater than means for Litte's nests in New York, but the maxima are in the same range.

Food-masses were shaped like those in Chandler's worker-and-male-producing cells, but were slightly larger, 4.5 × 4.5 × 2.8 mm, the last being the vertical measurement.

Colony size: Colonies in the tropics are markedly larger than those in the cool temperate regions and those excavated were not obviously eusocial, but seemed more nearly communal (terminology of Michener, 1974). Eleven tropical colonies have been partially or fully examined. The smallest which was excavated was from Costa Rica, with only four females (one from Trinidad had only one foraging bee and at least one other bee in the nest, but was not excavated). The largest colony fully studied was from Trinidad; it contained 16 females. Another, from Colombia, contained 11 foraging bees and an estimated 21 in total. In six fully-excavated, tropical nests, three opened in June and July in Costa Rica and Oaxaca, three in December and January in Trinidad, the mean number of females was 11.3.

Immature stages: The nests studied in Trinidad in December and January, Colombia in January, Costa Rica in July, and Oaxaca in July contained immatures of all stages. The climatic regimes in these areas are reasonably similar and production of young of both sexes is presumably continuous with the probable exception of the brief period when adults disappear from flowers (in Trinidad).

Guards: In Trinidad and Colombia guards were sometimes seen at the nest entrances. They are inconspicuous compared to those in northern, summer colonies and in many cases an apparent guard may be only a bee about to leave the nest. Usually, they retreat when disturbed, but one turned and blocked the nest entrance with her abdomen. Four guards were collected and subsequently measured and dissected. From this small sample no suggestion of consistent size or internal differences between guards and foragers was detected. The guards were of moderate size, little to considerably worn, mated or unmated, with varying amounts of ovarian enlargement.

Bees associated with nests: Data are available on 62 bees associated with nests in Trinidad. Except for one, possible nest-foundress and one or two possible, potential foundresses (large young bees), this sample is a reasonable tropical counterpart for Litte's sample of daughter bees from nests in New York. Data are presented in Table 2. The following features are worthy of comment: (a) Frequency of mated bees, amounting to 58.1 percent of all bees. (b) Existence of some worn, unmated bees. (c) Absence of bees with ovaries of class A (fully enlarged). (d) Abundance of bees with moderately enlarged ovaries (class B), amounting to 51.6 percent of the individuals, mostly mated. (e) Lesser abundance of individuals in ovarian class C, amounting to 38.7 percent, mostly unmated. (f) Scarcity of individuals with slender ovaries (class D), amounting to only 9.7 percent, mostly unworn and all unmated. The contrast with Litte's data is striking, as noted in the Discussion below. The mean size of bees associated with nests did not differ significantly from that of foragers.

For the few Trinidad nests which were completely excavated with all inhabitants captured, 47.5 percent of the 40 females were taken at the nest-entrances, returning with pollen. Pollen-collecting individuals have approximately the same mean head-width and variance thereof as do all females from Trinidad. Of the pollen-collectors, 63.8 percent were fertilized. They ranged from unworn to the most worn of all the individuals taken at the nests; nearly half had indices of wear less than 5. Nearly all showed some ovarian enlargement (classes B or C), although 3.2 percent of the pollen-collectors have ovaries placed in class D. Among pollen-collectors, 23.7 percent had an oocyte 2.0 mm long or longer, often apparently nearly ready to lay; such bees were all fertilized. Not a single nest-bee, including the most queenlike individual, contained an oocyte approaching 2 mm in length. Thus, it seems that the foragers are the principal reproductives, as in solitary bees.

It is clear, however, that not all the bees mate and lay eggs. Of the bees associated with nests, about one third had an index of wear of 5 or more and were therefore presumably the older individuals; of these 33.3 percent were not fertilized and had ovaries of classes C or D. Thus, about one sixth of the bees are apparently nonreproductive workers. Such individuals are not always small bees, but at least among foragers there was a significant, positive relationship among ovarian-width, mating, and head-width, suggesting that larger bees are more likely to become reproductive than smaller ones. (For details see material below on Foragers.)

Of the nest-bees (taken in the nests), over half were unmated, mostly with indices of wear of 1 or 2. Although such bees are presumably young adults that have foraged little if at all, some showed some ovarian enlargement (class C). Nest-bees showed a size-range and mean size essentially the same as those taken (nearly all carrying pollen) as they returned to their nests and as foragers in general.

Foragers: To elucidate the attributes of foraging bees, all the females taken in Trinidad in the special collections from flowers were measured and dissected. Nearly all these bees were collecting pollen. The few that had little or no pollen on the scopa were in no other way different from those that were collecting pollen. Hence, all are termed foragers and were analyzed together with the foragers caught returning to nests with pollen, making a total of 383 females. Head-widths of the specimens from Curepe, Trinidad, in the collection of the Commonwealth Institute of Biological Control were also measured, thus providing size data on 147 additional females.

The most noteworthy attribute of the foragers is the high percentage that have enlarged ovaries and are mated. Data on these features are shown in Table 2, and support, with some modifications, the comments on bees associated with nests, as follows: (a) Mated foragers, 55.6 percent of total, only slightly more numerous among worn than among little worn and presumably younger bees. (b) Existence of worn, unmated bees. (c) Small numbers of bees with ovaries in class A. (d) Abundance of bees with moderately enlarged (class B) ovaries, totaling 49.9 percent, the great majority mated. (e) Abundance of bees with less developed ovaries (class C), amounting to 45.4 percent, mostly unmated. (f) Scarcity of individuals

TABLE 2. Percentages of insemination (+, o) and ovarian classes (A-D) in bees from Curepe, Trinidad.

	Index of Wear	A+	Ao	B+	Bo	C+	Co	D+	Do	N
Associated with nests	< 5	....	....	36.8	7.3	17.1	26.8	....	12.2	41
	≥ 5	....	....	66.6	....	......	28.6	....	4.8	21
Foragers	< 5	4.1	....	41.0	8.5	10.0	35.8	....	0.7	271
	≥ 5	0.9	....	46.4	4.5	9.8	34.8	....	3.6	112

with slender ovaries (class D), only 1.5 percent, mostly worn, all unmated.

An analysis of variance demonstrated no significant heterogeneity among bimonthly means of head-widths. Thus, no seasonal size variation is recognizable. The frequencies of head-widths among all females from Trinidad are shown in Figure 18.

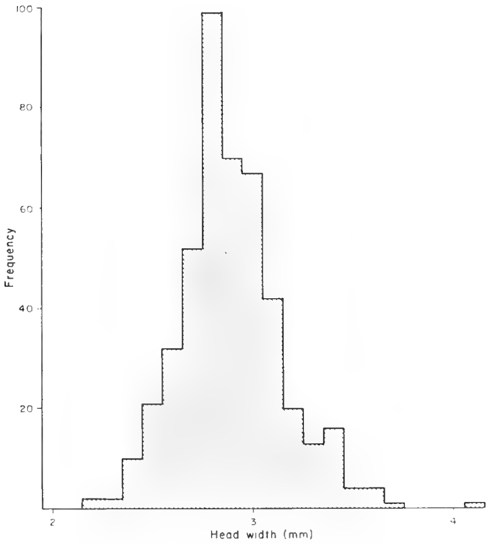


FIG. 18. Histogram showing frequencies of head-width classes of females from Curepe, Trinidad.

There is a general positive relation between size and insemination, so that the larger bees are more likely to be inseminated. Thus, of those whose spermathecae were examined, 51.4 percent of the 140 below the modal head-width were unmated while only 37.7 percent of the 159 above the modal head-width were unmated; the mean head-width of mated bees was significantly larger than that of unmated bees ($p << .001$). Nonetheless, both mated and unmated bees were widely scattered across the size range. Although the two smallest bees in the study were unmated, the third in size was mated. At the other end of the size scale, the largest of all the bees was unmated.

Large bees are also more likely to have considerably enlarged ovaries than small bees. There is a positive correlation ($r = .273$, $p < .01$) between ovarian width and head-width, and a similar but weaker correlation ($r = .205$, $p < .01$) between length of the longest oocyte and head-width. These relationships are not entirely a result of the limited space available for ovaries in small bees, as shown by the large ovaries of the smallest of all our dissected bees. Its longest oocyte was longer than average (1.53 mm), while at .71 mm in maximal ovarian width, only 7.6 percent of the bees had wider ovaries. (Not surprisingly, there is a strong correlation, $r = .729$, $p << .01$, between ovarian width and length of the largest oocyte.)

Since there are positive relationships between head-width and the percentage that have mated and between head-width and ovarian width, it is not surprising that there is also a strong positive relationship between ovarian width and mating, maximum ovarian width of mated females being greater than that of unmated ones ($p << .001$). Mean ovarian width of mated foragers is 0.59 mm, of unmated ones, 0.40 mm. There is no significant correlation ($r = .003$) between the index of wear and ovarian width; there are some extremely worn bees with slender ovaries and little-worn bees with strongly enlarged ovaries.

Probably, there is no meaningful relationship between mating and subsequent survival and work. Among 243 females with an index of wear of less than 7, 42.8 percent were not mated. Among the 55 females with an index of wear of 7 or more, 50.9 percent were unmated. Thus, one might suspect that unmated bees work harder, live longer, or visit flowers more when old, than do mated bees. The difference is neither great nor statistically significant, however. Among the 21 most worn bees there are both unmated and mated individuals at the frequencies of 11:10. Thus, there is no consistent evidence of a progressive change in the ratio of mated to unmated bees as the bees pass from unworn to much worn. This suggests that females mate when young or not at all.

There is a weak indication that larger bees tend to work more or longer than smaller ones, the correlation coefficient between head-width and wear being $r = .163$ ($p < .01$). However, the 45 bees whose indices of wear were 9 or above had almost exactly the same mean size as did all the bees from the special collections. The second and third largest bees in the study were much worn, with indices of wear above 15.

Table 3 summarizes the relationships described above.

Large bees: In cool, temperate climates, the overwintering gynes that establish nests in the spring and remain as queens through at least part of the summer are large as compared to the summer daughters, which are here called workers. A small percentage of the tropical females seem to be similarly large, and special attention to them seems worthwhile. Examining the largest 10 percent of the 403 dissected females from Trinidad and Colombia, we find unworn or nearly unworn individuals (indices of wear 1 and 2) among those taken in January, March, April, July, August, September, October, and December. Thus, large females seem to be produced in small numbers throughout the year. Much-worn, large individuals also occur throughout the year.

TABLE 3. Relations among attributes of females of *Halictus ligatus* from Curepe, Trinidad. The upper right represents individuals associated with nests in December, 1971, and January, 1972. The lower left represents foragers (mostly pollen collectors, hence the blank lower row) taken throughout the year. The numbers of the columns correspond to the numbers of the rows. + = a positive relationship; 0 = no significant relationship.

	1	2	3	4	5
1. Head width	....	+	+	0	0
2. Ovarian width	+	....	+	0	+
3. Insemination	+	+	....	0	+
4. Wing wear	+?	0	0	....	0
5. Pollen collecting	....	....	....	....	....

As is to be expected from the preceding subsection, most of the 40 large bees are mated and have enlarged ovaries, although the ovaries are not strikingly larger than those of many smaller bees. Of nine that were unmated, six were unworn and even though on flowers, some of them carrying pollen-loads, they would probably ultimately mate. The remaining three, unmated and worn, collecting pollen, including some of the largest bees in the study, show that not all large bees become reproductives. Most large bees, however, are more reproductive than most small bees: 31 of the 40 large bees had ovaries at or above the median ovarian width and 14 had an oocyte 2.0 mm long or longer. In terms of ovarian classes, 4 large females were in A, 27 in B, and 9 in C.

Since the only three tropical nests that have been seen early in establishment contained a lone large bee, and also in conformity with observations in the north, it seems probable that a nest is usually started by a large bee.

One nest excavated in Trinidad still contained a possible foundress, here hesitantly called a queen (head-width 3.63 mm, mated, index of wear 9, ovaries of type A with maximum width .81 mm). She was larger than any other bee in the nest except a fresh young adult of the same size, mated, but with rather slender ovaries (maximum width .30 mm). In addition to the queen, the colony contained seven foragers and four other bees that were in the nest, a total of 12 bees. In size, ovarian development, and frequency of being mated, the nonqueens were similar to the bees in other nests, all of which lacked individuals that were recognizable as old queens. Therefore, the queen seemed not to be playing a role in inhibiting reproductive development among her nest mates.

III. DISCUSSION AND CONCLUSIONS

With the existing information, there is no way to determine how much of the observed geographical variation in reproductive and nesting behavior is due to the direct effect of environmental differences among regions and how much to genetic differences among populations. Probably, both are involved. The duration of annual activity, of course, varies widely with the climatic zone, thus: Three and one half months at 47° latitude, five and one half months at about 40° latitude, eleven or twelve months at 27° latitude and eleven months (nine with full activity) at about 10° latitude. The seasonal period of inactivity in cool, temperate regions is related to low winter temperatures. Adult, mated females are the only overwintering form. In Florida and the tropics, the inactive period is brief and appears to be related to the dry season. Such inactivity probably occurs only in places where or years when there is a marked dry season. Survival occurs by adult females of all sorts and, if the dry season is short, by males and even developing immature stages. In the arid, Southwestern United States, the same is probably true, except that the inactive season may be long, due to protracted aridity and probably also winter. Data are needed regarding this species in the Southwest.

In cool, temperate regions *Halictus ligatus* lives in rather shallow, commonly aggregated nests. In Kansas (39°) and more southern localities, the nests are much deeper and are rarely aggregated.

In Trinidad and Colombia, guarding was rarely observed and there was no evidence of specialized, guarding individuals, as are found in *Lasioglossum zephyrum* (Brothers and Michener, 1974). In the cool, temperate zone, however, guarding is common, often by a large-headed bee, probably frequently the queen. Clearly, various types of individuals may be specialized as guards. However, the queen's large head seems to be especially advantageous for closing the burrow entrance. If the queen is essential for survival of the colony, it is surprising that she would often or even sometimes adopt the high risk activity of guarding, but similar behavior is known among large-headed females of certain other halictine species, in contrast to species whose queens have ordinary-sized heads. Perhaps the good guarding qualities of large heads outweigh the danger of being near the soil surface for long periods.

Little is known about colony-establishment in tropical and warm, temperate regions. In the few known cases, nests were started by lone females. This is apparently the strongly predominant method also at about 40° latitude (Indiana). However, at 42° (New York) 25 and 32 percent of the spring nests in two different years were inhabited by two or more gynes forming a semisocial colony. At 43° (Ontario), 60 percent of the spring-nests contained such colonies. In such a colony, the largest bee ordinarily becomes the queen, the others become auxiliaries or workers which may survive to forage with the daughters. It seems possible that where the active season is short, auxiliaries are important to start activity rapidly. Also, smaller and perhaps reproductively disadvantaged individuals might have lower fitness in such a climate than in warmer areas and hence might attain greater inclusive fitness by joining other females. The situation parallels that found in *Polistes fuscatus* in which gynes often join to form semisocial colonies in the northern, but not often in the southern part of the range (Heather Dew, personal communication).

In Ontario, males apparently are produced throughout the season when daughter females are produced. Thus, they first appear in late June. Perhaps this is important to provide males to mate with females to replace any overwintered queens that die, thus keeping the colonies developing as rapidly as possible through the short season. Farther south, in New York and Indiana, early-summer offspring are all females and males do not appear until late July. In the tropics and probably in Florida, as in Ontario, males are produced throughout the season when females are produced.

Overwintered queens die in July or August, after only a few months of post-hibernation activity, in the higher latitudes. In colonies whose queens die early, daughters can become replacement queens, but apparently they rarely attain fully queenlike ovarian development. In Trinidad, the bees that establish nests may be similarly short-lived, for only one colony was found to contain a probable foundress. Daughter bees and their descendants, however, regularly become reproductive and maintain the colony for months and perhaps years. Having higher reproductivity than workers in the north, they perhaps also found colonies.

In cool, temperate regions, daughter (i.e., worker) production is more or less continuous after the first daughters mature in late June (latitude 40°-43°) until overwintering females are produced in late summer. In Indiana and New York the maximum number of adult workers found in a nest at any one time was nine or ten. The mean number of mature females in nests in New York was only 4.3 and 3.4 in different years. In the tropics, colonies become larger. One from Trinidad contained 16 females and one from Colombia an estimated 21. The mean, adult female population (six nests only) was 11.3. The two Floridian colonies studied were relatively large and colonies there may attain sizes similar to tropical ones.

Probably, throughout the range, there is a continuum in size from smallest to largest females, with no bimodality. In cool, temperate regions, females produced in late summer have a large average size, mate, overwinter, and establish colonies in the following year. In Trinidad, such large females are produced throughout the season. They may well be important in establishing colonies, as in the north. If so, colony establishment must be scattered through the year. Not all large bees in Trinidad are queenlike, however. Some are unmated and have relatively slender ovaries.

Large females are reported by Chandler to be produced in unusually large cells with elongate rather than subspherical food-masses. Similar large, elongate food-masses were found in a Floridian nest by G. C. and K. R. Eickwort.

In Litte's New York study, the daughter bees that were mated totaled 5.7 percent in July, 17.3 percent in August. The numbers were small and the difference between the months, while reasonable in view of the increasing male population in late summer, may not be meaningful, as Litte points out. By contrast, in Trinidad, 58.1 percent of the bees that we found associated with nests and 55.6 percent of the foragers were mated. As only a few bees were suggestive of temperate zone queens in large size and much enlarged ovaries, the above comparison of mating frequencies seems reasonable.

Ovarian development, likewise, is much greater among tropical than New York bees. As shown in Table 4, Litte found only 12.6 percent of July and August daughters with ovaries of classes A and B. Probably, these were mostly or all replacement queens rather than workers. By contrast, in Trinidad, about 53 percent had enlarged ovaries. All the bees dissected with an oocyte nearly ready to be laid were foragers. In daughter bees in New York, positive relationships exist among head-width, mating, and wing-wear (longevity ?). Similar, although not identical, relationships hold in the Trinidad population. A small sample taken in April in south central Florida shows a high percentage of mated bees with enlarged ovaries there also.

Table 4. Percentages of bees (excluding nest foundresses) from New York and Trinidad having ovaries of various size classes (A-D).

Ovarian class	AB	C	D	N
New York (Litte)	12.6	23.3	64.2	151
Trinidad (associated with nests)	53.1	37.5	9.4	64
Trinidad (foragers)	53.6	45.1	1.3	384

In summary, different populations of *Halictus ligatus* have adopted different social strategies as adaptations to differing environments. In cool, temperate regions, spring-nests are occupied by lone individuals or semisocial colonies (sense of Michener, 1974) of foundresses. In either case a eusocial colony develops in the summer, the queen sometimes being replaced by one of her daughters. In tropical regions, the same sequence is probably followed although simple eusocial colonies with the queen as the only reproductive were not found and this condition is probably short lived. Many of the daughters become reproductive in the tropics but these daughters are not queenlike in behavior, for they regularly forage. The colony thus becomes more nearly semisocial, its maintenance being dependent on egg-laying daughters, or granddaughters, etc. By themselves, such individuals might also be regarded as communal, but there are also other daughters that are not reproductive and that are workers. Clearly, terms like communal and semisocial, while useful for many bees, fail to describe societies such as those in nests of *Halictus ligatus* in the tropics. Words like queen and worker also become difficult to apply successfully. They are helpful but must be used with caution and explanations.

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THE COMPARATIVE ANATOMY OF CAECILIAN MANDIBLES AND THEIR TEETH

By

EDWARD H. TAYLOR

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The Comparative Anatomy of Caecilian Mandibles and Their Teeth

Edward H. Taylor

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ABSTRACT

The dentary and splenial teeth on the mandibles were counted for 23 species of caecilians in 14 genera and 5 families. The genera *Scolecomorphus, Caudacaecilia, Dermophis* and *Siphonops* lack splenial teeth. However, lack of splenial teeth is a trait of the species for some caecilians in genera where other species have them and is therefore not a generic nor familial trait. The number of teeth on the mandible and their sizes are potentially useful in taxonomic identification of species.

INTRODUCTION

The teeth of caecilians were discussed at some length in my monograph on caecilians of the world (Taylor, 1968). The figures of the buccal region, drawn by the Persian artist Mr. Habib Kamrani, that appear in the monograph do not have photographic accuracy, but do present general relationships of the dental series to buccal anatomy. Additional information on the mandible and mandibular teeth is provided in the present review.

MATERIALS AND METHODS

The number of prepared skeletons in museums is small, but through the kindness of their curators I was permitted to extract the mandible or part thereof from certain specimens. In preparing the specimens, little attention had been given to opening the jaws and as a result many of the teeth are broken and often the bones on which the teeth are present are likewise injured.

The artist who prepared the figures, Mr. William Cutter, mounted the specimens in a stationary pan of water with a background of black velvet cloth. The camera was mounted on a mechanism that permitted it to be moved up and down. Unfortunately, the bones of the lower jaw were not always mounted at exactly the same angle, or the water permitted some movement while focusing, thus sometimes creating illusory differences where none exist. This must be taken into account when comparing the two sides of the jaw.

OBSERVATIONS

The actual number of teeth varies with age, new teeth being added on the distal portion of the bone. Teeth may be shed and replaced (as explained in the monograph, pages 26 and 27) as a "group" phenomenon.

The individual teeth tend to break off near their middle, thus exposing the fact that they are hollow. Near the base of each tooth is an opening that serves as a passageway for nerves and blood vessels. In counting the teeth, one must take into consideration these missing teeth, since in group replacement the full set is restored before the next group loss is begun.

The teeth of the second row in the lower jaw are designated splenials. These are usually very small and are often overlooked, because they may be partially concealed by the gingivae. They are smaller and almost always fewer than the dentaries. It may be necessary to remove parts of the gingivae on one side to find them. Certain genera may lack all traces of splenials.

Only brief comments in this paper are given on dentition of the various species and all pertain to the particular specimens illustrated. The figures serve to amplify those comments and to illustrate distinguishing characters.

Abbreviations for museums cited are: AMNH, American Museum of Natural History, New York; BMNH, British Museum of Natural History, London, England; EHT-HMS, Edward H. Taylor-Hobart M. Smith Collection, Lawrence, Kansas; DSBM, Division of Systematic Biology, Stanford University Collection (now in California Academy of Sciences, San Francisco); JAP, personal collection of the late James A. Peters; KUMNH, Museum of Natural History, Kansas University, Lawrence, Kansas; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; UIM, Museum of Natural History, University of Illinois, Urbana, Illinois; UMMZ, Museum of University of Michigan, Ann Arbor, Michigan; USNM, United States National Museum, Washington, D.C.

DESCRIPTIONS

Family SCOLECOMORPHIDAE Taylor

Genus *SCOLECOMORPHUS* Boulenger

Scolecomorphus kirkii kirkii Boulenger (Fig. 1). The dentary teeth are usually 14, but some larger preserved specimens I have seen have as many as 18. The dentary bone is relatively slender, the head and neck being distinctly narrower than the body. No splenial teeth.

The prevomerine and palatine series of teeth in all known members of this family are separated by a diastema, present in no other family.

Family TYPHLONECTIDAE Taylor
Genus *TYPHLONECTES* Peters

Typhlonectes compressicaudus (Duméril & Bibron) (Fig. 2A). There are 20 teeth indicated, 5 having been lost in a group long before preservation. Three splenial teeth. The dentary teeth are pointed, many broken near their middle, showing the teeth to be hollow. There are small basal openings on the inner side of the teeth, for passage of blood vessels and nerves. The anterior ventral edge of the dentary bone bears a short flange for the splenials.

Typhlonectes natans (Fischer) (Fig. 2B). There are 19 pointed, dentary teeth; posterior ones much smaller than anterior ones. The somewhat-widened, lower edge of the anterior part of the bone bears 6 or 7 very small splenials. The anterior dentary teeth are distinctly larger than in the preceding species.

These two forms and others of the family are aquatic, the young being born in the water, which they do not leave. Their large, baggy gills are absorbed before birth.

Family ICHTHYOPHIIDAE Taylor
Genus *ICHTHYOPHIS* Fitzinger

Ichthyophis mindanaoensis Taylor (Fig. 3A). Dentary teeth, 22; splenial teeth, 10, the series extending nearly half the length of the dentary bone.

Ichthyophis singaporensis Taylor (Fig. 3B). Dentary teeth, 20; splenial teeth, 10.

Ichthyophis kohtaoensis Taylor (Fig. 3C). Dentary teeth, 20-21; splenials, 17-18. The mandible is more slender than in the two preceding species and proportionately longer.

In this family, the postanal region has several transverse folds; the caudal terminus is usually pointed.

Genus *CAUDACAECILIA* Taylor

Caudacaecilia weberi (Taylor). In DSBM 21764 (Fig. 4A), there are 23 dentary teeth, almost equal in size. Splenials are absent. In DSBM 21758 (Fig. 4B), the dentaries are 22, all nearly the same size. No splenials. The tip of tail is bluntly rounded rather than pointed.

Splenials are absent in all members of this genus.

Family CAECILIIDAE Gray
Genus *CAECILIA* Linnaeus

Caecilia albiventris Daudin (Fig. 5). This species has most often been treated under the name *Caecilia tentaculata,* but that nominal species is in question as a *nomen dubium*, since it is based largely on a picture which cannot be verified with certainty. Dentaries, 12-13; splenials, 3 or 4.

Caecilia degenerata Dunn (Fig. 6). Anterior dentaries are elongate, slender, pointed, the 1st, 3rd, 5th and 7th teeth lost, most probably by group shedding before preservation. Six or 7 posterior teeth relatively very small. Two or 3 splenials present.

Caecilia nigricans Boulenger (Fig 7). Dentaries are relatively large, the 6 anterior teeth now broken, but elongate and sharply pointed in life. Nine or 10 smaller, posterior teeth. Anteromedian flange of the dentary bears 3 relatively very large splenial teeth.

Caecilia orientalis Taylor (Fig. 8). A badly damaged dentary bone, number of teeth indeterminate. The anterior teeth slender, pointed. Three splenial teeth. The posterior parts of the lower jaws are foreshortened, smaller than usual.

Genus *OSCAECILIA* Taylor

Oscaecilia bassleri (Dunn) (Fig. 9). Dentary bone relatively short, with 8 enlarged anterior teeth. The teeth numbered 1, 3, 5 and 6 showing a group loss; 3 much smaller, posterior teeth. Three small splenial teeth. Eye under bone, no eye socket (eye sometimes visible as a black dot through the transparent bone). A very slender species.

Oscaecilia ochrocephala (Cope) (Fig. 10). Six enlarged, anterior, dentary teeth and 4 much smaller posterior teeth. Four splenial teeth on the anterior, widened edge of the dentary. Eye under bone; subdermal scales present.

Genus *GYMNOPIS* Peters

Gymnopis proxima (Cope) (Fig. 11). The dentary teeth are 18-18, the posterior teeth not differing much in size from the anterior. The splenial teeth are 1-1 and a portion of the splenial area is broken from the dentary. Unfortunately, the dentary bones have been mounted at an incorrect angle and the teeth are pointing inwardly.

Gymnopis multiplicata multiplicata Peters (Fig. 12). Eight or 9 enlarged, anterior, dentary teeth, followed by 10 or 11 somewhat smaller teeth. The splenial flange of the dentary bone bears only a single tooth. Some preserved, young specimens have 12 to 15 teeth.

In this species there is no eye socket and the body folds have 5 rows of scales.

Genus *DERMOPHIS* Peters

Dermophis mexicanus mexicanus (Duméril and Bibron). In UIM 66889 (Fig. 13A), the dentary teeth are 15-15. The bone is broken on the right side of the figure. In MCZ 12121 (Fig. 13B), the dentary teeth are 13. In this genus no splenials are present.

Genus *SCHISTOMETOPUM* Parker

Schistometopum gregorii Boulenger (Fig. 14). Dentaries, 15-14, larger anteriorly, much reduced in size, posteriorly. Two splenials, one large and one very small on each bone.

Genus *SIPHONOPS* Wagler

Siphonops paulensis Boettger (Fig. 15). Dentaries, 15-15, bluntly pointed, diminishing in size posteriorly. No splenials in the genus.

Siphonops annulatus (Mikan). In EHT-HMS 1848 (Fig. 16), 11 or 12 teeth in dentary series, the tips somewhat rounded. In MCZ 19407 (Fig. 17), 14-16 dentaries.

Genus *GEGENEOPHIS* Peters

Gegeneophis ramaswamii Taylor (Fig. 18). Fragment of the dentary bone showing 13 teeth. Three splenials.

Genus *GRANDISONIA* Taylor

Grandisonia alternans (Stejneger) (Fig. 19). Dentary teeth, 20; splenial teeth, 6 or 7.

Genus *HERPELE* Peters

Herpele squalosoma (Stutchbury) (Fig. 20). Dentary teeth, 10-11. However, the number counted in preserved specimens usually varies between 10 and 15. The splenials in the figure are 3-3, although some other preserved specimens have 4 or 5.

Genus *GEOTRYPETES* Peters

Geotrypetes seraphini seraphini (A. Duméril) (Fig. 21). All teeth broken. Of the 9 anterior dentary teeth, 3 lost. The 9 posterior teeth, of nearly equal size, are much smaller than anterior 9. Splenials, 12-12.

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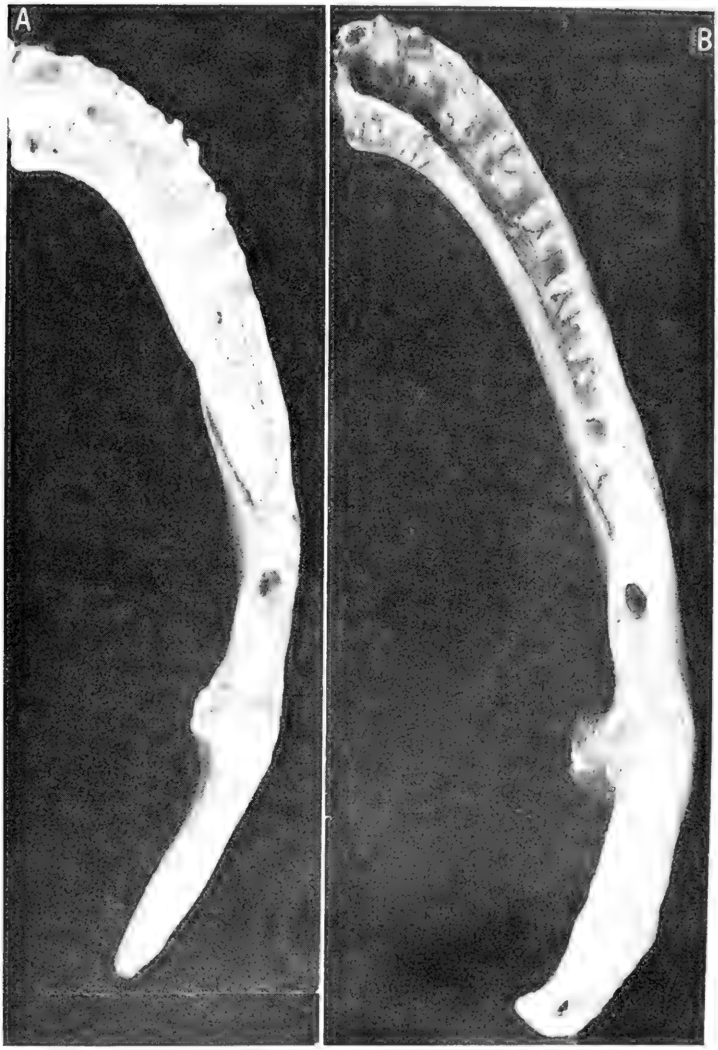

FIG. 1. *Scolecomorphus kirkii kirkii* Boulenger. MCZ 27120, Cholo Mts., Cholo District, Nyassaland.

FIG. 2. A. *Typhlonectes compressicaudus* (Duméril & Bibron). UMMZ 82854, Belém, Brasil. B. *Typhlonectes natans* (Fischer). AMNH 23418, Bogotá, Colombia.

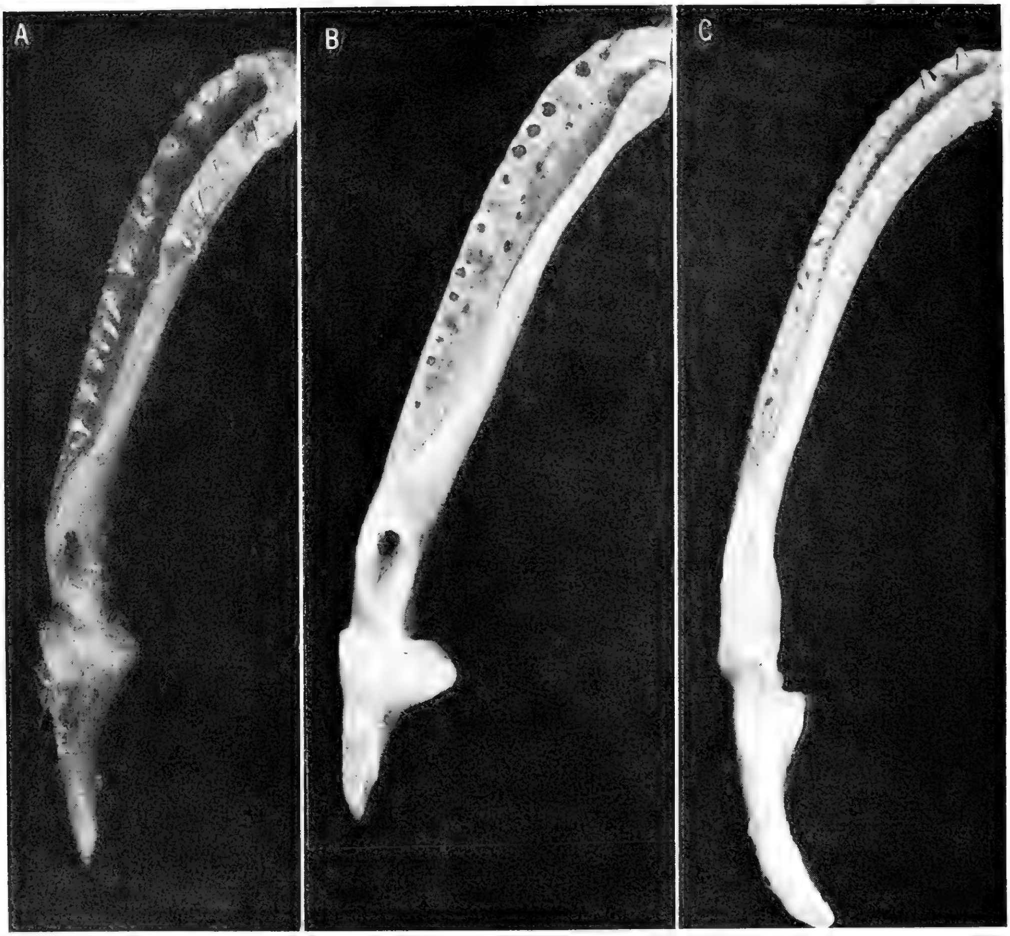

FIG. 3. A. *Ichthyophis mindanaoensis* Taylor. DSBM 20926, Dapitán, Misamis, Mindanao, Philippine Islands. B. *Ichthyophis singaporensis* Taylor. BMNH RR 1959-1-2-43 (holotype), Singapore Island, Malay Peninsula. C. *Ichthyophis kohtaoensis* Taylor. EHT-HMS 3935, 10 mi N Chiang Dao, Chiang Mai Province, Thailand.

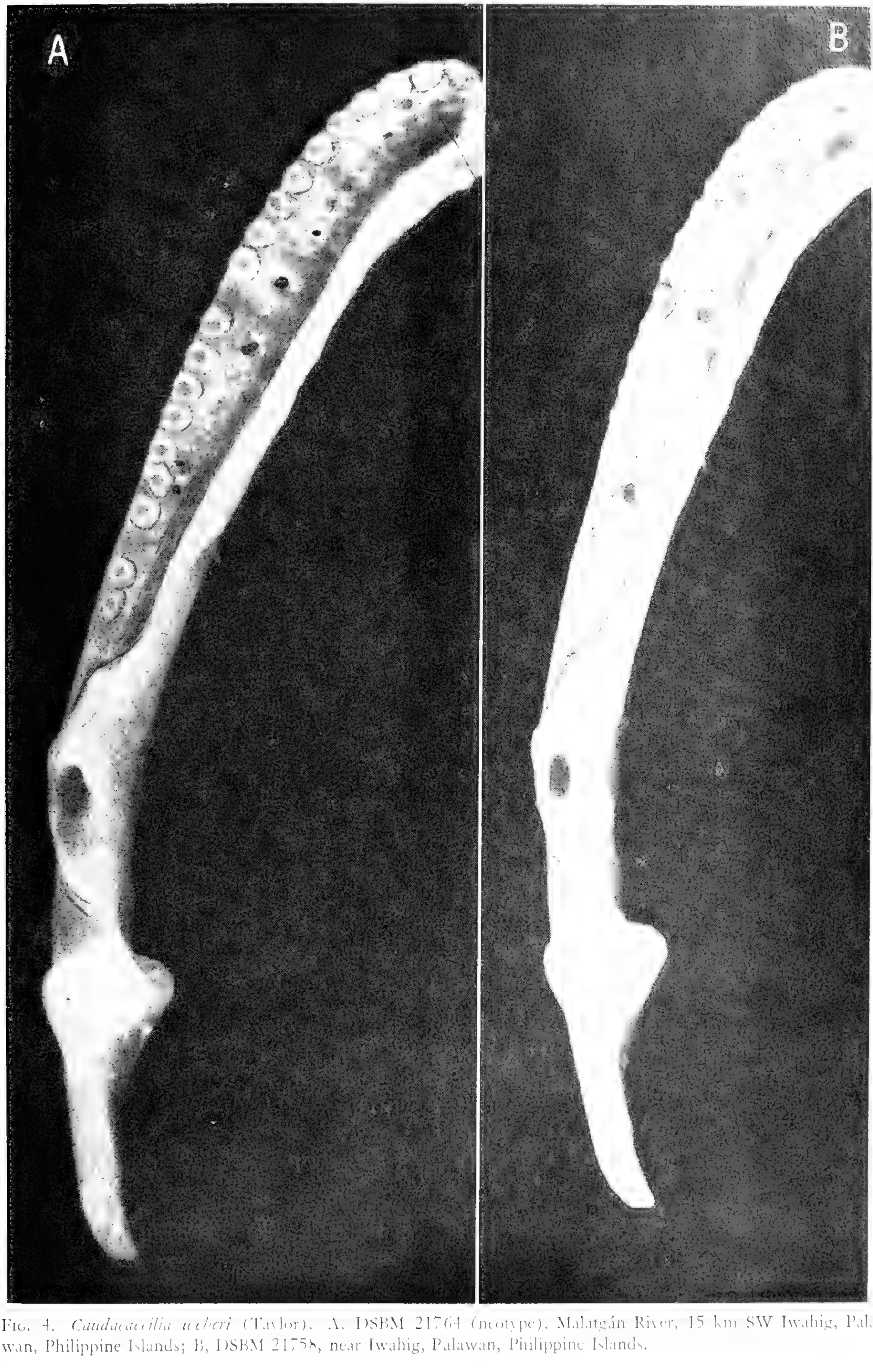

FIG. 4. *Caudacaecilia weberi* (Taylor). A, DSBM 21764 (neotype), Malatgán River, 15 km SW Iwahig, Palawan, Philippine Islands; B, DSBM 21758, near Iwahig, Palawan, Philippine Islands.

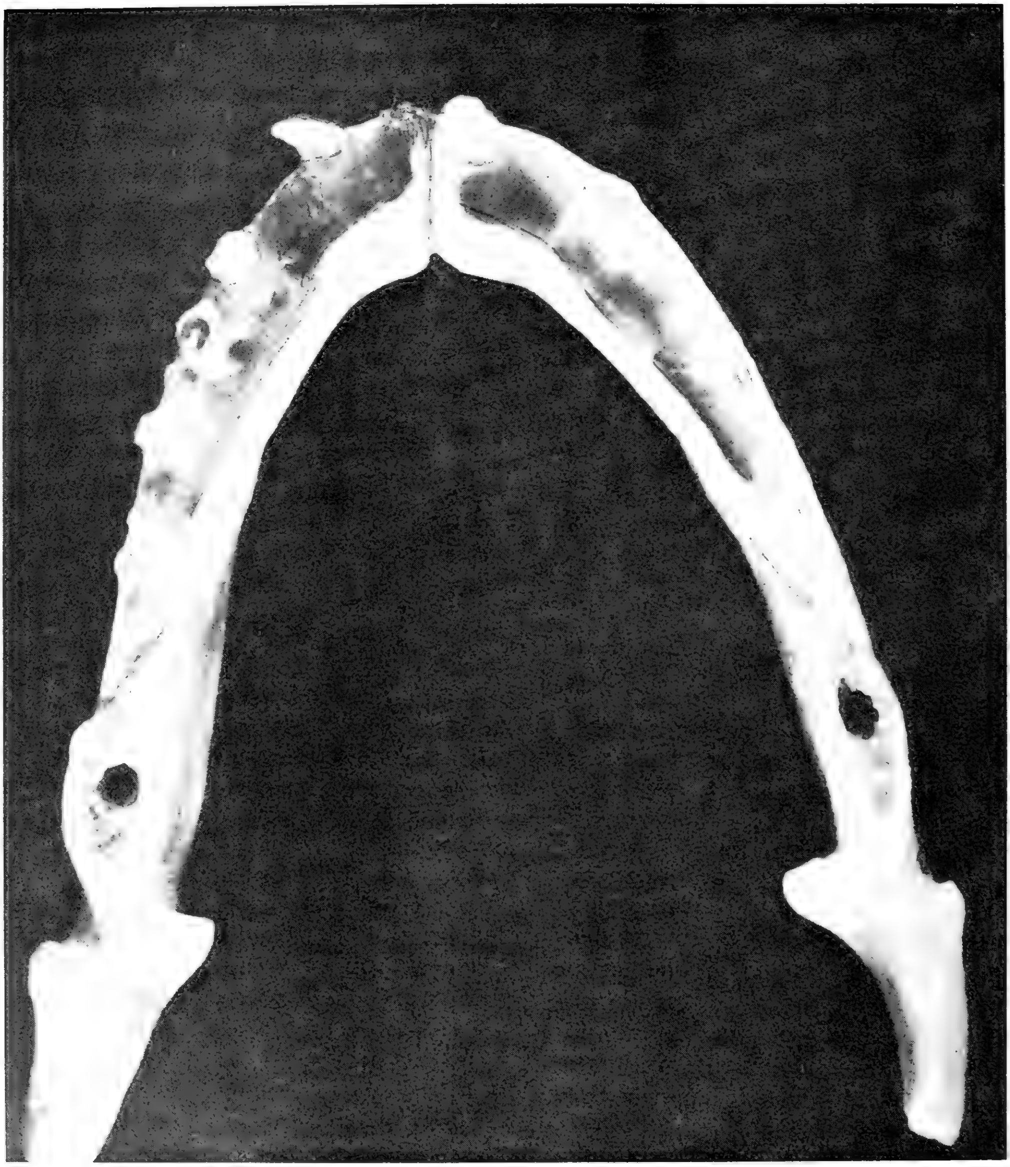

FIG. 5. *Caecilia albiventris* Daudin. AMNH 49960, Río Copataza, Ecuador.

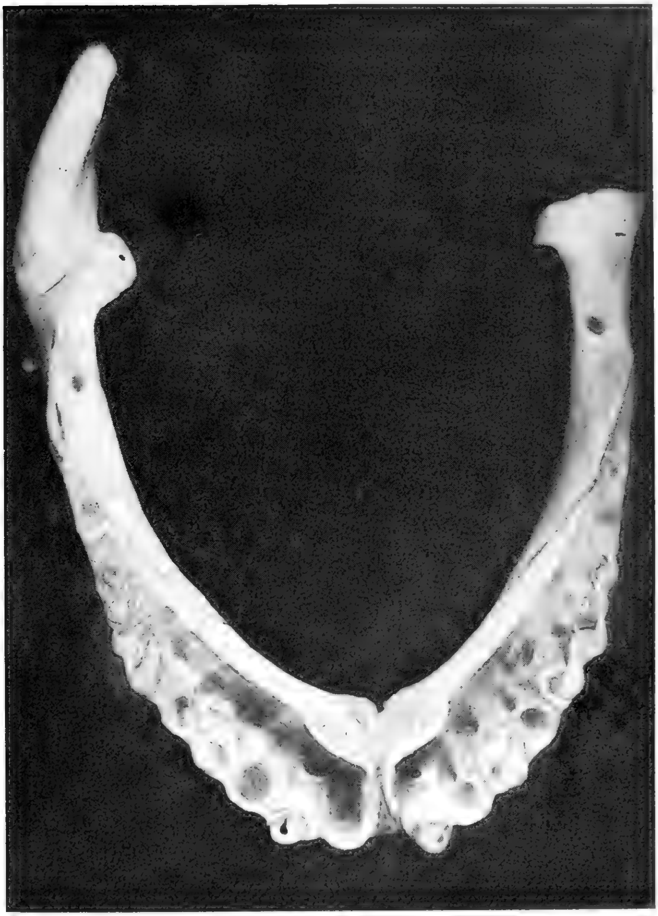

FIG. 6. *Caecilia degenerata* Dunn. AMNH 23354, either Boyaca or Condinamarca, Colombia.

FIG. 7. *Caecilia nigricans* (Boulenger). KUMNH 94377, Cana, Darién, Panamá, 500 m.

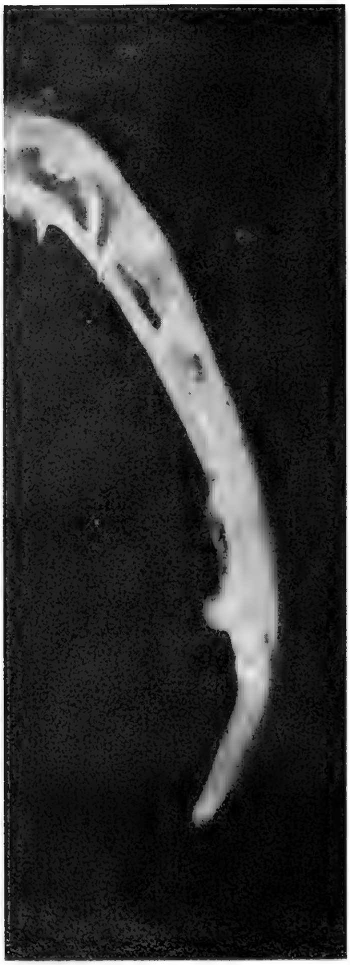

FIG. 8. *Caecilia orientalis* Taylor. JAP 4690, Napo Pastaza, Ecuador.

FIG. 9. *Oscaecilia bassleri* (Dunn). EHT-HMS 4675, Ecuador, specific locality uncertain; collected by Orces.

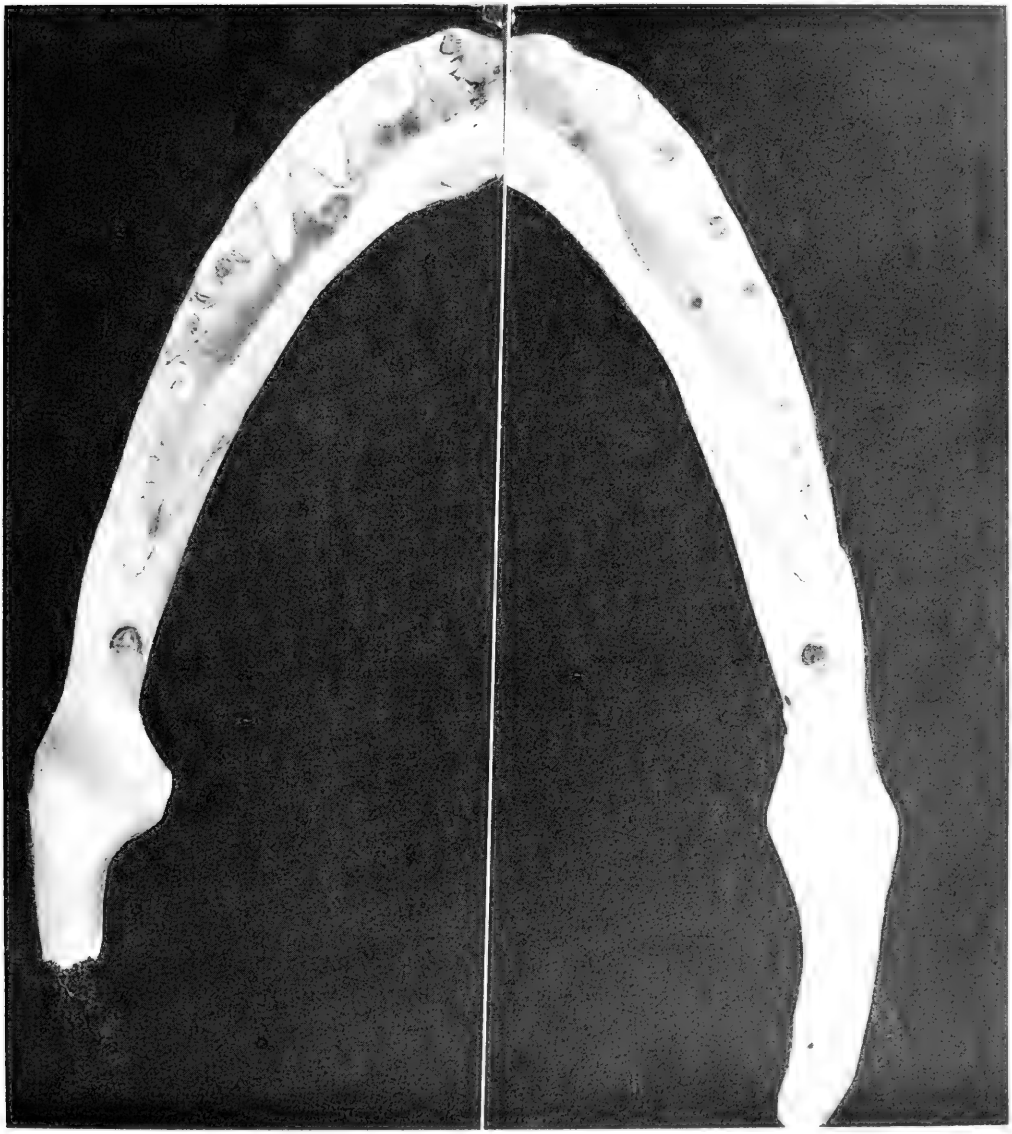

FIG. 10. *Oscaecilia ochrocephala* (Cope). EHT-HMS 1736 (41092), Gatún, Panamá Canal Zone.

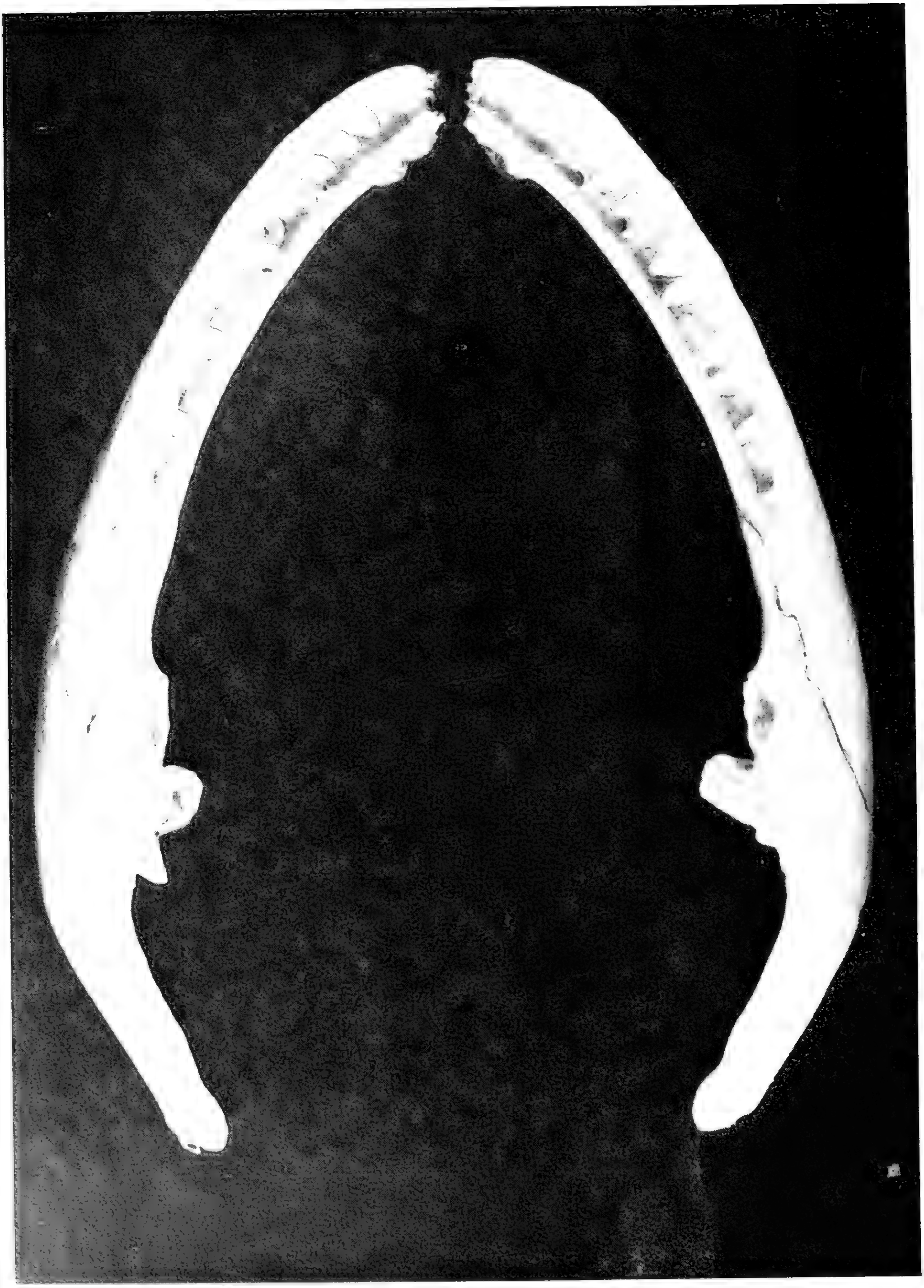

FIG. 11. *Gymnopis multiplicata proxima* (Cope). FHT-HMS 4712, Rancho Dominica, Turrialba, Limón Province, Costa Rica.

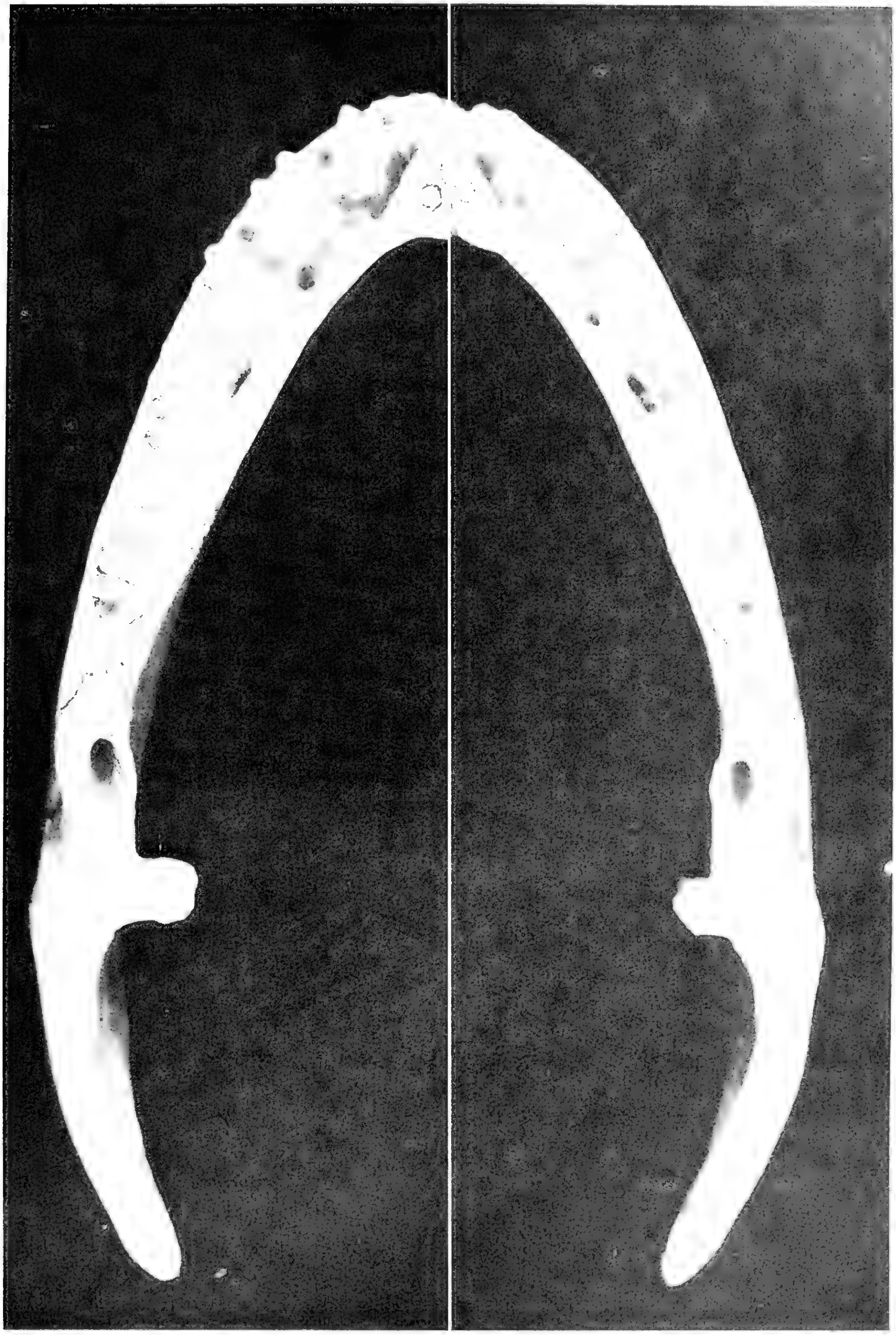

Fig. 12. *Gymnopis multiplicata multiplicata* Peters. EHT-HMS 4702, San Bosco, Tilarán, Guanacaste Province Costa Rica.

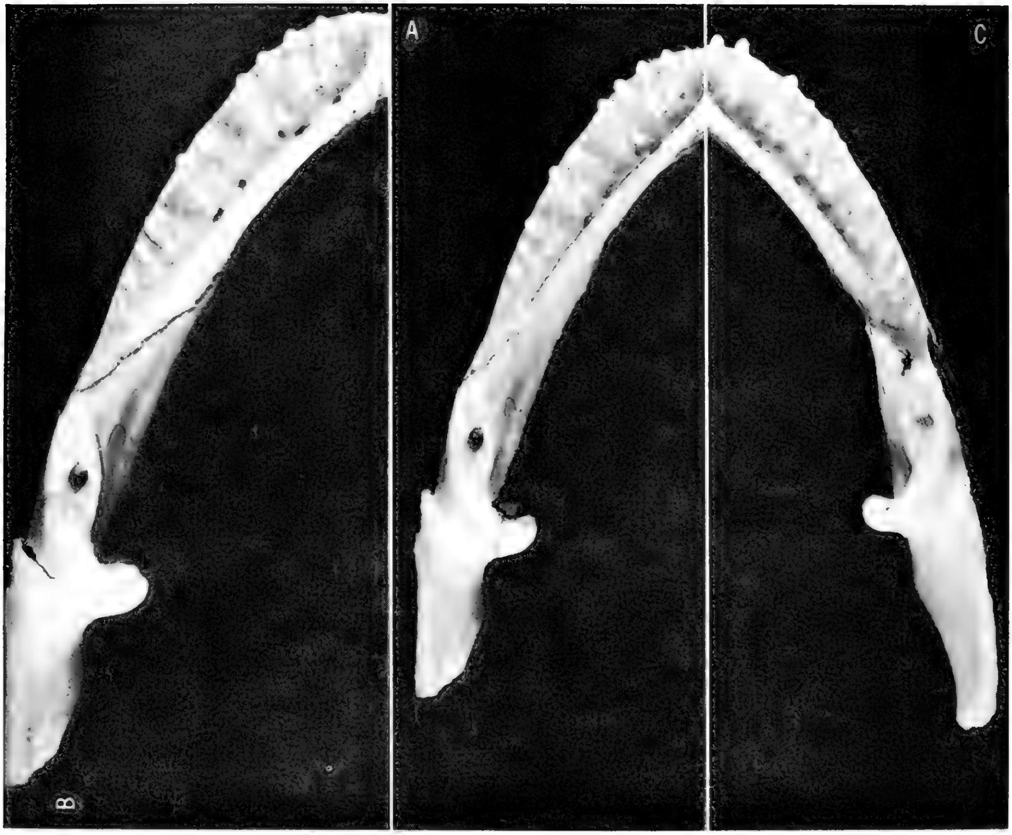

FIG. 13. *Dermophis mexicanus mexicanus* (Duméril & Bibron). A, B, UIM 66889, Finca El Naranjo, Suchitepequez, Guatemala; C, MCZ 12121, Guatemala.

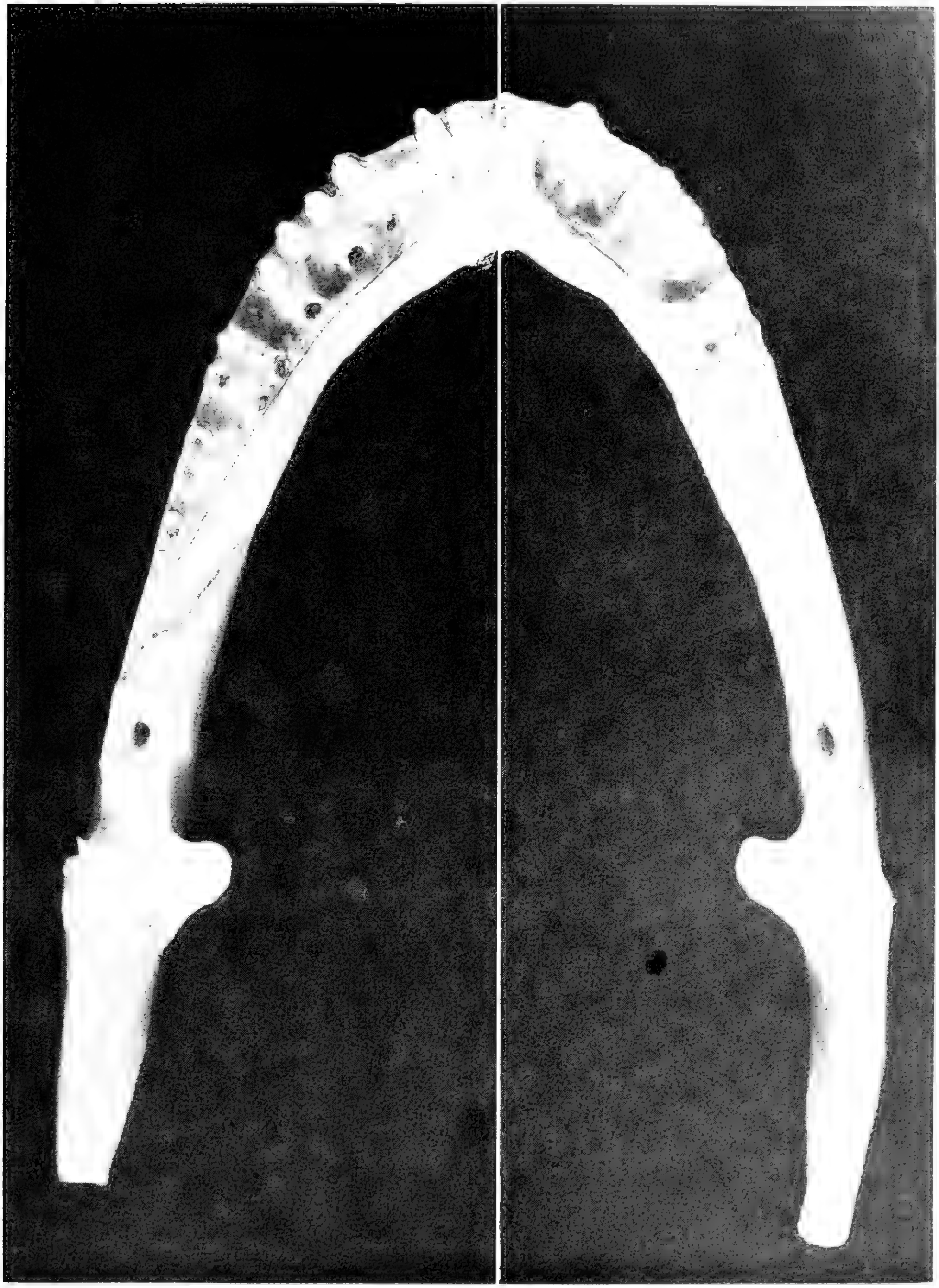

FIG. 14. *Schistometopum gregorii* (Boulenger). MCZ 20117, Lake Peccatoni, Kenya.

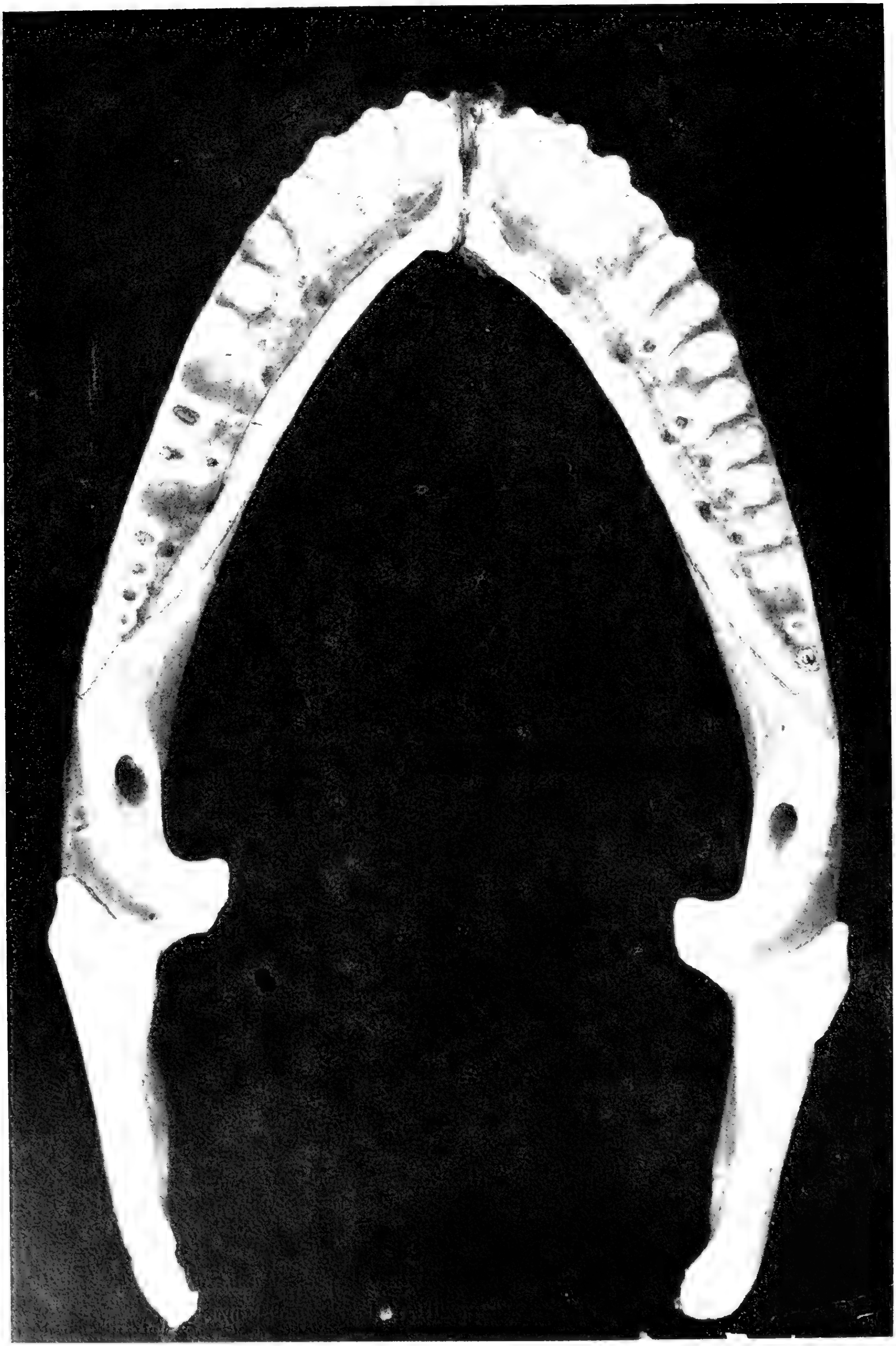

Fig. 15. *Siphonops paulensis* Boettger. EHT-HMS 3235, southern Brasil (no exact locality).

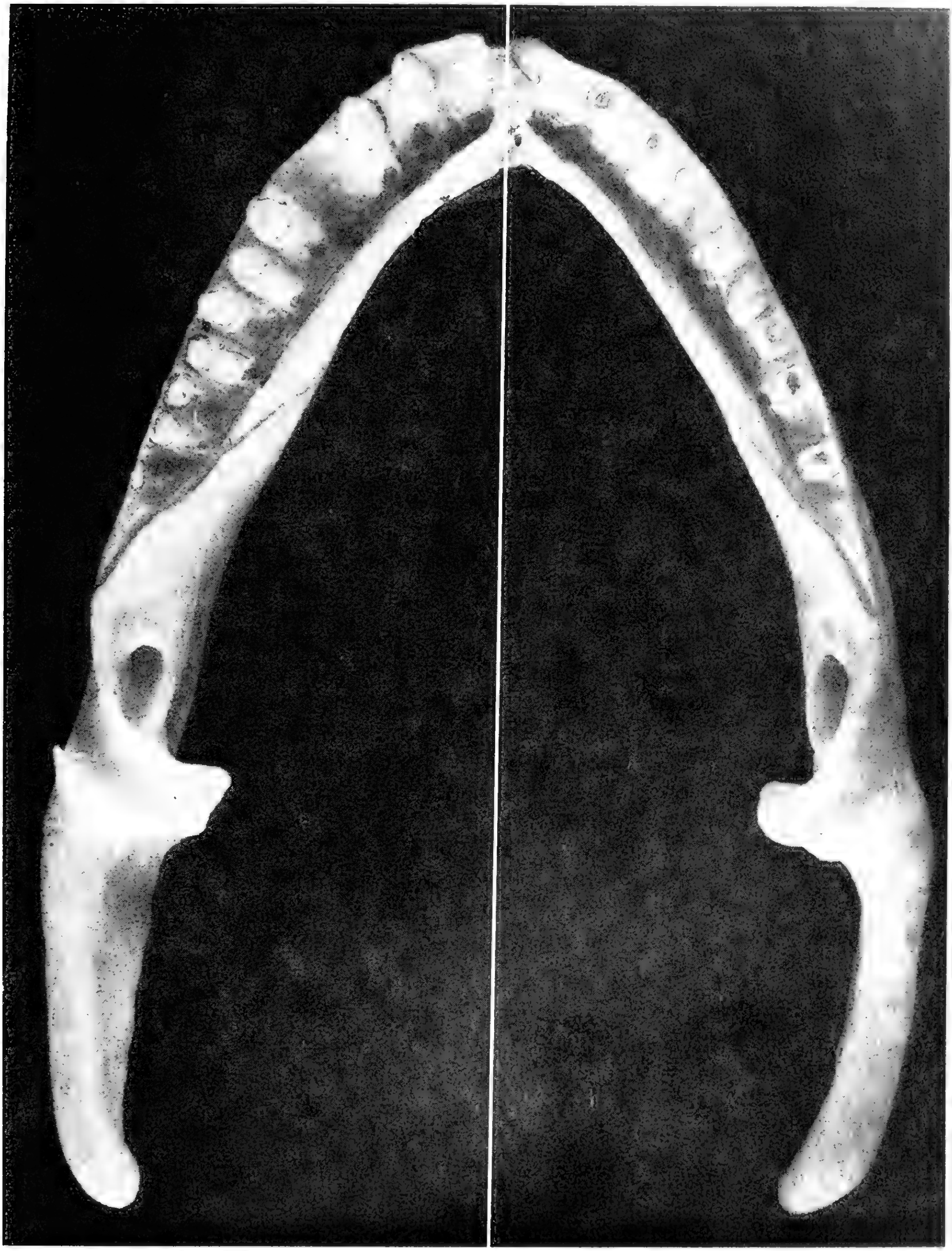

FIG. 16. *Siphonops annulatus* (Mikan). EHT-HMS 1848, Teresopolis, Guanabara, Brasil.

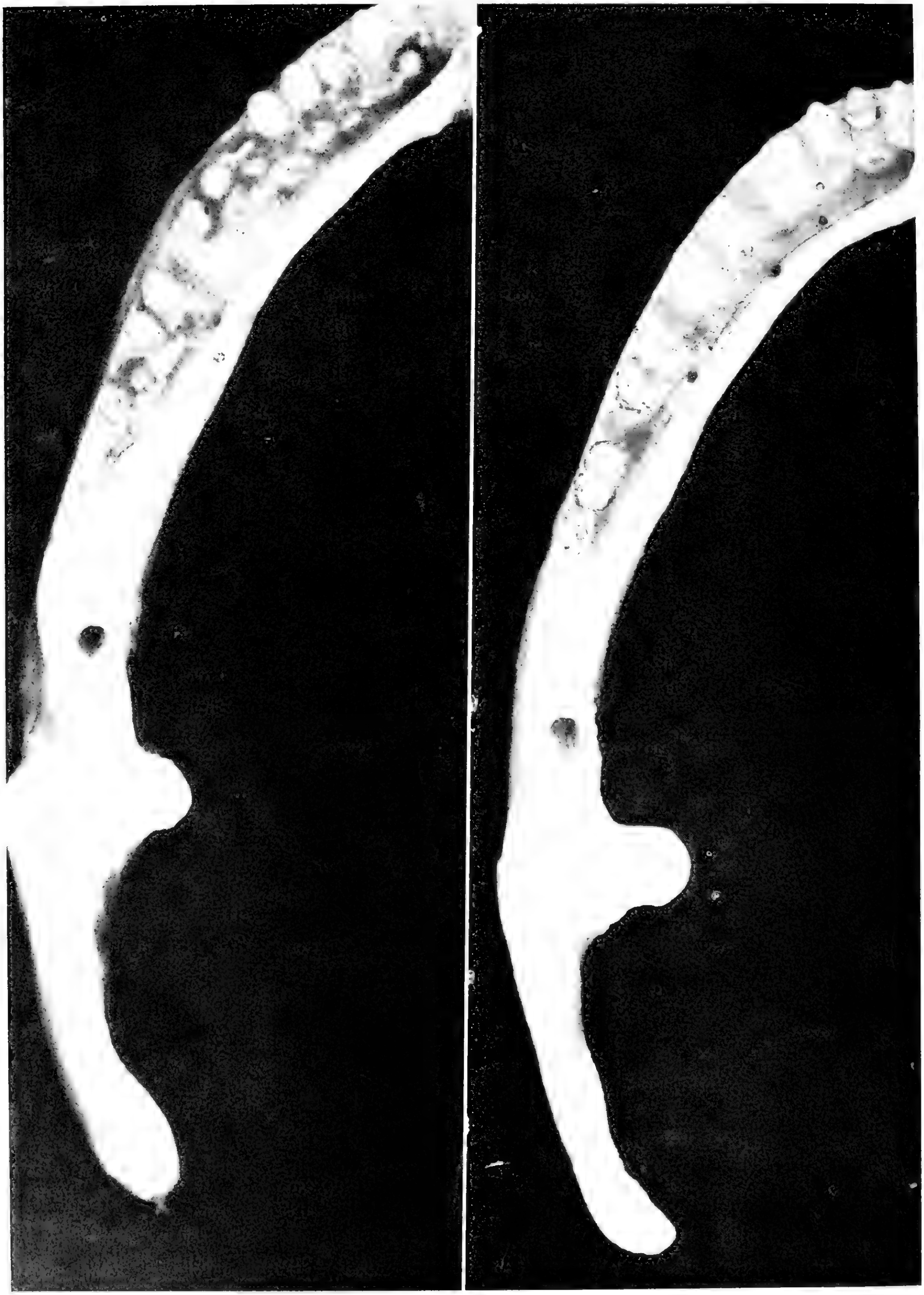

FIG. 17. *Siphonops annulatus* (Mikan). MCZ 19407, Ecuador, Pastaza River, "Canelos to Maranon," Ecuador.

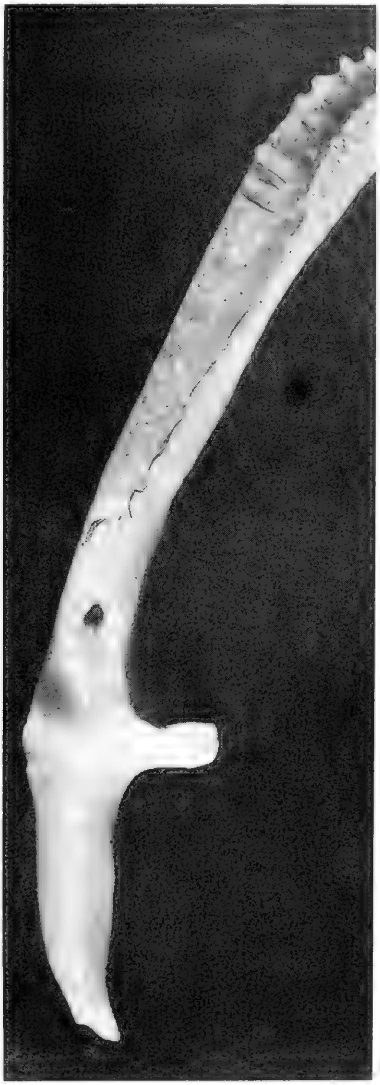

FIG. 18. *Gegeneophis ramaswamii* Taylor. MCZ 29452, Tenmalai Forest, Kerala State, India.

FIG. 19. *Grandisonia alternans* (Stejneger). EHT-HMS 4647 (formerly MCZ 15638), Silhouette Island, Seychelles Islands.

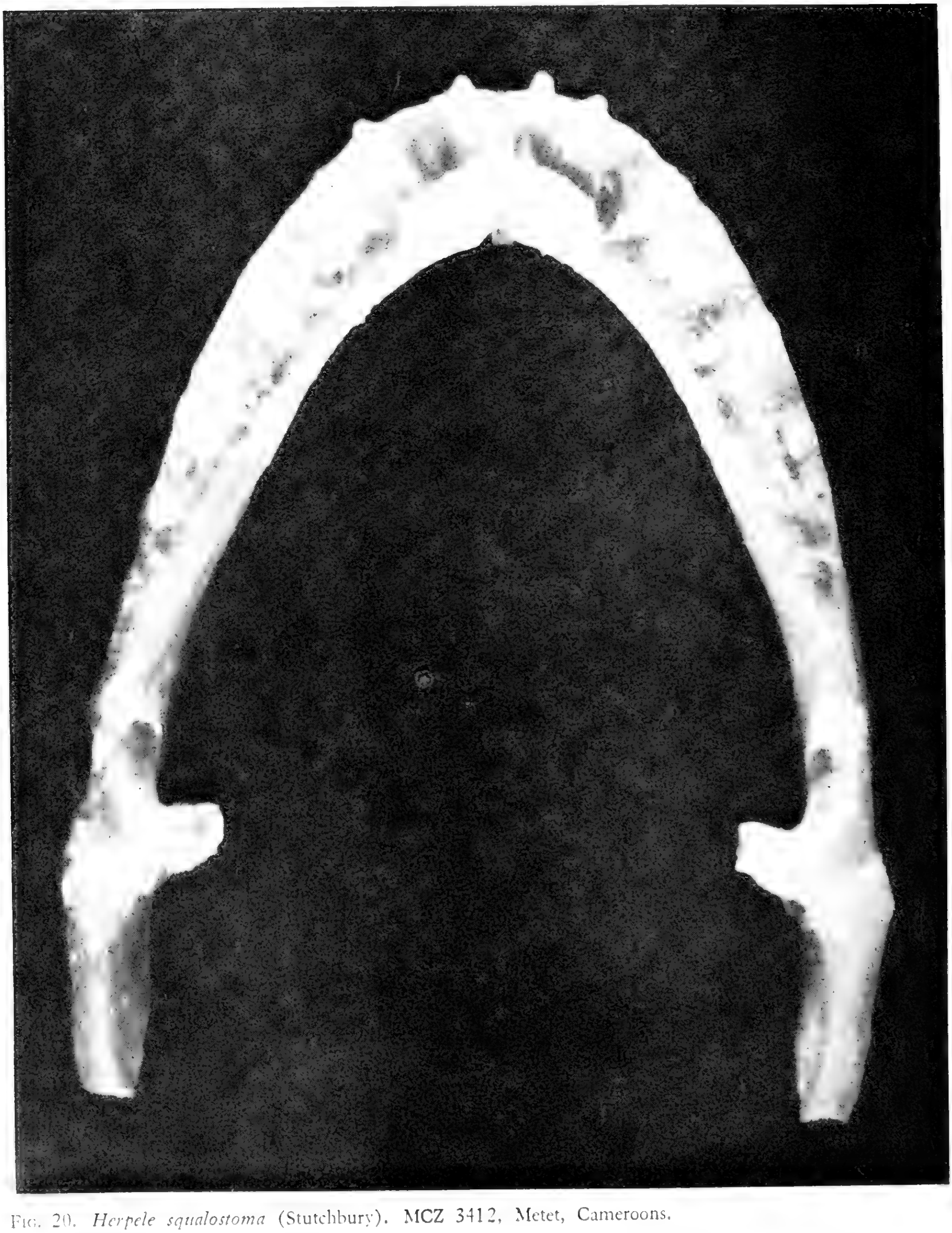

FIG. 20. *Herpele squalostoma* (Stutchbury). MCZ 3412, Metet, Cameroons.

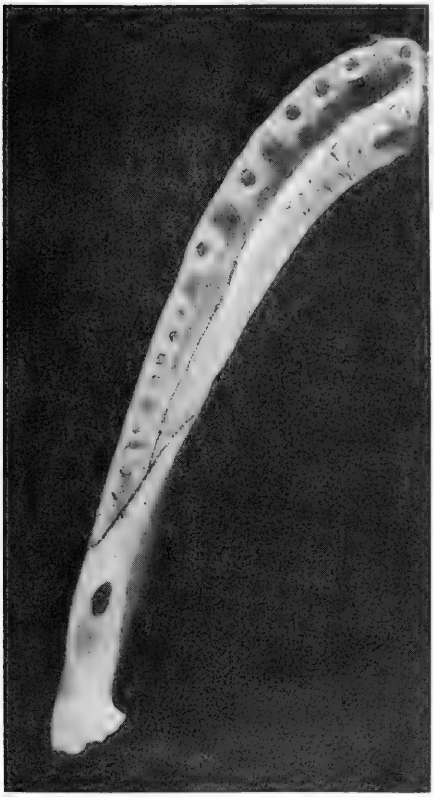

FIG. 21. *Geotrypetes s. seraphini* (A. Duméril). MCZ 3424, Metet, Cameroons.

THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

A NEW FERTILE SCHIZAEACEOUS FERN FROM MIDDLE PENNSYLVANIAN IOWA COAL BALLS

By

R. William Baxendale
and
Robert W. Baxter

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A New Fertile Schizaeaceous Fern from Middle Pennsylvanian Iowa Coal Balls

R. William Baxendale and Robert W. Baxter

Department of Botany, University of Kansas

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ABSTRACT

The morphology and anatomy of well-preserved, fertile-fern pinnules are described from coal-balls of the Desmoinesian Stage (Middle Pennsylvanian) of Iowa. The elongated, shortly-stalked sporangia show a rudimentary annulus in the form of a sub-apical band and contain a mass of highly-distinctive, ridged, monolete or alete, golden-brown spores. The spores are compared to those of the modern genus *Schizaea.* The somewhat problematic taxonomic status of the specimens is examined and a discussion presented, indicating the probable assignment of this fern to the leptosporangiate family, Schizaeaceae.

INTRODUCTION

As usually accepted, the family of ferns, Schizaeaceae, includes four extant genera (*Schizaea, Lygodium, Mohria,* and *Anemia*) as well as several fossil genera. Of these fossils, perhaps the best known is *Klukia exilis* (Phillips), described by Harris (1945, 1961) from the Jurassic strata of Yorkshire. Chandler (1955) reported species of *Anemia* and *Lygodium* from the Tertiary of Britain, and the genus *Schizaea* has been reported from the Upper Mesozoic of Kashmir (Lukose, 1964) and from numerous Tertiary and Quaternary deposits (Selling, 1944; Cookson, 1957). *Senftenbergia,* the earliest member of the Schizaeaceae has been described in detail by Radforth (1938, 1939) from the Lower Carboniferous of Britain and France and by Andrews (1943) from the Middle Pennsylvanian of Illinois.

Little is known of the earliest history of the schizaeaceous ferns. While several genera and species have been described from compression-material, to the authors' knowledge none have been previously reported as structurally preserved in coal-balls. The present paper describes the morphology and anatomy of a number of fertile-fern fragments found in cellulose-acetate peels taken from a coal-ball from Iowa. While there is strong evidence of schizaeaceous affinity, the material is so limited that the description is offered here as a matter of record without taxonomic assignment to any known or unknown species.

ACKNOWLEDGMENTS

We wish to thank Dr. R. W. Lichtwardt, Botany Department, University of Kansas, for the use of his photographic equipment and for many helpful suggestions during the preparation of this work. Thanks also go to Dr. G. A. Leisman, Biology Department, Kansas State Teachers College (Emporia) for reviewing the manuscript and to Mrs. E. C. M. Baxendale for her assistance in its preparation.

MATERIALS AND METHODS

All coal-ball materials used in this study were taken from the Lost Creek (Old Atlas) coal mine, which is located in Sec. 36, T.75N., R.16W., about 6 miles south of Oskaloosa, in Mahaska County, Iowa.

We employed the technique of making serial sections by taking successive, cellulose-acetate peels (Joy, et al., 1956). All photographs were taken by the senior author on normally-processed Kodak Panatomic-X film, using an AO Spencer microscope, and a Kodak "Color Snap 35" camera.

DESCRIPTION

The initial saw-cut through the coal-ball (I-1466) exposed the fragments of a fertile-fern pinnule and 3 associated sporangia. Fossil material removed in the saw-kerf included the actual physical attachment of these first-found sporangia to the pinnule, which thus remains uncertain. Subsequent, serial-peels revealed several, complete sporangia attached to the abaxial surface of the fertile pinnules. The attachment of 2 sporangia to a pinnule seen in transverse section is shown by Figure 1.

Transverse sections through a pinnule show a morphological form strongly resembling the old-fashioned pince-nez. A saggital section through such a pinnule and its associated sporangia might measure 1.8-2.0 mm. The uppermost epidermis (Figs. 1, 2) is composed of large, rectangular cells, elongated in the primary plane of the pinnule, measuring 92 μm radially by 63 μm tangentially. The epidermis is revolute at the margins of the pinnule and continuous with the epidermis of the abaxially clustered sporangia. The cells are sequentially smaller as they encircle the sporangia, becoming abruptly smaller and thinner-walled where they meet the basal stalk (Fig. 3).

Immediately below the epidermis is a zone of homogeneous-appearing parenchymatous mesophyll. This tissue is not perfectly preserved, but appears to have been composed of thin-walled cells, circular as seen in transverse section, having average diameters of about 25-30 μm.

The vascular bundle of the midrib is surrounded by the homogeneous mesophyll and is composed of a few (8-10) primary tracheids, each of which has very fine

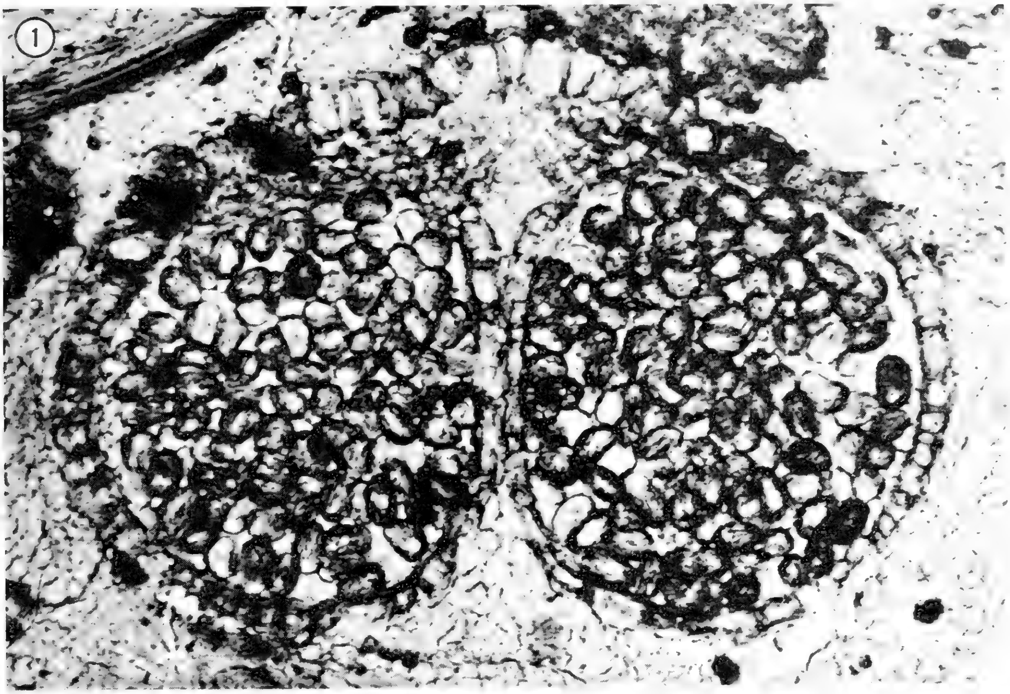

Fig. 1. Transverse section through a fertile pinnule showing the overall morphology and mode of attachment of two pendant sporangia. × 75.

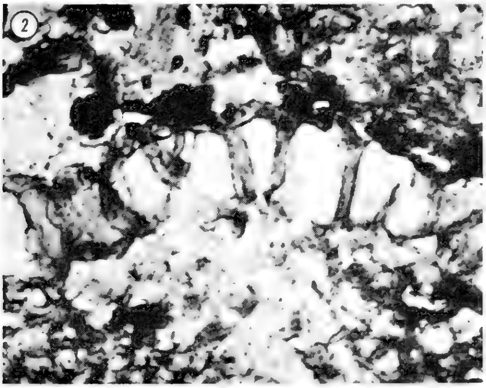

Fig. 2. Adaxial surface of fertile pinnule seen in transverse section. Note the greatly increased cell dimensions. × 260.

Fig. 3. Epidermis of the sporangium showing the abrupt termination of the layer in an enlarged cell (t). Spores (s) can be seen within the sporangium. × 550.

scalariform thickenings on its walls. Lateral tracheids depart from the midrib at approximately an angle of 180° from each other to vascularize the upper portion of each sporangium *via* the short sporangial stalk (Figs. 4, 5). Neither hairs nor papillate cells were found as parts of the sporangium.

The sporangia themselves are nearly circular when seen in median, transverse section (Fig. 6) with a maximal diameter of nearly 800 μm. The three-dimensional form of each sporangium, as reconstructed from serial peels, appears to be relatively large and somewhat like a spindle or a barrel, having an average length of 1.0-1.5 mm.

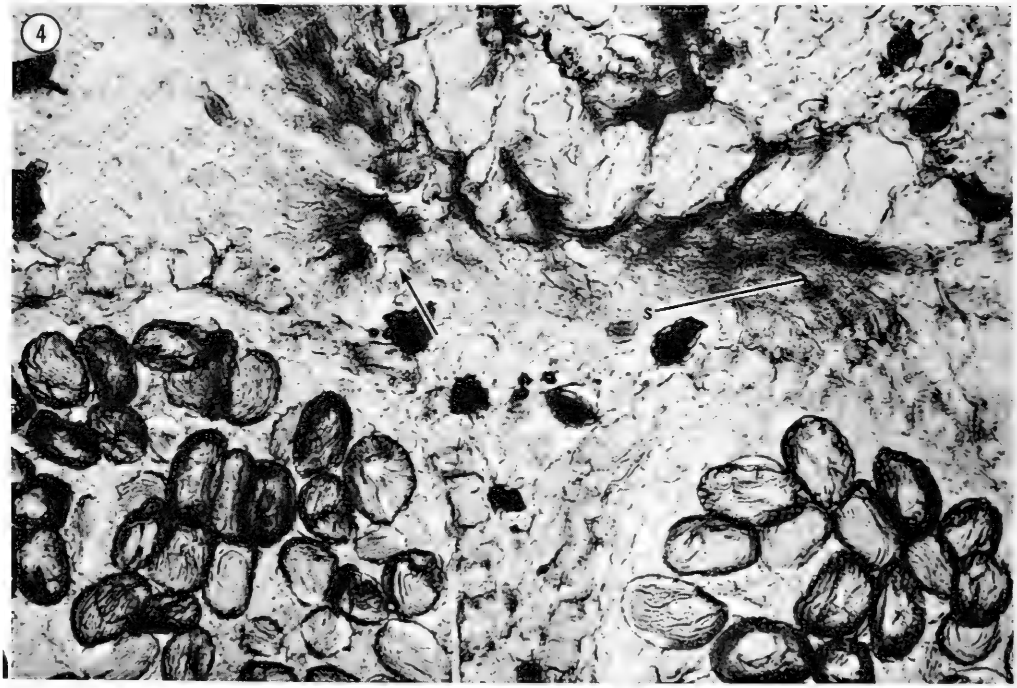

FIG. 4. Transverse section through a somewhat crushed pinnule illustrating vascularization of sporangium through the short sporangial stalk (s). Arrow indicates location of pinnule midrib vascular bundle. × 140.

As mentioned previously, the upper tissue-layer of the pinnule often appears continuous with the sporangial wall. Its cells are square to rectangular and of varying dimensions. Seen in face (tangential) view, however, the cells of the wall of the sporangium have a distinctive sinuous outline (Fig. 7). These sinuous cells were located at the distal end of several sporangia and usually measure 140 μm by 50 μm.

Although examination of initial sections suggested to us that each sporangium is sessile, more-complete sections, made later, revealed a short, but distinct, stalk by which the sporangium is attached to the abaxial surface of the pinnule (Fig. 8). A sporangial stalk, such as is illustrated in Fig. 8, is about 135 μm wide and not more than 180-200 μm in total length. Depending upon the individual section examined, a few, finely-scalariform vascular elements are seen centrally located within the stalk (Fig. 5).

In a few transverse sections through the more distal portions of sporangia, cells suggestive of a rudimentary annulus may be seen (Fig. 9). Morphologically, these cells differ from the ordinary, sporangial wall-cells only in having greatly-thickened cell walls. The radial walls appear to be especially thickened, often measuring up to 60 μm in width. The thick-walled cells appear to form a sub-apical band or ring rather than an apical cap. It is often difficult to clearly delineate the region of thick-walled cells, since the transition to typical, sporangial wall cells is usually gradual. No specialized line of dehiscence could be observed and an organized, apical plate appeared to be absent.

The spores themselves are strikingly characteristic, being relatively large, golden-brown, and somewhat bean-shaped (Fig. 10). A typical spore measures from 81-90 μm along the primary axis and 42-45 μm along the secondary axis. Approximately 840 spores are borne in each spo-

Fig. 5. Enlargement of portion of Fig. 4 showing the bundle of finely scalariform primary xylem tracheids. × 530.

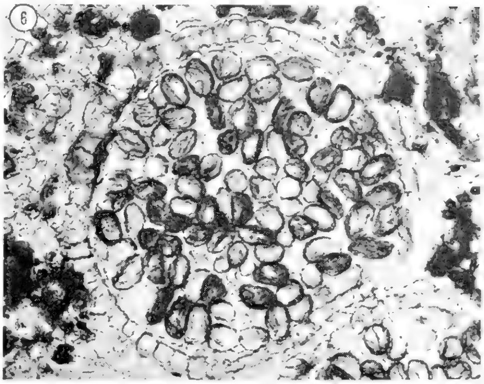

Fig. 6. A single sporangium seen to be nearly circular when viewed in median transverse section. × 100.

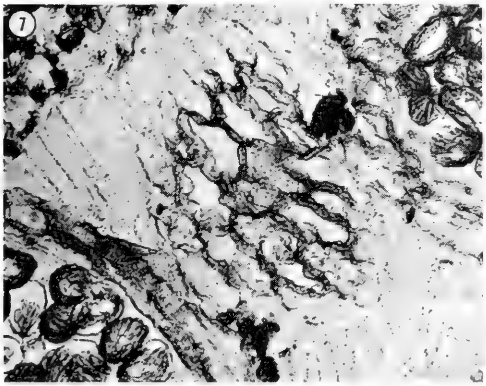

Fig. 7. Cells composing the sporangial walls seen in face view (tangential) showing their sinuous outlines. × 145.

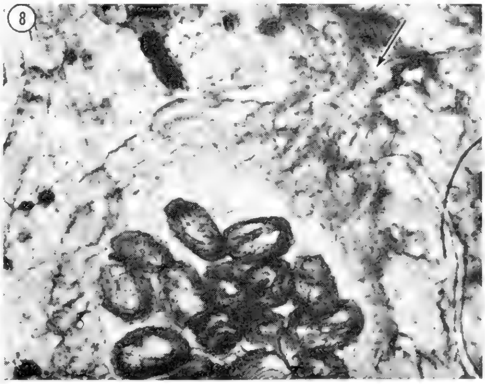

Fig. 8. Section through a sporangium showing its attachment to the abaxial surface by a short stalk (arrow). × 180.

Fig. 9. Portion of distal sporangial wall showing the elongate, thick-walled cells strongly suggestive of a rudimentary annulus. × 750.

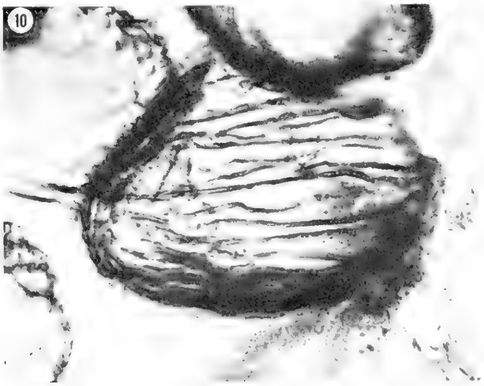

Fig. 10. Single bean-shaped spore showing the highly distinctive pattern of exine sculpturing. Note that some ridges bifurcate. × 890.

rangium. The spores are either monolete or alete and possess a distinctively sculptured exine. This exine-sculpturing is highly-consistent, being composed of broad, occasionally bifurcated and anastomosed ridges or muri, each typically 2.0-3.5 μm wide, running parallel to one another along the primary axis of the spore. Ridges are typically 1.5-2.0 μm high and from 4.0-6.5 μm apart. The exine of the spore is about 2.5-3.0 μm in thickness.

DISCUSSION

There is little doubt that the fertile-fern pinnules described here are assignable to the leptosporangiate fern-family, Schizaeaceae. This family has solitary sporangia not grouped into sori. Also, the sporangia are borne abaxially in two regular rows on either side of the midrib (in *Schizaea* and *Anemia*) and are often protected by an incurling of the pinnule margin. The sporangia are typically large and may be shortly-stalked or sessile. The first-formed tracheids are finely scalariform. The ring of thick-walled cells presumed to be an inconspicuous annulus is distinctly schizaeaceous and the highly-distinctive spore ornamentation closely resembles some species of the extant and fossil genus *Schizaea*. When considered together, the pinnule morphology, the sporangial form and arrangement, the nature of the annulus and the distinctive sculpturing of the spore-exine unquestionably place this fertile fern in the family Schizaeaceae.

The only genus of schizaeaceous fern previously described from the Carboniferous is *Senftenbergia* (Radforth, 1938, 1939), and is the only other member of the family Schizaeaceae of approximately equivalent age to that in the Middle Pennsylvanian coal-ball specimens described in this report. Boureau (1970) lists 5 species of *Senftenbergia*, several of which have morphological features similar to those described for our coal-ball specimens. The sporangia of *Senftenbergia ophiodermatica* are borne abaxially on the pinnule in two rows, one on either side of the midrib, arranged with their long axes parallel; each sporangium is shortly stalked. The pinnule margins, with their associated sporangia, are incurled toward the midvein, often giving the appearance of a crowded mass of sporangia. In both *S. ophiodermatica* and *S. sturi* the annuli are indistinct, the former species having been originally described by Kidston (1924) as exannulate. The sporangium of *S. sturi* is similar in form to that of our coal-ball specimens in being elongate, spindle-shaped, and shortly-stalked at the basal end. The spores of such species as *S. pennaeformis,* however, are basically spherical and have, on the irregular system of anastomosing ridges, stout peg-like projections. Also, all species of *Senftenbergia* produce spores with an obvious, triradiate commissure. These spore features are unlike those described for our coal-ball specimens, eliminating them from inclusion in the genus *Senftenbergia.*

Had the sporangia and highly-distinctive spores described in this report been associated with Upper Mesozoic or younger strata, a prompt and confident assignment could have been made to the genus *Schizaea.* Selling (1944) has reviewed several fossil, schizaeaceous ferns and without qualification referred two to *Schizaea* (*S. miocenica* and *S. skottsbergii*). Cookson (1957) described *S. digitatoides* from Pliocene-aged coal in New Guinea, and Lukose (1964) later added *S. kashmiriensis* from the Upper Mesozoic of India. The spores of *S. confusa,* described by Selling (1947) from specimens growing in Madagascar, are virtually identical with those described here from Middle Pennsylvanian-aged material. Cookson (1957) noted that such distinctively-ridged exospore sculpturing, considered along with a bilateral, monolete form, "provides a reliable basis" for assigning ferns with such spores to the genus *Schizaea.* Lukose (1964) is even more convinced of this, stating that "From the available knowledge of the morphology of the recent and fossil Schizaeaceae spores, bilateral bean-shaped, striated, monolete spores are met with only in the genus *Schizaea.*" We note, too, that Arnold (1947) considers *Schizaea* and *Senftenbergia* closely related.

We believe that the botanical affinity of the fertile-fern specimens here described clearly lies with the Schizaeaceae. No other group of ferns, fossil or extant, resembles those specimens so closely as does the family Schizaeaceae. The available material strongly supports classification of this fern to the Schizaeaceae. This paper is believed to represent the first report of the remains of a fertile schizaeaceous fern from the North American coal-balls, establishing the presence and describing the morphology of distinctive, large, ridged, monolete spores from Middle Pennsylvanian-aged deposits.

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THE PARASITIC GROUPS OF HALICTIDAE (HYMENOPTERA, APOIDEA)

By

Charles D. Michener

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The Parasitic Groups of Halictidae[1] (Hymenoptera, Apoidea)

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ABSTRACT

Eight parasitic genera of halictid bees are recognized, derived from five different nonparasitic ancestral groups. The parasites vary from those, like *Paralictus,* which are similar to their nonparasitic relatives and are presumably recent derivatives of them, to others, like *Sphecodes,* which appear to be ancient parasitic groups derived from nonparasitic ancestral genera that quite likely no longer exist. Convergent morphological features among parasites include reduction or loss of structures for pollen collecting and carrying and of structures used in nest construction.

A review of host relationships is provided, as is speculation on the relationships between type of parasitization and structure within the genus *Sphecodes.*

In the taxonomic treatment, a new genus (*Ptilocleptis*) and three new species (*P. tomentosa, polybioides,* and *eickworti*) are described, as are *Sphecodes* subgenus *Austrosphecodes* and the species *S.* (*A.*) *convergens* and *Eupetersia guillarmodi* and *flava.*

INTRODUCTION

Among most families of bees there are genera or species that do not make or provision their own nests, but put their eggs in, or actually live in, the nests of other species of bees. Larvae of such social parasites or cleptoparasites do not feed on the hosts, but eat the provisions supplied by the host. In some cases, adult hosts are killed by the female parasite, but in most cases only the eggs or young larvae in cells are killed, either by the adult female parasite or by the young larvae of the parasite. In the large bee family Halictidae, parasitic forms have arisen at least five times from different nest-making ancestors. The subjects of this paper are the parallel evolution that has occurred among these forms, their host relationships, and their taxonomic groupings.

Although some of them have not yet been reared from nests of their hosts, parasitic halictids can be recognized by the absence of pollen-gathering and pollen-carrying structures in the females. There are parasitic species of other families of bees that have not lost pollen-handling equipment (*Bombus, Braunsapis;* see Michener, 1974), but no such forms are known in Halictidae, although individuals of nest-making species sometimes usurp nests of the same or other species (Knerer and Plateaux-Quénu, 1967).

The parasitic halictid genera and their antecedents are listed in Table 1. Characters supporting the judgments as to which are the ancestral groups are indicated in the taxonomic treatment. Convergent features characteristic of the parasitic groups are listed below and in Table 2.

CONVERGENT FEATURES

Parasitic halictids are characterized by numerous similarities. These are among the principal characteristics by which they differ from the nonparasitic or nest-making genera from which they arose. Many of these features involve reduction or loss of pollen-gathering, pollen-carrying, and nest-making structures, while others appear to be defensive and offensive equipment for encounters with nest owners. In either case, the structures are those of females, and the rest of this section pertains only to female characters. Some of these characters, such as the reduced hairiness, relatively coarse punctation, and sometimes even spine-like setae on the hind tibiae, occur in males of some species also. Their functional significance is probably limited to females, however; presumably the developmental mechanisms happen to operate in some males.

In this section each feature which seems to be an adaptation of parasites to their way of life and which appears to have arisen independently in different parasitic groups, is lettered *a* to *s*. Each of these features is scored on a scale 0 to 1, 0 representing the structure as found in nest-making ancestral halictids, 1 representing the extreme modification found among parasites. The intermediate conditions are subjectively assigned scores such as 0.2 or 0.6 to give an idea of the morphological degree of difference from the extremes, 0 and 1. Scores for the parasitic genera are shown in Table 2 and many of them are indicated in parentheses in the following account.

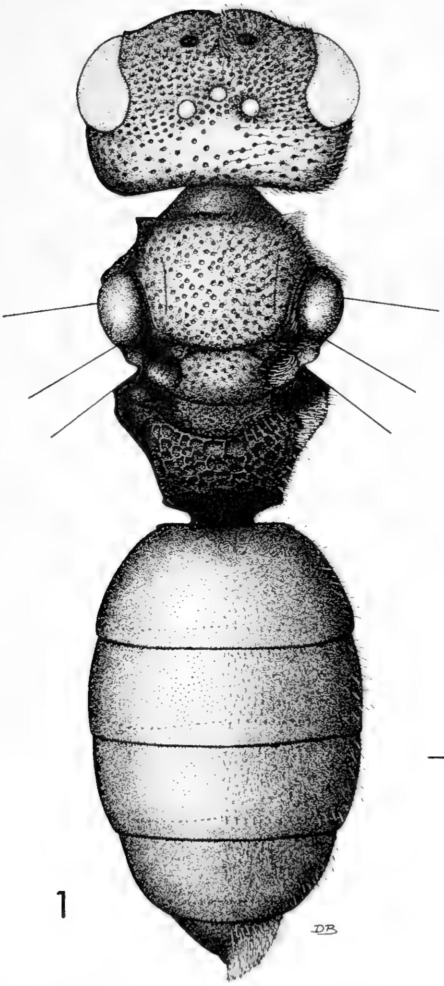
Reduction and Loss of Structures of Nest-Making Halictids:

(a) The body and legs of nest-making Halictidae are usually hairy, most of the longer hairs and many short ones being plumose (Fig. 1). This extensive vestiture presumably serves to capture loose pollen, which can later be brushed together and transferred to the scopa by modified grooming movements (Jander, 1976). Comparison of the right sides of Figures 1 and 2 shows the difference in vestiture of a typical host and a highly modified parasite. *Paralictus* (0) has the hairiness of its presumed ancestor; all other parasites (1) are markedly less hairy than their presumed ancestors. In *Ptilocleptis* and some species of *Austrosphecodes* a dense covering of short plumose hairs occurs on certain parts of the body, but this is very different from the longer, more or less erect hairs of nest-making halictids.

(b) The front basitarsus of most pollen collecting halictids is somewhat flattened with a sharp ridge or carina along the posterior (i.e., outer) margin of the segment, the distal half or more of this ridge giving rise to a row of closely placed setae forming a comb, the anterior basitarsal comb (the anterior basitarsal brush of Eickwort, 1969b). The entire segment except for the strigilar area is covered with a brush of hairs which are usually longer than those of the comb, so that the latter may be inconspicuous. The hairs of the brush are usually rather dense but are sparse in small forms like *Homalictus* and *Lasioglossum* (*Dialictus*). The brush and the comb contained within it appear to be important in removing pollen from anthers

Table 1. Parasitic Halictidae and the Groups from which they Presumably Arose.

Parasites	Probable Ancestors	Distribution
1. *Paralictus*	*Lasioglossum* (*Dialictus*)	North America
2. *Echthralictus*	*Homalictus* s. str.	Samoa
3. *Parathrincostoma*	*Thrinchostoma*	Madagascar
4. *Temnosoma*	Augochlorini	Neotropical
The *Sphecodes* Group:	*Halictus-Lasioglossum* Group of Genera	
5. *Ptilocleptis*	*Sphecodes* (*Austrosphecodes*)	Neotropical
6. *Microsphecodes*	*Sphecodes* (*Austrosphecodes*)	Neotropical
7. *Eupetersia*	*Sphecodes* s. str.	
7a. *Eupetersia* s. str.		Africa
7b. *Nesoeupetersia*		Madagascar to India
8. *Sphecodes*		
8a. *Sphecodes* s. str.		Holarctic, Oriental, African; also penetrating Australian and Neotropical regions
8b. *Austrosphecodes*		Neotropical



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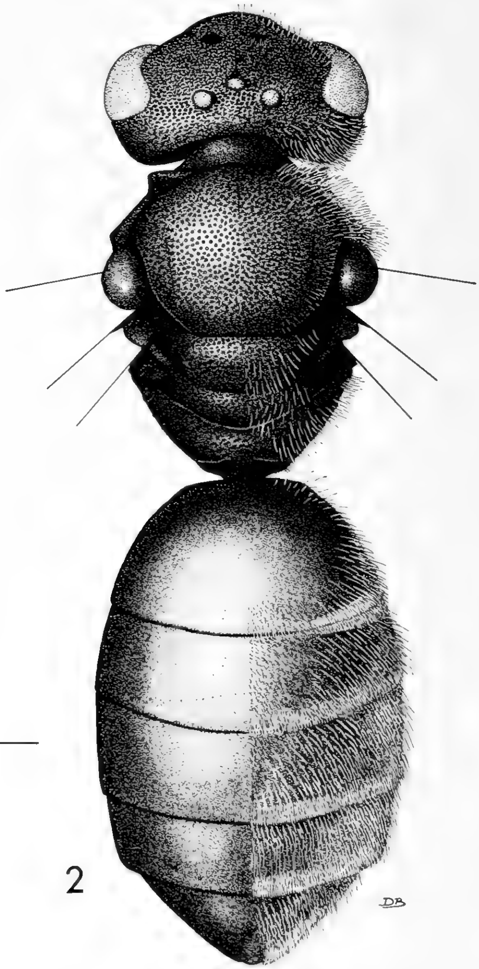

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Fig. 1. *Sphecodes monilicornis* (Kirby), female, hairs omitted on left. Fig. 2. *Lasioglossum malachurum* (Kirby), female, hairs omitted on left. Scale line represents 1.0 mm.

as well as various parts of the body. The posterior ridge and the comb arising from it vary from essentially unmodified (0) to lacking (1) among parasitic groups. When they are lacking, the basitarsus is more nearly round in cross-section, less flattened than in nest making forms. Although development of the comb varies in the Augochlorini and it seems to be absent in some unrelated, nonparasitic genera, its loss especially in the Halictini seems clearly related to parasitism.

(c) The base of the mid femur and the apex of the mid tibia of pollen collecting halictids each bears a comb or brushlike row of hairs on the under surface, that on the tibia arising from an oblique ridge. They were termed the mesofemoral brush and mesotibial comb by Eickwort (1969b). As pointed out by Jander (1976), these structures are opposable and serve to remove pollen from the fore legs. In parasites the tibial brush is retained but the femoral brush varies from little modified (0) to absent (1). Usually the tibial brush is more brushlike, less comblike, than in many nest making bees.

(d) In pollen-carrying forms, there are

long and usually branched hairs on the underside of the hind trochanter (Fig. 4). On the femur in the Halictini, there are some long branched hairs at the base on the underside, but otherwise the underside is nearly bare. Long branched hairs from the anterior (= outer) surface (Figs. 4, 5) and a longitudinal row of similar hairs from near the middle of the posterior (= inner) surface (Fig. 6) curl down and meet below the femur to form a femoral corbicula, the cavity of which is somewhat enlarged by the straight or usually concave, rather than convex, under surface of the femur. The pollen carrying corbicula is less specialized in the Augochlorini. Long branched hairs arise from a more extensive basal area on the under side of the femur; on the posterior surface, while the hairs are directed downward, there is no row of unusually long curled hairs. The corbicula is shorter than in Halictini because of the larger basal hairy area and is open, since very long curled hairs arise only from the anterior side of the femur. Earlier illustrations and accounts of halictid scopas are those of Eickwort (1969b) and Eickwort and Fischer (1963). In all parasitic forms the scopa is reduced (Figs. 3, 7-14). In *Paralictus* the trochanteral scopa is unmodified while the long branched femoral hairs are either somewhat reduced in number and density but curled to form a corbicula which often contains some pollen grains (0.2), or the scopa is further modified by loss of the long hairs on the anterior surface of the femur (0.5). In all other parasitic genera the trochanteral hairs are short and the femoral hairs are short, relatively sparse, and not or little branched. The underside of the femur is relatively bare, however, and the hairs are directed about as in the pollen carrying forms. In some (0.9) the underside of the femur is about as in the pollen collecting ancestral groups (concave in *Echthralictus,* straight in *Temnosoma*) while in others (1) the curvature of the under surface is slightly to markedly convex.

(e) The posterior tibia in nest making forms is covered with long plumose pollen carrying hairs except for the relatively bare under surface. Near the anterior (outer) margin of the bare area, i.e., along the lower margin of the outer surface of the tibia, the hairs are especially long (except in *Homalictus*) and coarsely branched and while the main axes are directed downward and distally, the apical parts are curled upward and distally. The tibial scopa is modified in all the parasitic groups (Figs. 7-14). In *Paralictus* (0.3) the long hairs near the lower margin of the outer surface are not much larger than other tibial hairs, are only gently curved, and lack the characteristic coarse plumosity of these hairs in pollen carrying forms. In *Echthralictus* (0.5) the same is true but the hairs are even shorter, those of the lower margin of the outer surface being quite short. In other parasitic genera, the ventral relatively bare area is not or weakly evident, the hairs have few barbs or are simple, and those along the lower margin of the outer surface are smaller than those elsewhere on the tibia. Forms having a relatively uniform coverage of simple hairs are scored (1) while those with more plumose hairs and a sparsely hairy under surface are scored as (0.8) or (0.9).

(f) The hind basitarsus is flattened, usually as long as the remaining tarsal segments, the hairs of its lower margin unusually long, coarse, straight, simple or with branches only basally. Probably these features function to comb pollen off of the metasoma. In parasitic genera they vary from almost unmodified (0.2), to less flattened and lacking most or all of the coarse, straight hairs (0.7), to those in which the basitarsus is also markedly shorter than the remaining tarsal segments (1). Because of variability this feature is rather weak, but seems worth more

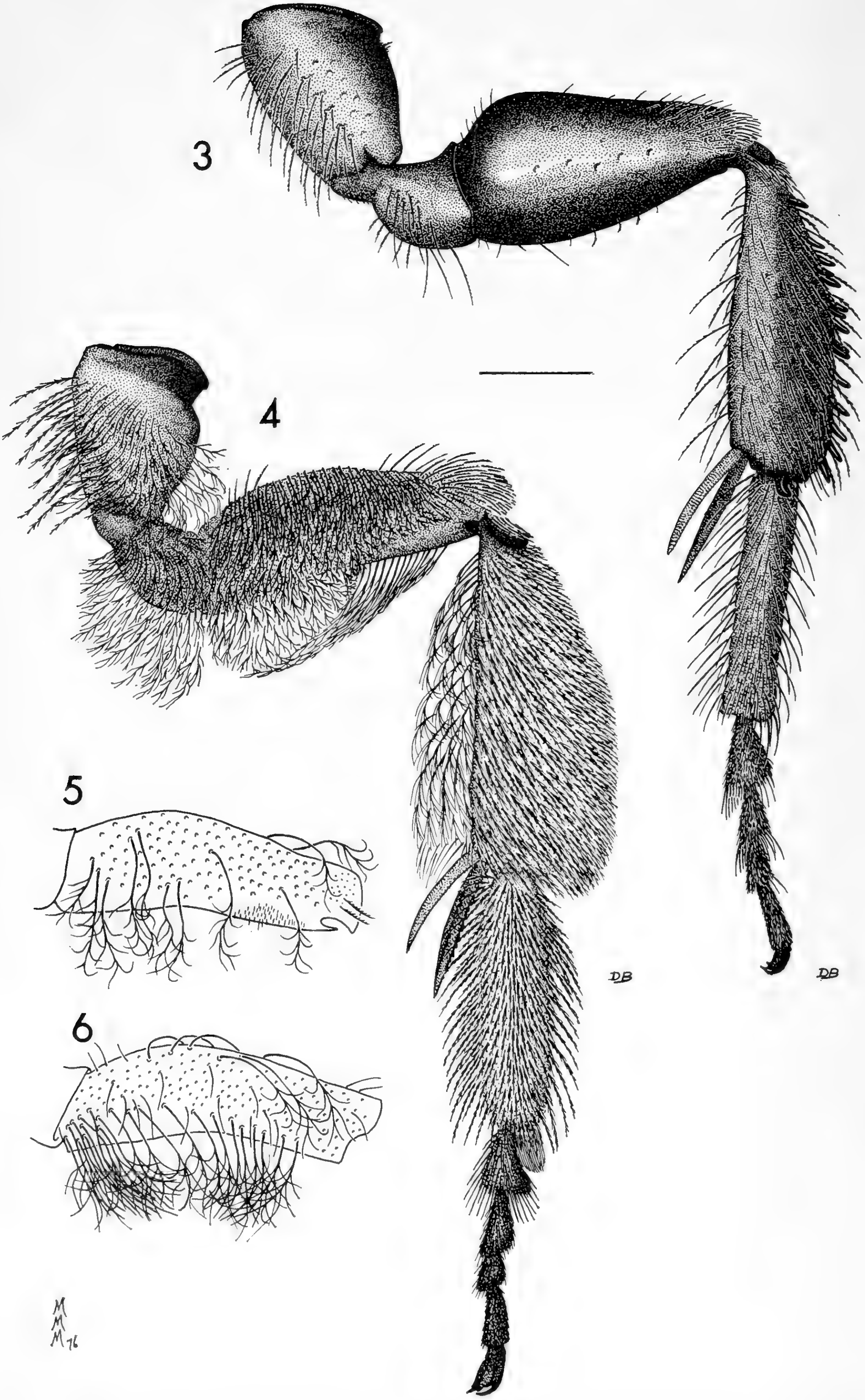
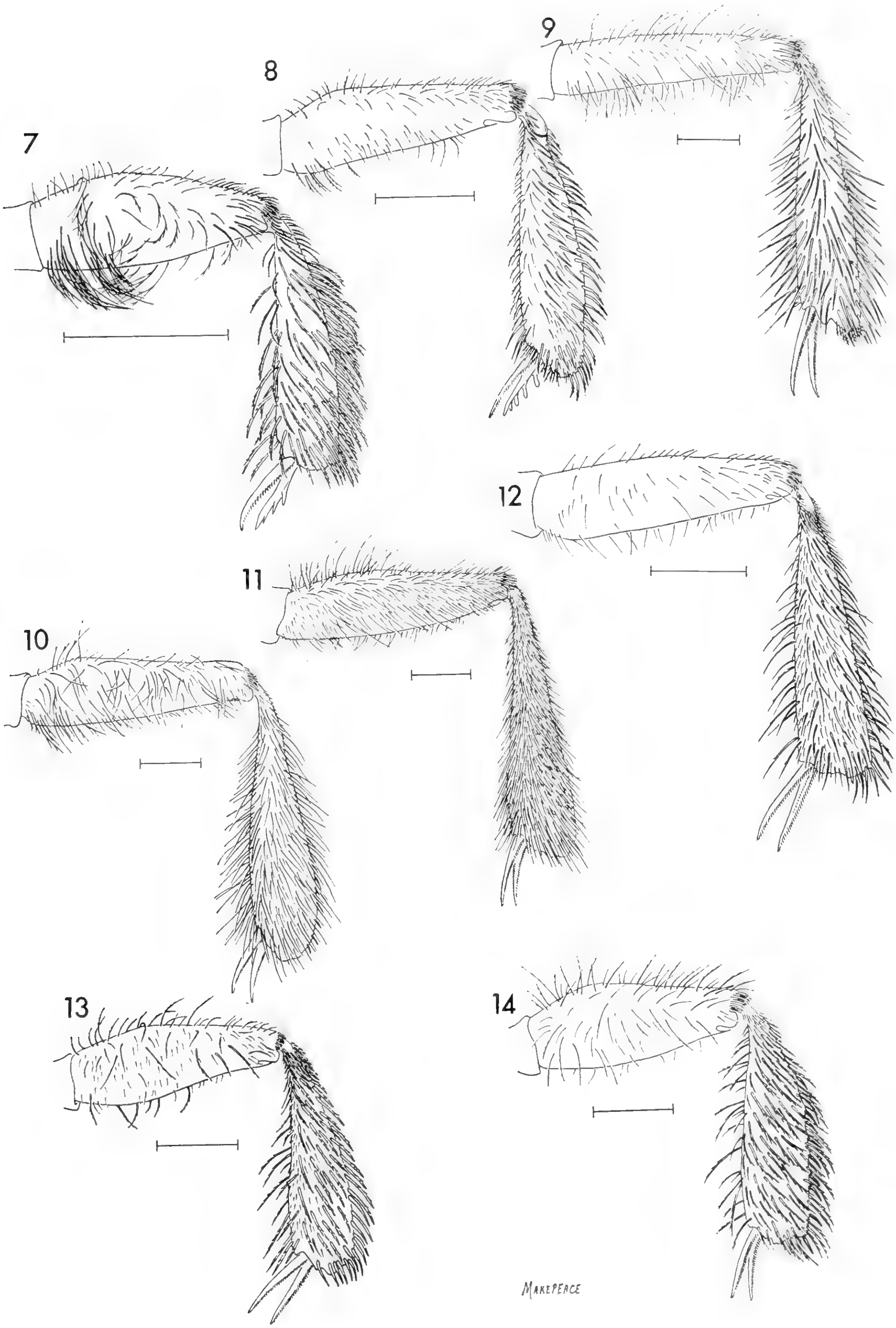


FIG. 3. Outer (= anterior) surface of hind leg, *Sphecodes monilicornis* (Kirby), female. FIG. 4. Same, *Lasioglossum malachurum* (Kirby). FIGS. 5, 6. Anterior and posterior views of hind femur of *Lasioglossum malachurum* (Kirby), female. Most hairs are indicated only by their sockets. Scale line represents 0.5 mm.



FIGS. 7-14. Outer views of posterior femora and tibiae of females. FIG. 7. *Paralictus asteris* Mitchell. FIG. 8. *Echthralictus extraordinarius* (Kohl). FIG. 9. *Parathrincostoma seyrigi* Blüthgen. FIG. 10. *Temnosoma smaragdinum* Smith. FIG. 11. *Ptilocleptis tomentosa* Michener. FIG. 12. *Eupetersia coerulea* Blüthgen. FIG. 13. *Sphecodes* (*Austrosphecodes*) *chilensis* Spinola. FIG. 14. *Sphecodes* (*Sphecodes*) *confertus* Say. Scale lines represent 1.0 mm.

TABLE 2. Scores for Various Characters of Females of Parasitic Halictid Genera 1 to 8.* 0 = same condition as in nest making ancestral group; 1 = extreme of modification among parasites.

	1	2	3	4	5	6	7	8
a. Vestiture	0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
b. Tarsus I	0	0	1.0	1.0	1.0	1.0	1.0	1.0
c. Mid-femoral brush	0.5	0	1.0	1.0	1.0	1.0	1.0	1.0
d. Femoral scopa	0.2-0.5	0.9	1.0	0.9	1.0	1.0	1.0	1.0
e. Tibial scopa	0.3	0.5	1.0	1.0	1.0	1.0	1.0	0.9
f. Hind basitarsus	0.2	0.7	0.7	0.7	0.7	0.7	0.7	0.7-1.0
g. Ventral scopa	0.2	0.6	1.0	0.8	0.9	0.9	1.0	0.9-1.0
h. Basitibial plate	0.1-0.3	0	0.9	0.7	1.0	1.0	0.7	0.7-1.0
i. Prepygidial region	0.5	0.6	1.0	1.0	1.0	1.0	1.0	1.0
j. Sixth tergum	0.3	0.3	0.4	0.6-1.0	0.9	0.9	0.9	0.9
k. Labrum	0.5-0.7	0.2	0.2	0.8	1.0	0.9	0.9	0.9
l. Tibial spur	0.2	0.2	1.0	1.0	1.0	1.0	1.0	1.0
m. Penicillus	0.5-0.8	0.8	0.5	1.0	1.0	1.0	1.0	1.0
n. Sculpturing	0	0	0.8	1.0	0	0	0-0.6	0.4-0.8
p. Mandible	0.5-1.0	1.0	0	0.5	0.5	1.0	1.0	0 -1.0
q. Head	0.5-1.0	1.0	0	0	0	1.0	1.0	0 -1.0
r. Legs	0	0	0.1	0	0.5	0.5	0.5	0 -1.0
s. Spines	0	0.2	0	0	0.1	0.1	0.1-0.3	0.1-1.0
Mean	0.25-0.38	0.44	0.64	0.72-0.74	0.76	0.83	0.82-0.87	0.69-0.97

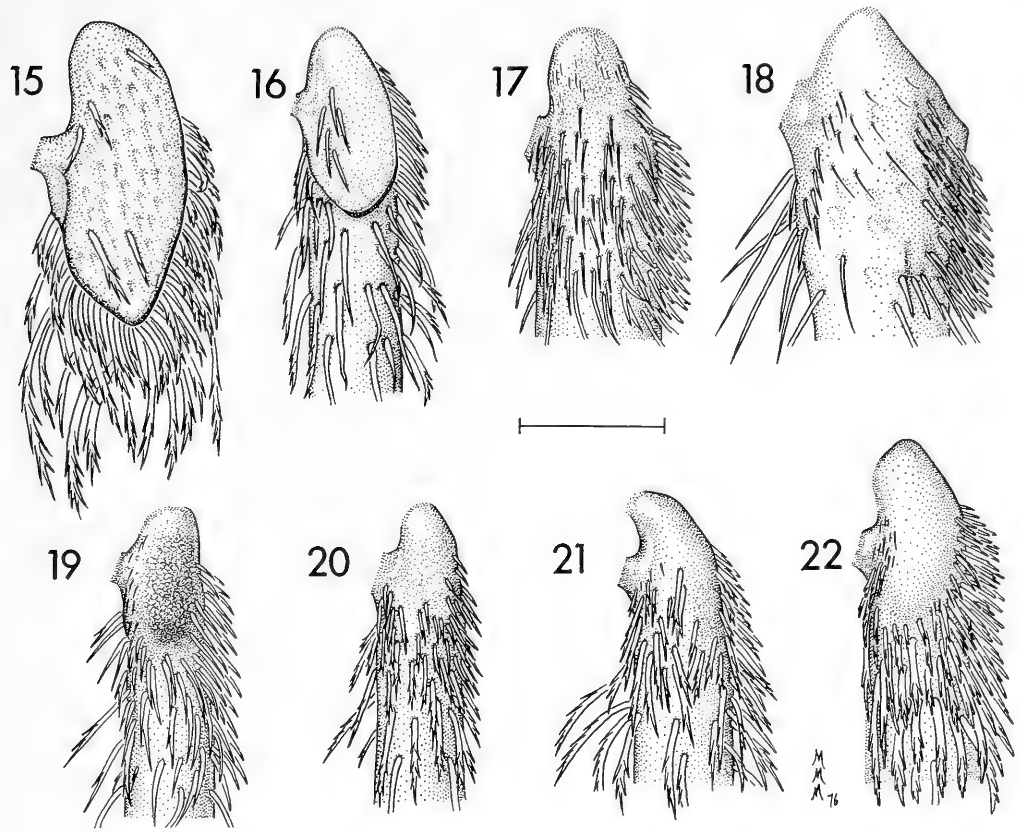
* 1 = *Paralictus*, 2 = *Echthralictus*, 3 = *Parathrincostoma*, 4 = *Temnosoma*, 5 = *Ptilocleptis*, 6 = *Microsphecodes*, 7 = *Eupetersia*, 8 = *Sphecodes*.

consideration than mere inclusion under general hairiness (feature *a*, above).

(g) Nest making Halictinae vary in the extent to which there is a ventral metasomal scopa for carrying pollen. Usually there is a preapical zone of rather long plumed hairs, often simple but curled at the tips, across each metasomal sternum, these hairs being longer and more erect and therefore more important in pollen carrying on basal than on apical sterna. In *Homalictus*, however, the ventral scopa becomes the main pollen carrying structure. The bands of hairs are reduced, usually to a single row on each sternum, but these hairs are enomous, coarsely plumed, directed posteriorly and at their tips often upward toward the sterna to form a corbicula behind each row. Moreover, similar giant hairs arise on the lateral, ventral parts of the terga and are directed postero-mesally. In all parasitic forms the sternal scopa is reduced. In *Paralictus* (0.2) the hairs are only somewhat shorter and less plumose than in the presumed ancestral type. In *Echthralictus* (0.6), a *Homalictus* derivative, the large sternal hairs are much reduced in numbers, curvature, and in plumosity, some being simple, but are still evident as a few, unusually large hairs; large lateral tergal hairs are absent. The other parasitic genera have only simple hairs of moderate length on the areas concerned, and are scored 0.8 to 1 depending on the density of the hairs, the latter indicating the lower density.

(h) The basitibial plate is defined, at least along its posterior margin, and commonly around the whole margin by an elevated carina in nest making species (Fig. 15). It functions to support the bee working in the nest as it pushes its legs out against the burrow walls (Batra, 1964). In parasitic genera (Figs. 16-22) it may be essentially normal (0), less well defined with the marginal carina lower (0.1-0.3), feebly defined and often only posteriorly (0.7), barely detectable (0.9) or entirely absent (1).

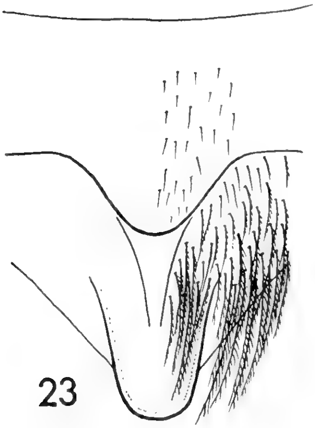
(i) The fifth metasomal tergum of nest-



Figs. 15-22. Outer views of bases of posterior tibiae of females, including basitibial plates. The scale line represents 0.25 mm. Fig. 15. *Lasioglossum malachurum* (Kirby). Fig. 16. *Echthralictus extraordinarius* (Kohl). Fig. 17. *Ptilocleptis tomentosa* Michener. Fig. 18. *Temnosoma smaragdinum* Smith. Fig. 19. *Eupetersia coerulea* Blüthgen. Fig. 20. *Sphecodes chilensis* Spinola. Fig. 21. *Sphecodes confertus* Say. Fig. 22. *Sphecodes monilicornis* (Kirby). Scale line represents 0.25 mm.

making species has a dense prepygidial fimbria of hairs extending across the segment, apically. This hair band is broadened middorsally where the hairy region extends toward the base of the segment. In the middle of this broad area is a sharply defined specialized longitudinal zone lacking ordinary hairs but covered with minute dense hairs. The surface in this zone is very minutely punctate. There is a deep cleft in the tergal margin, dividing this zone longitudinally in the Augochlorini but not in the Halictini. In all parasitic forms this elaborate structure is modified. In no case is there a sharply defined specialized longitudinal zone. In *Paralictus* there is an ill-defined longitudinal area or a small, median, apical region of minute punctation and fine hairs. Although superficially the tergal surface and vestiture are uniform from side to side, there is a broad triangular, median wedge lacking long hairs but with scattered hairs of moderate length. This zone includes the small median apical region and is roughly an equilateral triangle; posterolaterally it is continuous with the apical impuctate tergal margin (0.5). In *Echthralictus,* the specialized zone is also broadened posteriorly to form a wide, hairless, triangular wedge, only minutely roughened and shiny, cutting into the hairy part of the tergum (0.6). Posterolaterally this zone is continuous with the bare posterior marginal band of the tergum. The posterior margin of the zone is longer than the other two margins which are about at right angles to one another. The zone is similar to that of *Paralictus* but it is larger and much better defined. Both genera have hairs along the extreme tergal margin. In other parasitic genera the tergal surface and margin show no specialized region, dense to sparse hairs being distributed across it (1). When the hairs form a dense fimbria it is often less dense medially; such a sparsely hairy area may or may not be a rudiment of the specialized zone found in nest-making forms. In all cases it lacks the short fine hairs and dense minute punctation of this zone in nest making forms.

(j) The sixth metasomal tergum of pollen-collecting halictids is provided with two heavily sclerotized plates (Fig. 23) which perhaps contribute to the effectiveness of the tamping movements characteristic of halictid nest building (Batra, 1964). The gradulus is strongly arched to the rear and forms a carina delimiting posteriorly and laterally the more anterior, elevated plate, the suprapygidial plate of Eickwort (1969b). An inclined zone, broad anteriorly and tapering posteriorly, slopes downward as it extends backward from the suprapygidial plate and merges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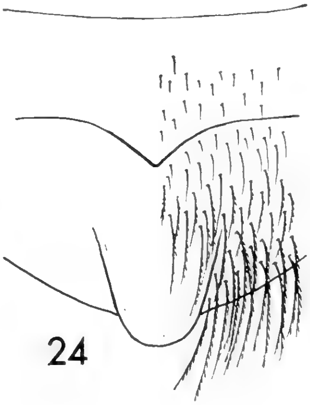
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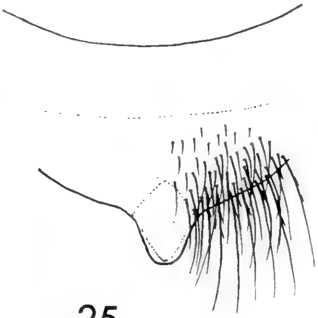
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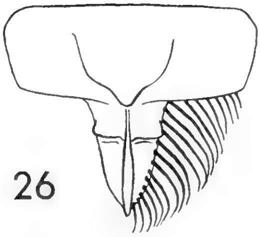
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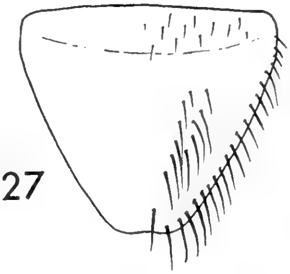
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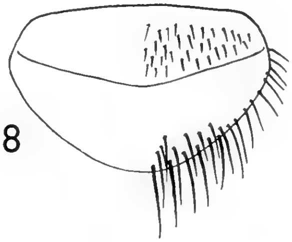
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FIGS. 23-25. Median parts of sixth metasomal terga of females. FIG. 23. *Lasioglossum malachurum* (Kirby). FIG. 24. *Paralictus asteris* Mitchell. FIG. 25. *Ptilocleptis polybioides* Michener.

FIGS. 26-28. Labra of females. FIG. 26. *Lasioglossum malachurum* (Kirby). FIG. 27. *Sphecodes monilicornis* (Kirby). FIG. 28. *Ptilocleptes tomentosa* (Michener).

with the median basal part of the pygidial plate, which is a flat process projecting beyond the rest of the tergal margin. On either side of the pygidial plate is a hairy region, the hairs constituting the pygidial fimbria, which is broken by the pygidial plate and the inclined zone anterior to it. All parasitic forms have these plates less well developed (Figs. 24, 25). In *Paralictus* (0.3), the arch of the gradulus is less prominent although distinct, the suprapygidial plate being a relatively small elevated area, delimited by a carina which is angulate rather than rounded posteriorly. The inclined zone is absent, and the pygidial fimbria is sparse, but continuous, across the tergum where the inclined zone would be if it were present. *Echthralictus* (also 0.3) is similar, but the gradulus is very weak, not carinate, and the suprapygidial plate therefore is inconspicuous; however, the pygidial fimbria is interrupted medially. *Parathrincostoma* (0.4) agrees with the comment on *Echthralictus* except that the whole gradulus is almost invisible and some *Temnosoma* (0.6) likewise agree except that the gradulus is absent lateral to the suprapygidial plate. In the *Sphecodes* group (0.9) the gradulus is only weakly arcuate posteriorly in the middle, there being no hint of a suprapygidial plate, and the fimbria or hairy zone is continuous or narrowly interrupted medially. In some *Temnosoma* (1) the gradulus and of course the suprapygidial plate are absent and the fimbria is continuous.

(k) The labrum of nest making forms (Fig. 26) consists of a transverse, more or less rectangular, thick sclerite or body, sometimes called the basal area of the labrum, from the distal margin of which projects an apical process which is flattened, depressed below the surface of the body, relatively thin, pointed or rounded, and provided with a strong dorsal keel and a row of coarse bristles along the margins. The keel is reduced in parasitic forms, and the process is usually less pointed (Figs. 27, 28). In the genera scored 0.2 in Table 2, the labrum is modified principally by the reduction of the keel on the process to a carina. In *Paralictus* (0.5-0.7) the line between the body of the labrum and the process is not sharp, the surfaces sometimes being at or nearly at the same level, and the process is broad and lacks the keel completely, and is bluntly pointed, rounded, or subtruncate at the apex. In one species there are scattered bristles on the surface of the process. In *Temnosoma* (0.8) the labrum is similar, but the process is relatively short, truncated or emarginate, and its bristles scattered. In the *Sphecodes* group, the body of the labrum is reduced to a transverse basal ridge, the process lacks a keel and is broadly rounded, truncate, or bilobed, and there are often bristles other than the marginal ones or the row of bristles is mesal to the margin (Figs. 27, 28). Most members of this group are scored 0.9, but *Ptilocleptis,* because of the greatly shortened process, is scored 1.0.

(l) The hind tibial spurs each has two margins between which is a concave surface. Both margins of the outer spur and the outer margin of the inner spur are minutely serrate. The inner margin of the inner spur, in nest making species, varies from more coarsely serrate to wavey, even almost straight, to produced into one or a few long processes. In genera scored 0.2 the inner margin of the inner hind tibial spur is produced into a few large projections, as in the forms ancestral to these parasites, but the projections are smaller (as noted for *Paralictus* by Eickwort and Fischer, 1963). In all the rest (1), that margin is minutely serrate like the other margins.

(m) In nest-making forms, the apex of the hind basitarsus, on the outer surface, is prolonged as a flat process bearing a dense brush of hairs, the penicillus, shaped like a paint brush and used for spreading liquid on the cell lining (Batra, 1964). A small but slender penicillus is present in *Parathrincostoma* (0.5); in genera scored 0.8, a small projection remains but the brush is absent, while in those scored 1 both projection and brush are absent.

ENLARGEMENT AND SPECIALIZATION OF STRUCTURES AMONG PARASITES:

(n) Nest-making Halictinae vary greatly in the coarseness of the punctation and propodeal areolation. Moreover, there is no single measure of such coarseness for a specimen or species. Yet in general it seems clear that parasitic forms are more coarsely sculptured, and the cuticle firmer, than in their nest-making relatives. *Temnosoma* is noteworthy for the coarse pitting of the first two metasomal terga which end in thickened margins instead of thin margins as in other forms, for the coarse transverse ridges on the constricted bases of the second and third terga, and for the coarsely punctate tegulae. Presumably such features provide defense against the stings and jaws of host bees. The numbers in Table 2 for this feature are more subjective than for others, but nonetheless give a general idea of sculpturing.

(o) The proccipital carina and the anterolateral angles of the pronotum are highly variable in nest-making forms, as also in the parasites. In general, however, they appear to be more prominent in parasites, probably providing defense for the neck. Acute produced prothoracic angles occur in *Echthralictus* and *Parathrincostoma.* The latter also has an unusually prominent preoccipital carina. In *Temnosoma* the head is unusually produced backward forming a sharp ridge behind the vertex, protecting the neck region. Perhaps this explains the lack of enlargement of the pronotal angles in this genus. These features are not scored for Table 2.

(p) Mandibles in nest-making Halictinae have a preapical inner tooth. They are unmodified in forms scored 0 in Table 2. In those scored 0.5, the mandibles are of more or less normal length but lack the inner tooth, or in some *Paralictus,* are elongate with a small inner tooth; 1 indicates mandibles that are very long, pointed, and simple.

(q) Most nest-making Halictinae have heads about as wide as the thorax, the clypeus less than three times as wide as high, and the eyes usually converging below. Various parasitic groups (0) retain these characteristics. Others (1) have heads usually wider than the thorax, the clypeus over three times as wide as high, and the eyes not converging below. This places the mandibles farther apart, presumably making them more effective in grasping hosts, and is generally associated with long mandibles.

(r) In nest-making species the legs are relatively slender, the hind femur being straight or concave on the under surface (see *d*) (Figs 5, 6). Similarly shaped femora are found in some parasitic forms (0). In *Parathrincostoma* the legs are extraordinarily slender but the under surface of the hind femur is slightly convex (0.1). In others, the under surface of a moderately slender femur is slightly convex (0.5) or the femur is more thickened (1), with the under surface slightly convex and the upper surface especially near the base strongly so. Thickened legs presumably house stronger muscles for pushing resistant host bees along the burrows (see Figs. 7-14).

(s) Nest-making Halictinae lack spine-like tibial setae and the outer surface of the apex of the hind tibia often has a mere tubercle representing the apical tibial spine. Some parasitic groups (0) are similar, others (0.1) differ only in having a somewhat more recognizable tibial spine, but broader than long. *Echthralictus* (0.2) has the numerous setae of the outer margin of the hind tibia thickened, tapering, mostly simple, and thus spinelike. Other forms (0.3) have spinelike setae intermixed among hairs on the outer margin of the hind tibia, although the tibial spine is broader than long. In many *Sphecodes* the spinelike setae become more prominent, shorter, stouter, often almost peglike and in some species similar setae occur on the middle tibia. Along with such strengthening of the spinelike setae, the hind tibial spine is much better developed, becoming two or three times as long as broad. Such forms are scored as 1 (Fig. 3). Probably the spinelike setae and the apical tibial spines provide for a firm grip on the burrow walls when a parasite pushes a host bee.

The means in Table 2 give an idea of the amount of morphological evolution that a parasitic group has undergone since diverging from its nest making ancestors. Obviously *Paralictus* is less different from *Lasioglossum* (*Dialictus*) than other parasitic genera are from their nest making ancestral groups. *Echthralictus,* also, is moderately close to *Homalictus* from which it was derived. Every genus has scores ranging from 0 to 1, showing that acquisition of the characteristics of parasites has not followed the same sequence in all. The genera from *Temnosoma* to *Sphecodes* are all highly modified as parasites, *Temnosoma* being more specialized than the least modified *Sphecodes,* according to the table. This is probably true, but it should be noted that the range of means for a genus is based on the scores in the column above. There may not be any species having such extreme means, however. For example, in *Paralictus,* there is no species that combines all the low scores, nor is there a species that combines all the high scores. Thus there is no *Paralictus* species with a mean score as low as .25, nor is there one with a mean score as high as .38.

SIMILARITY OF PARASITIC FEMALES TO MALES

Males of halictids leave the nests early and play no roles in nest making, defense, or parasitization. It is therefore not surprising that in most features relating to pollen gathering and transport and nest construction, the parasites approach males. Specifically, this applies to characters *b* to *m* of the preceding sections and Table 2. In character *p* also, parasites often resemble halictid males and it may be that loss of the mandibular tooth should be looked at as loss of a structure important in nest-making, rather than as acquisition of simple, sicklelike mandibles for fighting. Indeed, the *Sphecodes* species famous for fighting and killing hosts with its mandibles [*S. monilicornis* (Kirby)] is one that retains the inner mandibular tooth.

In gross appearance, however, most halictid males, whether belonging to parasitic genera, or not, are quite different from females, having longer, more slender metasomas and longer antennae than females. Some nest-making forms have males that look like females [*e.g., Lasioglossum lustrans* (Cockerell)], and some parasites have sexes that look alike, more or less intermediate in shape between typical halictid males and females (*e.g., Eupetersia*).

RELATIVE DIVERSITY OF PARASITIC AND NONPARASITIC HALICTINAE

The nonparasitic Halictinae constitute an enormous group of species of impressive, morphological homogeneity. The similarity in morphology is suggested by the series of papers by Vachal and Blüthgen. Vachal, who was a specialist in halictines early in this century, placed all nonparasitic species of the subfamily in a single genus, *Halictus*. Blüthgen, a later specialist who was a "splitter" at the generic level in other groups with which he worked, placed nonparasitic groups as isolated as *Homalictus, Lasioglossum, Pachyhalictus,* and *Halictus* in a single genus. Only intensive studies and long searches for group characters have made possible the present classification of nonparasitic halictines, dividing the subfamily into two tribes, Augochlorini and Halictini, and many genera (Eickwort, 1969a, b).

By contrast, parasitic halictines have almost consistently been accorded generic rank since their species were first studied, and it is perfectly obvious that they are morphologically markedly different from the nonparasitic forms and from one another. No numerical phenetic study has been made to demonstrate the differentiation of the parasitic genera quantitatively, but such a study hardly seems necessary for that purpose alone.

It seems clear that on all continents, in spite of a wide diversity of habitats, social organizations, nesting substrates, and floral relationships, the nonparasitic forms remained basically similar, presumably as a result of selection favoring their various characteristic structures. The peculiarities of the labrum, scopa, pygidial plates and pygidial and prepygidial fimbriae, for example, vary only within narrow limits.

Among parasites, however, these structures and others listed above, mostly involved in nest construction and pollen gathering and carrying, appear to have escaped from the forces that elsewhere limit their variation. The result is the structural diversity found among parasitic genera.

HOST RELATIONSHIPS

Most parasitic bees have their own close relatives as hosts. This rule appears to apply to the majority of parasitic Halictinae, although some species of *Sphecodes* are exceptions. Table 3 gives known or probable hosts for parasitic halictids. All hosts are halictids except as otherwise indicated.

Of course, the most indisputable host data are those in which the parasite has been reared from host cells, or its larvae, pupae, or teneral adults found there. Such records are annotated (R) in the table. Finding a female parasite in the burrow of another bee is not entirely convincing, unless repeated, since parasitic bees may enter various burrows at night, in bad weather, or in searching for host nests. Such records, as well as reports of the parasites flying about nesting sites of the hosts, are annotated (N) in Table 3. Reports of hosts based on finding the parasite in the vicinity of or on the same flowers as the supposed host, the latter being the only local bee of the appropriate size and seasonality, are mere surmises, but probably are commonly correct, and are annotated (S). Less definite associations have been ignored, except for genera like *Echthralictus* and *Parathrincostoma* for which no host data exist, but whose hosts are probably correctly surmised.

In the table, each parasite name begins a separate paragraph. Specific names of hosts are omitted to save space when different host species of the same genus or subgenus are reported. The publications cited after host names provide such information.

Examination of the table suggests no high level of host specificity by most species of parasites. Some appear to attack any halictines of the right size that are available to them, while different-sized individuals of a parasitic species are reported by several authors to be associated with host species of different sizes. Other parasites are doubtless more host specific. Some are primarily or exclusively parasites of halictids, others of andrenids. Certain species of *Sphecodes* are believed to parasitize both halictids and andrenids, however, and *S. albilabris* has been reared from an andrenid and probably from a colletid, but appears to be primarily a parasite of large halictids.

Larvae of parasitic Halictinae are very similar to those of other Halictinae, having no specialized structures and behavior, such as characterize the parasitic anthophorid and megachilid larvae that attack host eggs or larvae. In halictid parasites whose behavior has been examined, the adult female parasite opens a host cell, destroys the egg, replaces it with her own egg, and recloses the cell. Evidence for this statement is largely that in repeated excavations of nests parasitized by *Paralictus* (Michener, unpublished), *Microsphecodes* (Eickwort and Eickwort, 1972), and *Sphecodes* (various authors), many cells containing immature stages and presumably eggs of parasites must have been seen, although often such cells were not distinguished from unparasitized cells. G. Eickwort (personal communication) was able to distinguish the shorter, straighter eggs of *Sphecodes autumnalis* and sp.? from those of hosts (*Perdita* and *Evylaeus*). The *Sphecodes* eggs were in the typical halictine egg position on the provisions and were not easily distinguishable from those of the hosts in the field, although measurements served to permit recognition in the laboratory. All cells, both those examined by Eickwort and by other authors, contained only one egg or young, indicating destruction of the host-egg by the adult parasite. All were closed, except, no doubt, in those species of *Lasioglossum* (*Evylaeus*) whose cells are left open part of the time. In no case was a partly eaten pollen ball found with an egg, indicating that the parasites do not destroy host larvae and replace them with eggs, but only attack fully provisioned cells in which the host larva has not started to feed. Hosts quickly oviposit in and close any fully provisioned cell. Hence, in nearly all cases, destruction of a host egg or possibly freshly hatched larva must precede laying of the egg of a parasite.

Parasites enter the nests of both solitary and eusocial hosts. After ovipositing in appropriate cells, they close the cells and either leave, or remain inside the nest to deposit more eggs on subsequent days, depending at least in part on the number of cells available for parasitization (Knerer and Atwood, 1967; Ordway, 1964). *Paralictus, Microsphecodes,* and some species of *Sphecodes* accomplish parasitization without killing adult hosts (Ordway, 1964; Eickwort and Eickwort, 1972; Michener, unpublished) while other *Sphecodes* species regularly do so. Legewie (1925) recorded the results of 76 attacks of *Sphecodes monilicornis* on colonies of *Lasioglossum malachurum*. The *Sphecodes* succeeded in 75 cases and 283 *Lasioglossum* were killed. *S. pimpinellae,* however, appears to chase away the hosts, *Augochlorella,* spp., without killing them (Ordway, 1964).

Species such as *Sphecodes monilicornis* and *pimpinellae* attack social hosts and the attack appears to result in destruction of the colony.

In the case of solitary hosts, the *Sphecodes* may lay in appropriate cells and depart before the host returns, thus being cuckoo-like, as is *Nomada.*

Eickwort and Eickwort (1972) give an account of *Microsphecodes kathleenae,* females of which enter nests of *Lasioglossum* (*Dialictus*) *umbripenne,* a eusocial host, either by passing the guard like a *Lasioglossum* or by locating unguarded nests. Female *Microsphecodes* were found in nests along with workers and queens of the host and are believed to locate the host cells, open them, eat the eggs, deposit their own, and close the cells. More than

TABLE 3. Hosts of Parasitic Halictid Bees. (R) = reared or immature parasite taken from host cell, (N) = found in or about nests, (S) host surmised on the basis of seasonal and local occurrence.

Paralictus asteris Mitchell—*Lasioglossum* (*Dialictus*) *imitatum* (Smith), (R) Michener and Wille, 1961, parasite misidentified as *P. cephalotes* (Dalla Torre); (N) Michener, unpublished.

Paralictus cephalotes (Dalla Torre)—*Lasioglossum* (*Dialictus*) *zephyrum* (Smith), (N) Robertson, 1901, 1926.

Paralictus simplex Robertson—*Lasioglossum* (*Dialictus*) *versatum* (Robertson), (N) as unidentified *Paralictus*, Michener, 1966; (N) Michener, unpublished.

Echthralictus spp.—*Homalictus* spp. *Homalictus* is the only possible host in the islands where *Echthralictus* occurs.

Parathrincostoma sp.—*Thrinchostoma* sp. Probable host as judged by size and relationship.

Temnosoma spp.—Augochlorini such as *Augochloropsis* or *Augochlora*. Probable hosts as judged by size, abundance, similar coloration, and relationship.

Microsphecodes kathleenae (Eickwort)—*Lasioglossum* (*Dialictus*) *umbripenne* (Ellis), (R) Eickwort and Eickwort, 1972.

Microsphecodes russeiclypeatus (Sakagami and Moure)—*Lasioglossum* (*Dialictus*) *seabrai* (Moure), (N) Sakagami and Moure, 1962.

Microsphecodes sp.—*Lasioglossum* (*Evylaeus*) sp., (R) Michener, unpublished.

Microsphecodes sp.—*Habralictus* sp., (N) Michener, unpublished.

Sphecodes albilabris (Kirby) (= *fuscipennis* Germar)—*Halictus* spp., (N) Blagoveshchenskaya, 1955; (N) Blüthgen, 1919; (N) Fahringer, 1922; (N) Friese, 1926; (?) Stoeckhert, 1954. *Colletes cunicularius* (Linnaeus), COLLETIDAE, (N) Alfken, 1912; (S) Blüthgen, 1930; (R?) Malyshev, 1927; (N) Möschler, 1938. *Meliturga clavicornis* Latreille, ANDRENIDAE, (R) Rozen, 1965. *Andrena ovina* Klug, ANDRENIDAE, (N) Friese, 1926. Major hosts of this species are apparently *Halictus quadricinctus* (Fabricius) and *sexcinctus* (Fabricius) but the only actual rearings from cells are from *Colletes* and *Meliturga*.

Sphecodes alternatus Smith—*Lasioglossum* (*Evylaeus*) *nigripes* (Lepeletier) (N) Knerer, 1968; (N) Knerer and Plateaux-Quénu, 1970.

Sphecodes arvensis Patton (det. Cockerell)—*Halictus rubicundus* (Christ), (N) Hicks, 1934.

Sphecodes atlantis Mitchell—*Lasioglossum* (*Dialictus*) *pilosus* (Smith), (R) G. Eickwort, personal communication.

Sphecodes autumnalis Mitchell—*Perdita octomaculata* (Say), ANDRENIDAE, (R) G. Eickwort, personal communication.

Sphecodes barbatus Blüthgen—*Lasioglossum* (*Lasioglossum*) *caspicum* (Morawitz), (S) A. W. Ebmer, personal communication.

Sphecodes brachycephalus Mitchell—*Calliopsis andreniformis* Smith, ANDRENIDAE, (S) Mitchell, 1956.

Sphecodes chilensis Spinola—*Corynura lepida* Alfken, (R?, N) Claude-Joseph, 1926; (R? N) Janvier, 1933.

Sphecodes crassus Thomson (= *variegatus* Hagens)—*Lasioglossum* (*Evylaeus*) spp., (N) Alfken, 1912; (N) Blüthgen, 1919, 1923a; (R) Blüthgen, 1934; (N) Rapp, 1945; (R) Stoeckhert, 1933. Stoeckhert (1933) depreciates reports that *Halictus maculatus* Smith is a host and Valkeika (1962) reports but gives no evidence that *Lasioglossum* (*Lasioglossum*) *sexnotatulum* Schenck is a host.

Sphecodes cristatus Hagens—*Lasioglossum* (*Evylaeus*) *nigripes* (Lepeletier), (S) Blüthgen, 1934.

Sphecodes davisii Robertson—*Agapostemon virescens* (Fabricius), (R) G. Eickwort, personal communication.

Sphecodes divisus Kirby—*Lasioglossum* (*Evylaeus*) spp., *L.* (*L.*) spp., and *Halictus* spp., (N) Alfken, 1913a; (N) Blüthgen, 1916, 1919, 1934; (N) Chambers, 1949; (S) Morice, 1901; (N) Rapp, 1945; (N) Scholz, 1912. There are also scattered records of this species entering *Andrena* nests, ANDRENIDAE, (N) Alfken, 1913a; (N) Morice, 1901.

Sphecodes fasciatus Hagens—*Lasioglossum* (*Dialictus*) spp., *L.* (*Evylaeus*) spp., and *Halictus* (*Seladonia*) *tumulorum* (Linnaeus), (N, S) Alfken, 1912, 1913b; (S) Blüthgen, 1934; (S) Morice, 1901; (N) Perkins, 1887.

Sphecodes ferruginatus Hagens (= *rufescens* Hagens)—*Lasioglossum* (*Evylaeus*) spp., (S) Blüthgen, 1934; (N) Stoeckhert, 1933.

Sphecodes near *fragariae* Cockerell—*Perdita nuda* Cockerell, ANDRENIDAE, (R) Torchio, 1975.

Sphecodes friesei Herbst—*Leioproctus* (*Lonchopria*) *zonalis* (Reed), COLLETIDAE, (R?) Janvier, 1933.

Sphecodes gibbus (Linnaeus)—*Halictus* spp., (N) Aflken, 1913a, 1939; (N) Blüthgen, 1923a, 1934; (R) Breitenback, 1878; (N) Fahringer, 1922; (S) Friese, 1926; (N) Möschler, 1938; (R) Nielsen, 1903; (S) Perkins, 1887; (S) Sanders, 1948; (N) Stoeckhert, 1933. *Lasioglossum* (*Evylaeus*) *malachurum* (Kirby), (N) Blüthgen, 1934; (N) Stoeckhert, 1933. *Lasioglossum* (*Lasioglossum*) *leucozonium*, (N) Perkins, 1887. Records of this species in or near nests of unrelated bees involve *Dasypoda hirtipes* (Fabricius), MELITTIDAE (Friese, 1920, 1923, 1926), *Andrena* spp., ANDRENIDAE (Morice, 1901; Minkiewicz, 1935, but see Stoeckhert, 1954), and *Eucera longicornis* (Linnaeus), ANTHOPHORIDAE (Friese, 1920). Of these only the *Dasypoda* record appears to be based on repeated observations.

Sphecodes granulosus Sichel and *rugulosus* Sichel—*Caenohalictus rostraticeps* (Friese), (R?, N) Claude-Joseph, 1926; (R?, N) Janvier, 1933. *Corynura* (*Callochlora*) *chloris* (Spinola), (R?) Janvier, 1933.

Sphecodes hyalinatus Hagens—*Lasioglossum* (*Evylaeus*) spp., (N) Blüthgen, 1934; (N) Rapp, 1945; (N) Stoeckhert, 1933.

Sphecodes levis Lovell and Cockerell (?)—*Lasioglossum* (*Evylaeus*) *quebecense* (Crawford), (R) G. Eickwort, personal communication.

Sphecodes longuloides Blüthgen—*Lasioglossum* (*Evylaeus*) *aglyphum* (Pérez), (N) Blüthgen, 1934.

Sphecodes longulus Hagens—*Lasioglossum* (*Evylaeus* and *Dialictus*) spp., (N) Alfken, 1912; see also Blüthgen, 1934 and Valkeila, 1962.

Sphecodes majalis Pérez—*Lasioglossum* (*Lasioglossum*) *pallens* (Brullé), (S) Blüthgen, 1934; (S) Stoeckhert, 1954.

Sphecodes marginatus Hagens (= *nigritulus* and *atratus* Hagens)—*Lasioglossum* (*Evylaeus*) spp., (N) Alfken, 1913a, 1939; (N) Blüthgen, 1934; (S) Möschler, 1938.

Sphecodes miniatus Hagens (= *dimidiatus* Hagens)—*Lasioglossum* (*Evylaeus*) spp., (N) Alfken, 1939; (N) Blüthgen, 1919; (S) Perkins, 1887; (N) Stoeckhert, 1933. Blüthgen (1916) reported *Halictus* (*Seladonia*) *tumulorum* as a probable host.

Sphecodes minor Robertson—*Lasioglossum* (*Evylaeus*) *cinctipes* (Provancher), (R) Knerer and Atwood, 1967. (R, Atwood, 1933, probably also concerns *S. minor*.)

Sphecodes monilicornis Kirby (=*subquadratus* Smith, *quadratus* Meyer)—*Lasioglossum* (*Evylaeus*) *malachurum* (Kirby), (N) Blüthgen, 1934; (N) Ferton, 1898, 1923; (N) Grandi, 1961; (N) Knerer, 1968, 1973; (R) Legewie, 1925; (N) Marechal, 1894; (N) Rapp, 1945; (N) Stoeckhert, 1933, 1954. *L.* (*Evylaeus*) spp., (N) Alfken, 1913a, b; (N) Blüthgen, 1934; (N) Fahringer, 1922; (N) Grandi, 1961. *Halictus rubicundus* (Christ), (N) Alfken, 1913a, b; (S) Perkins, 1887. *L.* (*Lasioglossum*) spp., (N) Alfken, 1913a, b; (N) Frisby, 1914. Many of the references marked (N) report the *Sphecodes* killing nest guards or burrowing into nest entrances.

Sphecodes niger Sichel—*Lasioglossum* (*Evylaeus*) spp., (N) Blüthgen, 1916, 1934; (N) Rapp, 1945.

Sphecodes pellucidus Smith—*Andrena* spp., ANDRENIDAE, (N) Alfken, 1913a; (N) Blüthgen, 1934; (N) Chambers, 1949; (N) Fahringer, 1922; (N) Friese, 1920; (N) Möschler, 1938; (S) Perkins, 1919; (N) Stoeckhert, 1933. *Dasypoda hirtipes* (Fabricius), MELITTIDAE, (N) Friese, 1923. *Lasioglossum* (*Evylaeus*) *nigripes* (Lepeletier), (N) Grandi, 1961. *Lasioglossum* (*L.*) spp., (S) Morice, 1901; (?) Valkelia, 1962.

Sphecodes pimpinellae Robertson—*Augochlorella* spp., (R) Ordway, 1964.

Sphecodes puncticeps Thomson—*Lasioglossum* (*Evylaeus*) spp., (N) Alfken, 1912, 1913a, but see 1939; (S) Blüthgen, 1919, 1934.

Sphecodes reticulatus Thomson—*Andrena* spp., ANDRENIDAE, (N) Alfken, 1913a, b, 1939; (N) Blüthgen, 1919, 1934; (N) Legewie, 1925; (S) Perkins, 1919; (S) Richards, 1944. *Dasypoda hirtipes* (Fabricius), MELITTIDAE, (N) Friese, 1920, 1923.

Sphecodes rubicundus Hagens—*Andrena* spp., ANDRENIDAE, (N) Alfken, 1912, 1913a; (N) Blüthgen, 1934; (N) Chambers, 1949; (N) Möschler, 1938; (S) Perkins, 1919; (N) Saunders, 1898; (R) Saden, 1895; (N) Stoeckhert, 1919, 1933; (N) Torka, 1913.

Sphecodes ruficrus (Erickson) (= *hispanicus* Wesmael)—*Lasioglossum malachurum* (Kirby), (N) Ferton, 1898.

Sphecodes rufiventris (Panzer) (= *subovalis* Schenck)—*Halictus maculatus* Smith, (N) Blüthgen, 1934; (N) Stoeckhert, 1933. *Lasioglossum* (*Evylaeus*) spp., *L.* (*Lasioglossum*) spp. and *Halictus* (*Seladonia*) sp., (S) Blüthgen, 1923.

Sphecodes schencki Hagens—*Lasioglossum* (*Lasioglossum*) *discum* (Smith) [= *morbillosum* (Kriechbaumer)], (R) Grozdanić, 1971.

Sphecodes spinulosus Hagens—*Lasioglossum xanthopus* (Kirby), (?) Alfken, 1912; (S) Blüthgen, 1916, 1934; (N) Perkins, 1889. *Halictus rubicundus* (Christ), (S) Yarrow, 1943. Records for *Andrena* are probably incorrect (Stoeckhert, 1933).

Sphecodes subovalis Schenck—*Halictus maculatus* Smith, (N) Rapp, 1945.

Sphecodes sp.—*Calliopsis* spp., ANDRENIDAE, (N) Ainslie, 1937; (R) Michener, 1953 (misidentified as *Neopasites*); (N) Mitchell, 1960; (N) Rau and Rau, 1916; (N) Shinn, 1967.

Sphecodes sp.—*Perdita* spp., ANDRENIDAE, (N) Michener, unpublished; (N) Mitchell, 1960.

one *Microsphecodes* was often found in a single nest and the parasites appear to remain in the host-nest for up to a day or so. The Chilean *Sphecodes* reported upon by Claude-Joseph (1926) and Janvier (1933), all of them probably in the subgenus *Austrosphecodes,* probably behave similarly. The several North American species of *Paralictus* are parasites in *Lasioglossum* (*Dialictus*) nests and adults of host and parasite are regularly found together in the same nest. Probably they, too, have habits similar to those of *M. kathleenae.*

There are probably morphological correlates in females of *Sphecodes* related to the manner of parasitization. Thus, those that actively dig and push their way into nests, against the defense of hosts, have heavy legs, strong hind-tibial spines, spinelike or peglike tibial setae, and a partially recognizable basitibial plate, all features which presumably make the parasite more effective in pushing its hosts. *S. monilicornis* has these features very well developed (Figs. 3, 22) and also has a heavy, quadrate head, which provides space for the strong mandibular musculature; the females of this species puncture or crush the heads of the host with their long mandibles. On the contrary, the subgenus *Austrosphecodes* and the genus *Microsphecodes,* whose females apparently live more or less peacefully in nests of the host, have slender legs without the projections and basitibial plates to improve traction.

Unlike many *Sphecodes,* which commonly visit flowers, adults of *Microsphecodes* perhaps feed only in cells of their hosts. Most of the known specimens have been collected only recently, by persons studying nests of halictine bees. No specimens are known to have been taken on flowers although *M. russeiclypeatus* was obtained in a place where much floral collecting has been done by me and by those associated with Padre J. S. Moure. Published observations of *M. kathleenae* in Costa Rica indicate that it was not found on flowers (Eickwort and Eickwort, 1972). I found the unnamed species listed in Table 3 as parasites of *Habralictus* and *Lasioglossum* (*Evylaeus*) to be common flying about nesting sites of their hosts in Colombia, as well as in the nests, yet not one was seen on a flower. Another Colombian species was taken about a bank inhabited by *Lasioglossum* (*Dialictus*) where extensive sweeping of the flowers visited by the *Dialictus* failed to reveal even one *Microsphecodes.* These observations suggest that the principal, if not the only, feeding place of *Microsphecodes* adults may be in the nest of the host, where they probably feed on food masses stored in cells. Such behavior is suggestive of that of the parasitic genera of allodapine bees which likewise do not visit flowers but feed in the nests of the host.

SYSTEMATIC TREATMENT

For genera 1 to 4 of Table 1, the commentary in this section indicates the placement relative to their nonparasitic ancestors. For genera 5 to 8, the *Sphecodes* group, however, more detailed, comparative descriptions are given, because these genera are closely related and require substantiation. Moreover, they probably had a common parasitic *Sphecodes* or *Sphecodes*-like ancestor and thus constitute a natural group, unlike genera 1 to 4, each of which arose from a different nest-making ancestor (Table 1).

GENUS PARALICTUS ROBERTSON
(Figs. 7, 24, 29)

Paralictus Robertson, 1901, Canadian Ent., 33:229. Type species: *Halictus cephalicus* Robertson, 1892 (not Morawitz, 1873) = *Halictus cephalotes* Dalla Torre, 1896, by original designation.

This is a North American group of several species, resembling and presumably derived from the subgenus *Dialictus* of *Lasioglossum*. It resembles *Dialictus* in small size, presence of some greenish coloration on the head and thorax, weakened second and third transverse cubital veins (second sometimes absent) and second recurrent vein, presence of a few (two to four) coarse teeth on the inner margin of the inner, hind tibial spur (but these teeth smaller than is usual in *Dialictus*), male genital structure including the large, retrorse, ventral lobe on the base of the gonostylus, as well as various other features marked as zero or near zero in column 1, Table 2.

Paralictus differs from *Dialictus* in those features having high numbers in column 1, Table 2. Included among these are reductions in various pollen-handling and nest-making structures, such as characters *c* to *j* and *m*. (For details, see the explanations for the characters listed in Table 2). Other outstanding features of *Paralictus* are the following: (*k*) Apical process of labrum of female rounded at apex, without keel. (*p*) Mandible of female large, sometimes with subapical tooth, although mandible narrower and more pointed than in most *Dialictus*, sometimes acutely pointed, without distinct, subapical tooth. (This feature is approached in some *Dialictus*, as is the next.) (*q*) Head of female often quadrate, inner margins of eyes sometimes parallel or diverging below so that face is wide below, genal areas commonly greatly broadened, much wider than eye.

The males are not distinguishable from those of *Dialictus* by characters that appear to be of generic importance (but see Mitchell, 1960).

As emphasized to me by Dr. George C. Eickwort, who has studied *Paralictus* in some detail and who provided me with an identified set of specimens for study, there is considerable diversity among the species, some being more like *Dialictus* than others (see variation indicated in column 1, Table 2). *P. michiganensis* Mitchell and *simplex* Robertson are perhaps the most *Dialictus*-like, having a relatively unmodified head (especially in *simplex*), bidentate mandibles (inner tooth smaller and narrower than in *Dialictus*), the body of the labrum distinctly elevated above the apical process, and the carina margining the basitibial plate strong. On the other hand, in some features the same species are quite different from *Dialictus*. Thus the hind femur lacks long, scopal hairs on the anterior surface, the penicillus is much reduced, and the labral process in *simplex* is subtruncate and bears scattered bristles other than those near the margin. At the other extreme are species such as *P. cephalotes* (Dalla Torre) and *asteris* Mitchell which have large heads, the inner orbits nearly parallel or diverging below, the mandibles enormous and untoothed, the labral process weakly differentiated from the body of the labrum, and the carina margining the basitibial plate weak. The long, curled, scopal hairs on the anterior surface of the hind femur in *asteris* and the well formed penicillus in *cephalotes*, however, are *Dialictus*-like features of these species. (The largest penicillus, but still reduced compared to *Dialictus*, occurs in an undescribed species from Lawrence, Kansas.)

The question arises as to whether *Paralictus* is a monophyletic group or consists of parasites derived independently from different species of *Dialictus*. Perhaps this question can be answered if *Dialictus* becomes well enough known that the group or groups from which *Paralictus* arose can be determined. At present it is impossible to reach a decision. Obviously, if *Paralictus* is polyphyletic it must either be divided into two or more genera (or subgenera of *Lasioglossum*) or synonymized with *Dialictus*. For the present, I maintain *Paralictus* as a genus because it differs from *Dia-*

lictus by many more, and more striking, characters than those that separate the nonparasitic groups such as *Dialictus, Evylaeus, Lasioglossum* s. str., and even *Halictus* from one another.

GENUS ECHTHRALICTUS
PERKINS AND CHEESMAN
(Figs. 8, 16, 30)

Echthralictus Perkins and Cheesman, 1928, Hymenoptera—Apoidea, Sphecoidea and Vespoidea, *in* Insects of Samoa, British Museum (Natural History), p. 14. Type species: *Halictus extraordinarius* Kohl, 1908, by original designation.

This genus contains at least two species restricted to Samoa, where it presumably arose from *Homalictus* (*Homalictus*) species. As indicated by Michener (1965) it resembles *Homalictus* proper in the following features: small size; presence of some greenish or bluish coloration on the head and thorax; presence of a frontal carina; weakened third transverse cubital and second recurrent veins; presence of a few, coarse teeth on the inner margin of the inner, hind tibial spur; presence of a few, very long hairs representing the distinctive sternal scopa of *Homalictus;* rather elongate male genitalia with short gonostyli and without a basal, retrorse, gonostylar lobe, as well as various other features marked as zero or near zero in column 2 of Table 2.

Echthralictus differs from *Homalictus* in those features having high numbers in column 2, Table 2. Among these are reductions in pollen-carrying structures (characters *d* to *g*) and in some probable nest-making structures (characters *i, j, m*), as explained in the paragraphs about characters listed in Table 2. The femoral scopa is not recognizable, except for the row of long hairs on the posterior surface which is reduced to simple hairs, the longest about two-thirds as long as the maximum femoral diameter. The tibia has a distinct, relatively bare, under surface, but the hairs margining it are not longer than those elsewhere on the tibia and have only short


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FIGS. 29, 30. Facial views of females of *Paralictus asteris* Mitchell and *Echthralictus extraordinarius* (Kohl).

branches. Except for some long hairs arising near the tibial spurs, the longest tibial hairs are the thick, mostly-simple bristles along the outer margin (character *s*). Other outstanding generic characters of *Echthralictus* are: (*k*) Apical process of labrum of female rather narrowly rounded (rather than pointed) at apex; the keel reduced to a strong carina. (*o*) Dorsolateral angle of pronotum produced to acute spine, rounded at apex. (*p*) Mandible of female acute, without subapical tooth. (*q*) Head of female quadrate, inner margins of eyes subparallel, so that face is wide below, genal area much wider than eye.

Another distinctive feature, perhaps related to the loss of the tergal and great reduction of the sternal scopa, is the rounded lateral metasomal margin. In *Homalictus,* the metasoma is compressed so that its lateral margin is a strong bend, or crease, in the terga where their ventral surfaces join the dorsal surfaces. The inner margin of the inner, hind-tibial spur of the male is coarsely pectinate, suggesting a female.

In features such as the wide head and the coarse teeth on the inner hind-spur of the male, *Echthralictus* suggests *Homalictus ctenander* Michener from Australia, but in the labral process, female mandible, scopa, etc., that species does not show evidence of parasitic behavior (Michener, 1965). While the male of *Echthralictus* is easily distinguished from that of most *Homalictus,* species like *H. ctenander* eliminate useful, constant, generic characters for males.

Genus PARATHRINCOSTOMA Blüthgen

(Figs. 9, 31-38)

Parathrincostoma Blüthgen, 1933, Mitt. Zool. Mus. Berlin, 18:389. Type species: *Parathrincostoma seyrigi* Blüthgen, 1933, by original designation and monotypy.

This genus, known only from Madagascar, was first described from the male. Although Blüthgen could not determine whether the pollen-carrying scopa of the female was present or absent, he suggested that the genus was probably a parasite derived from *Thrinchostoma.* Benoist (1962) described the female and noted the absence of the "brosse collectrice aux tibias III," but made no point of this finding, nor did he note the lack of a femoral scopa. Presumably he was confused by the fact that one of his two, supposed species was a *Nomia* with pollen-collecting apparatus (see Appendix). Thus the parasitic nature of the genus is here established for the first time, based on the lack of the pollen-carrying apparatus.

Parathrincostoma agrees with *Thrinchostoma* subgenus *Eothrincostoma* in the characters listed below:

Both sexes: Nonmetallic black, large and slender, 11-14 mm long; metasoma elongate, widest at third segment. Clypeus produced downward and strongly protuberant forward, a line tangent to the lower ends of eyes crossing clypeus near middle or at lower third; malar space conspicuous, but shorter than basal mandibular width. Paraocular area extending as a strong, right-angular lobe into clypeus. Mouthparts long and slender, glossa linear and much exceeding the short galea and palpi. Pronotum with horizontal, dorsal surface rather broad, margined anteriorly by high carina or lamella, not overhung by scutum. Dorsal surface of propodeum much longer than metanotum. Apical wing veins strong; first transverse cubital arising well away from margin of stigma, vein *r* being about three times as long as wide, first recurrent vein approximately interstitial (or in one specimen of *P. seyrigi,* second transverse cubital absent so that there are only two submarginal cells); no area of dense hair along second transverse cubital vein, this vein not angular or thickened; anterior margin of third submarginal cell about half as long as posterior margin; marginal cell minutely truncate and appendiculate at apex. Apical margins of terga 1-4 of females and 1-6 of males broadly impunctate and slightly depressed.

Male: Labrum with strong, median, apical process similar to that of female, this process margined with bristles, without keel, but with feeble, longitudinal, median ridge. Basitibial plate an elongate, hairless, shining area, not defined by a carina.

Parathrincostoma differs from *Thrinchostoma* in the features represented by high scores in column 3, Table 2, and discussed in the paragraphs associated with that table as well as below: (*a*) Body and legs largely without short hairs except behind pronotal lobe, sparsely across dorsum of pronotal collar, and in males on large areas with short, dense, brown hairs on terga 3-5. Depressed apical tergal margins without laterally directed hairs in female or in male with such hairs poorly represented. (*h*) Basitibial plate of female feebly elevated, shining, not clearly defined. (*i*) Fifth metasomal tergum of female hairy, with hairs nearly to margin, without any evidence of median specialized area, surface not hidden by hairs, apical margin weakly produced medially. (*j*) Sixth tergum with pygidial and suprapygidial plates united, the gradulus weak or absent. (*k*) Labral keel of female reduced to a strong carina, high and almost a keel apically.

Other distinctive features of *Parathrincostoma* are as follows: Dorsolateral, pronotal angle obtuse or produced to acute spine, connected mesally with carina or lamella across anterior margin of collar. Propodeal triangle broader than in *Thrinchostoma,* posterior margin curving onto posterior pronotal surface. Male: Face and legs black; flagellum of moderate length, all segments longer than broad or second

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FIGS. 31-34. *Parathrincostoma seyrigi* Blüthgen. FIGS. 31, 32, male and female. FIGS. 33, 34, faces, male and female.

as broad as long; hind tibia slender, black, unmodified, the spurs in normal positions; first two hind tarsal segments not fused, but articulation much broader than more distal articulations; seventh tergum without pygidial plate, but with broadly rounded, apical margin as seen from above, this margin being a sharp separation of dorsal and ventral surfaces of tergum. Sterna 4 and 5 unmodified.

It is interesting that the unmodified fourth and fifth sterna and hind tibia of the male and the nonfused first and second hind tarsal segments of the male appear to be ancestral to those of any *Thrinchostoma.* Relative to most *Thrinchostoma,* several other characters, especially those of the wings, are ancestral, being more like ordinary halictids. It is in these latter characters that *Parathrincostoma* resembles the subgenus *Eothrincostoma. Eothrincostoma* is restricted to Africa, so far as known not being found in Madagascar or Asia. Unless the ancestral wing, leg, and sternal characters are reversions somehow related to parasitic behavior, the implications are that *Parathrincostoma* is an ancient parasite that arose from a common ancestor with *Eothrincostoma* either in Africa or at a time when *Eothrincostoma* was in Madagascar. *Eothrincostoma* and *Thrinchostoma* have the common derived male features of modified sterna, fused first and second hind tarsal segments, and enlarged and modified hind tibiae.

Genus TEMNOSOMA Smith
(Figs. 10, 18)

Temnosoma Smith, 1853, Catalogue of hymenopterous insects in the collection of the British Museum, 1:38. Type species: *Temnosoma metallicum* Smith, 1853 (monobasic).

Micraugochlora Schrottky, 1909, Rev. Mus. La Plata, 16:138. Type species: *Micraugochlora sphaerocephala* Schrottky, 1909 (monobasic).

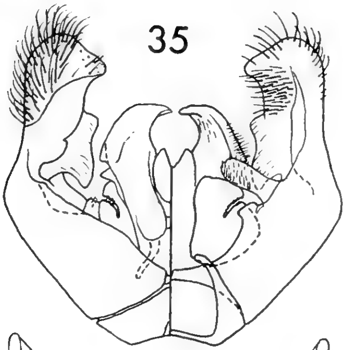
Temnosomula Ogloblin, 1953, Bol. Soc. Ent. Argentina, 2:2. Type species: *Temnosoma (Temnosomula) platensis* Ogloblin, 1953, = *Temnosoma sphaerocephala* (Schrottky, 1909), by original designation and monotypy.

This genus, which ranges from southern Arizona to Argentina, consists of brilliant metallic-green species with coarse punctation (suggestive of chrysidids), the only known parasites in the tribe Augochlorini. (All other forms treated in this paper are in the tribe Halictini). *Temnosoma* has been described and illustrated by Eickwort (1969b) and its features related to the presumed parasitic behavior are summarized in Table 2 and the accompanying text and figures. More detailed treatment is not necessary here.

In some respects there is more variation in the genus than Eickwort recognized. Thus the labral process of the female is sometimes emarginate instead of truncate and the body of the labrum may have a single median elevation instead of a pair of them. The gradulus of the sixth tergum of the female may be absent, so that there is no suprapygidial plate and the hairy zone or pygidial fimbria extends across the tergum in front of the pygidial plate uninterruptedly. On the other hand, as illustrated by Eickwort, there may be a weakly defined, small, suprapygidial plate and behind it, a break in the hairy zone.

THE SPHECODES GROUP

The content of this large and widespread group is indicated in Table 1. It contains halictids that are highly modified as parasites. Probably because of its antiquity, its most closely related nonparasitic relatives are not readily identifiable. The distal veins of the forewing are strong, a character shared with *Halictus* and differentiating the parasites from *Lasioglossum, Homalictus,* and their rela-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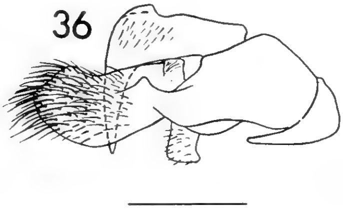
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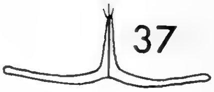
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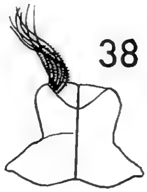
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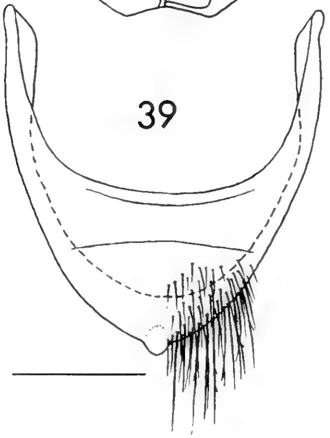
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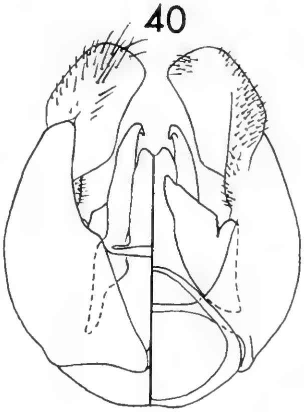
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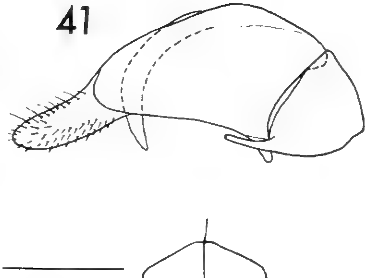
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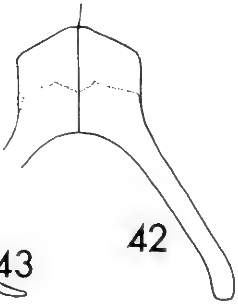
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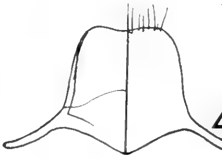
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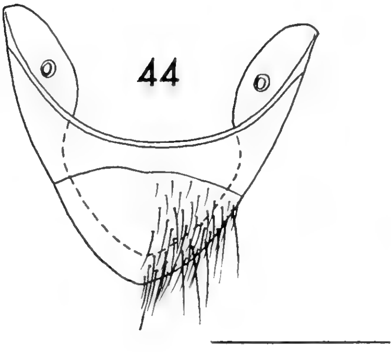
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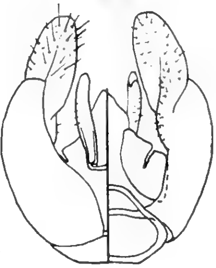
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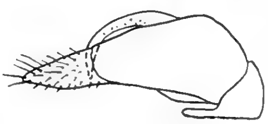
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FIGS. 35-38. *Parathrincostoma seyrigi* Blüthgen, male. FIGS. 35, 36. Dorsal-ventral and lateral views of genitalia. FIGS. 37, 38. Seventh and eighth metasomal sterna, dorsal at left.

FIGS. 39-43. *Ptilocleptis tomentosa* Michener, male. FIG. 39. Seventh tergum. FIGS. 40, 41. Dorsal-ventral and lateral views of genitalia. FIGS. 42, 43. Seventh and eighth metasomal sterna, dorsal at left.

FIGS. 44-46. *Ptilocleptis eickworti* Michener, male. FIG. 44. Seventh tergum. FIGS. 45, 46. Dorsal-ventral and lateral views of genitalia. Scale lines represent 0.5 mm.

tives. Unlike *Halictus,* however, the distal margins of the metasomal terga are usually rather broadly hairless, never with hair bands. Also, unlike *Halictus,* the male gonostylus often has a small basal ventral lobe, probably homologous to the retrorse lobe that is widespread in the *Lasioglossum-Homalictus* group. The rather large gonostyli, however, are suggestive of those of some *Halictus.*

Partly because of the great variability among species of *Sphecodes,* the genera of the *Sphecodes* group are not easily defined. The more diagnostic characters are italicized in the following descriptions.

PTILOCLEPTIS New Genus

(Figs. 11, 17, 25, 28, 39-54)

Type species: *Ptilocleptis tomentosa* new species.

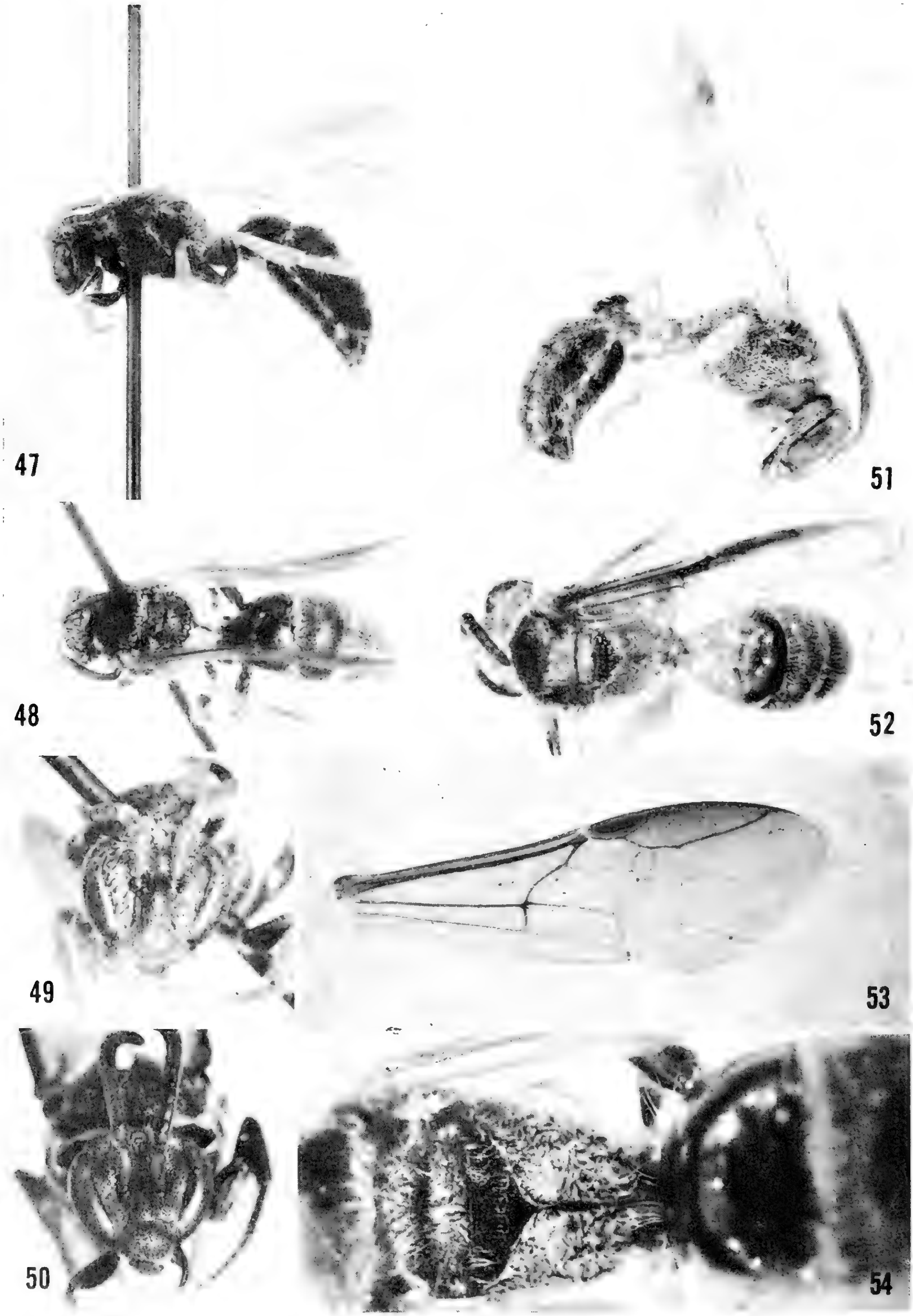
The three species of this genus, all of them described in the Appendix, resemble certain polybiine wasps because of the elongate body, dark costal margins of the forewings, and in some cases the yellowish integumental markings, in others the pattern of yellow brown pubescence.

Both sexes: Punctation moderate, dense on head and thorax, not involving coarse pitting as is usual in *Sphecodes. Head little wider than long, eyes strongly converging below, clypeus only about twice as broad as long, not biconvex. Eyes with scattered hairs,* extremely short to about one-fourth as long as diameter of scape. Hypostomal carina a very high, thin lamella, gradually reduced toward posterior end, abruptly reduced near angle so that transverse part is low. Hairs of flagellum mostly short, but dorsal side with some hairs one fifth as long as diameter of flagellum, basal segments with some as much as one third that length. *Preoccipital carina present, complete.* Pronotum with horizontal surface of collar very-short medially, *a strong carina across anterior margin of collar between lateral angles;* lateral angle right-angular, extended downward as strong vertical carinate ridge which merges with a laterally directed lamella that extends toward coxal base; a carina from lateral angle of pronotum onto posterior lobe, continuing at least two thirds of way across lobe. Anterior extremity of scutum narrowly vertical, then abruptly curving onto dorsal surface, vertical area that lacks punctures present, but small, or absent in *P. polybioides* Michener. Scutellum rather flat medially or biconvex. Propodeum with dorsal area bearing strong longitudinal carinae, the area about as long as or longer than metanotum, distinctly *shorter than scutellum; posterior and lateral surfaces of propodeum with short plumose hairs.* First metasomal tergum as long as or longer than wide.

Wings with rather long hairs over entire surface; stigma of moderate size; marginal cell with apex narrowly rounded almost on wing margin, free part beyond submarginal cells much longer than part subtended by marginal cells; *marginal cell unusually broad because vein beyond submarginal cells is gently curved almost its entire length;* submarginal cells extending well beyond apex of stigma; second and third submarginal cells each receiving a recurrent vein, or second transverse cubital vein absent, so that there are only two submarginal cells, the second receiving both recurrent veins.

Female: Mandible without subapical tooth, relatively short. Labrum with apical process a little over twice as wide as long to four times as wide as long.

Legs slender, hind femur well over four times as long as wide; basitibial plate totally absent; *tibia rather densely covered with relatively short, slender, essentially simple hairs,* some near upper margin with a few short barbs, some shorter plumed hairs interspersed, no spinelike setae; *hind tibial spine absent.*



FIGS. 47-54. *Ptilocleptis.* FIGS. 47-49. *P. tomentosa* Michener, holotype female. FIG. 50. Face of allotype male of *P. tomentosa.* FIGS. 51, 52. *P. polybioides* Michener, holotype female. FIG. 53. Wing of *P. tomentosa,* allotype male. FIG. 54. Propodeum and base of metasoma of *P. tomentosa,* holotype female.

Fifth tergum with apical fringe of plumose hairs longer than those of preceding terga. *Pygidial plate a thin slightly upturned apical process* in front of which a bare zone extends anteriorly toward middle of tergum in *P. tomentosa.*

Male: Antenna of moderate length as in female, not thickened, first flagellar segment broader than long or as long as broad, others longer than broad or second about as long as broad. Labrum with apical process two to four times as broad as long.

Second hind tarsal segment shorter than to longer than third, base broader than base of third.

Gonocoxite not striate, without depression; gonostylus without basal lobe.

This genus is known from Mexico (unknown locality) to southern Brazil. It differs from *Sphecodes* in the features italicized above, especially those of the labrum, clypeus, and hind tibia. Moreover, it does not look like a *Sphecodes,* not only because of its form and relatively fine punctation, but because of lack of red coloration and the extensive coverage of the body with short plumed hair, as indicated in the descriptions of the species.

In its elongate body, slender legs and relatively fine punctation this genus suggests *Eupetersia.* It is much less similar to *Sphecodes* than is *Eupetersia,* however. Presumably it is an independent derivative of *Sphecodes,* as indicated by the characters emphasized above as well as by the relatively narrow head and short mandibles, features suggestive of *S. convergens* which may represent the group from which *Ptilocleptis* arose.

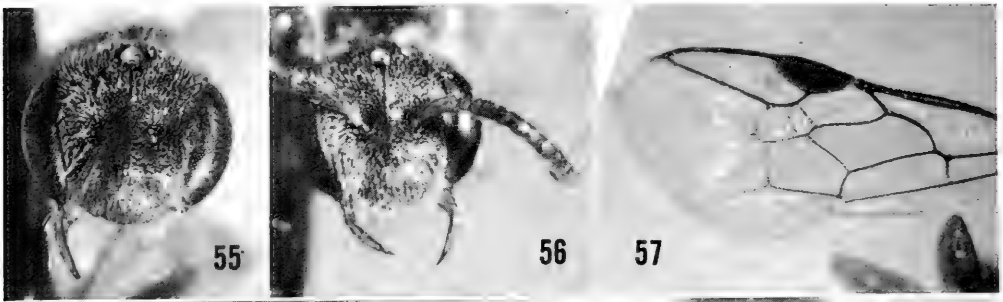
The generic name is based on *ptilon,* feather or plume, and *kelptis,* thief, and is feminine in gender.

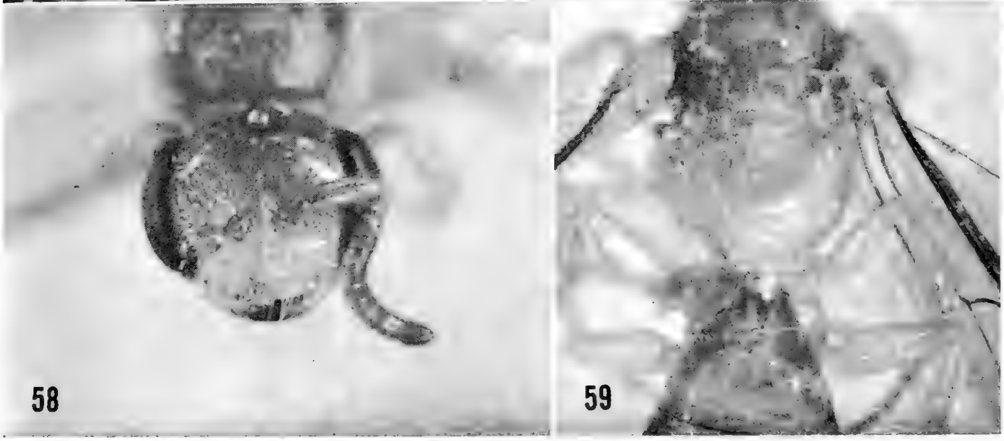
Genus MICROSPHECODES
Eickwort and Stage
(Figs. 55-57)

Microsphecodes Eickwort and Stage, 1972, Jour. Kansas Ent. Soc., 45:501. Type species: *Sphecodes kathleenae* Eickwort, 1972, by original designation.

Both sexes: Punctation rather weak, not involving such coarse pitting as is usual in *Sphecodes.* Clypeus three to four times as broad as long, not biconvex. Eyes with only very short, scattered hairs. Hairs on upper surface of antennal flagellum often one third as long as diameter of flagellum or more, such long hairs present on all flagellar segments. Preoccipital carina present or absent. Pronotum with horizontal surface or collar poorly defined, rounded onto declivous anterior surface, narrow medially, *lateral angle rounded or obtusely angulate with no marked vertical ridge extending downward from it* and no carina or lamella extending toward coxal base; a weak ridge extending to pronotal lobe, but not continued as a carina across lobe. *Anterior extremity of scutum gently convex* except adjacent to pronotum, no large strongly convex or vertical region, but with small transverse more or less vertical area without punctures. Scutellum biconvex or not, the midlateral areas (convexites when present) largely impunctate. Propodeum with dorsal area slightly shorter than or as long as scutellum, semilunar, with a few, often irregular carinae. Posterior and lateral surfaces of propodeum with numerous, short, plumose, white hairs in addition to scattered longer hairs.

Wings *with rather long hairs over entire surface; stigma large;* marginal cell pointed at or near wing margin; *free part of marginal cell more than twice as long as part subtended by submarginal cells, which do not extend beyond apex of stig-*





Figs. 55-57. *Microsphecodes kathleenae* (Eickwort and Stage). Figs. 55, 56. Faces of female paratype and allotype male. Fig. 57. Wing of allotype male.

Figs. 58, 59. *Eupetersia flava* Michener, face and dorsum of propodeum and base of metasoma.

ma; second and third submarginal cells each receiving a recurrent vein.

First tergum slightly longer than broad, more elongate in male; metasoma moderately elongate, more slender in male than in female. Almost no constriction between first and second terga as seen in lateral view.

Female: Mandible without subapical tooth. Labrum as usual in *Sphecodes,* with broad rounded apical process about twice as broad as long.

Legs slender, hind femur over three times as long as wide, upper surface near base scarcely convex; basitibial plate entirely absent; hairs on outer side of hind tibia simple or nearly so, upper margin of hind tibia without spinelike setae or pegs; hind tibial spine absent or nearly so.

Fifth tergum with apical margin bare, broadly impunctate, like preceding terga. Pygidial plate narrow, rounded apically, parallel-sided, marginal carinae extending only a short distance onto tergal disc.

Male: Antenna not much longer than in female, *flagellum not thickened,* first two flagellar segments both a little broader than long. Labrum as in female.

Second hind tarsal segment slightly longer than third, narrowed toward base and articulated like third.

Gonocoxite not striate, without depressed area. Gonostylus broadly rounded, its basal ventral setose lobe rather small and directed apically.

This is a neotropical genus of minute species, 3.25 to 6 mm long, often with more or less extensive yellowish areas on the head and thorax. Species are known from Costa Rica to southern Brazil. The characters italicized in the above description separate *Microsphecodes* from most

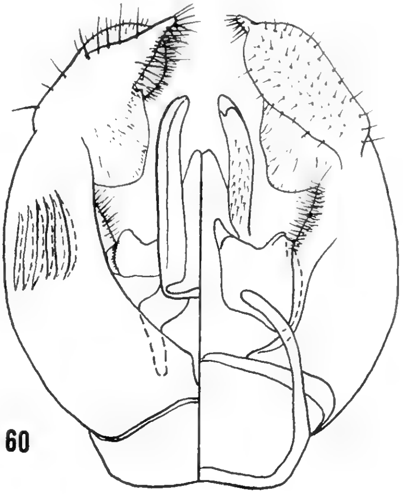
Sphecodes. Some of these characters, such as the simple mandibles, occur also in various groups of *Sphecodes,* but others seem very distinctive and have led me to elevate *Microsphecodes* to the genus-level. Among such characters are the gently convex anterior part of the scutum, the enlarged stigma and short submarginal cells relative to the marginal cell, and the lack of an apical fringe on the fifth tergum of the female. Thus *Microsphecodes* is fully as distinctive as *Eupetersia.*

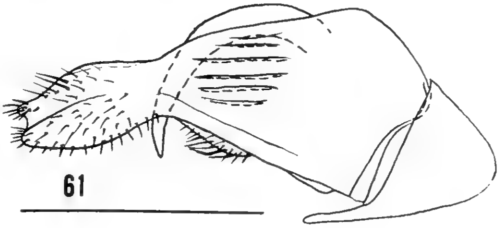
The described species of the genus are listed and discussed by Eickwort and Stage (1972).

Various small species of *Sphecodes* resemble *Microsphecodes* in appearance and some species of *Austrosphecodes* from South America may represent a group of *Sphecodes* related to *Microsphecodes.* In other areas, similar species obviously result from convergence. For example, *Sphecodes (Sphecodes) antennariae* Robertson has the size, coloration, shining thorax with small punctures, lack of areolation, and simple female mandibles of *Microsphecodes.* However, the distinct origin of *S. antennariae* is shown by most of the above italicized characteristics and by the presence of a few spinelike setae on the outer margin of the hind tibia of the female, the partially recognizable basitibial plate of the female, the thickened articulation between the first and second hind tarsal segments of the male, etc.

Genus EUPETERSIA Blüthgen
(Figs. 12, 19, 58-66)

Both sexes: Punctation moderate to fine, varying from dense to sparse, not involving such coarse pitting as is usual in *Sphecodes.* Head much wider than long, clypeus three or more times as wide as long, not or feebly biconvex. Eyes hairless or with scattered very-short hairs. Hairs of antennal flagellum all short or some as much as one-fifth as long as diameter of flagellum. *Preoccipital carina present,* at least at sides where lower extremities approach or join posterior extremities of hypostomal carinae.





Figs. 60, 61. *Eupetersia guillarmodi* Michener, dorsal-ventral and lateral views of male genitalia. Scale lines represent 0.5 mm.

Pronotum with horizontal surface of collar reduced almost to the vanishing point medially (broader in *guillarmodi*), but forming lateral angle which is usually prominent (weak and rounded in *coerulea* Blüthgen and *ruficrus* Blüthgen and relatives) and below which vertical ridge extends downward, a carina usually evident from lateral angle onto posterior lobe. Anterior extremity of scutum strongly convex, the vertical anterior surface sometimes lacking punctures and therefore with an area sharply different from rest of scutum.

Scutellum variable. Propodeum with dorsal area coarsely-rugose, aerolate, *markedly longer than scutellum,* usually slightly concave, broad laterally so that it is semilunar and broadly rounded posteriorly (not triangular); *posterior and lateral surfaces of propodeum with numerous short plumose pale hairs in addition to scattered longer hairs.*

Wings with rather long hairs over entire surfaces; stigma of moderate size; marginal cell narrowly truncate to pointed on or near wing margin; *free part of marginal cell beyond submarginal cells much longer than part subtended by submarginal cells,* which usually extend but little beyond apex of stigma.

First tergum usually about as long as broad; *metasoma in both sexes moderately elongate,* usually more slender than in most female *Sphecodes* and not as slender and parallel sided as in most male *Sphecodes.* (In *E. guillarmodi,* metasoma relatively robust, same shape in male and female.) In lateral view, a constriction between first and second terga (except in *E. guillarmodi*). Posterior margins of terga 2-4 broadly depressed, hairless, impunctate.

Female: Mandible without subapical tooth. Labrum as usual in *Sphecodes* with broad, rounded apical process about twice as broad as long.

Legs slender; hind femur over three times as long as wide, upper surface near base scarcely convex; basitibial plate entirely absent or slightly elevated; long hairs on outer side of hind tibia simple or nearly so; upper margin of hind tibia with or without spinelike setae; hind tibial spine broad, blunt, not longer than broad.

Fifth tergum with apical margin fringed, unlike preceding terga, and sometimes with a conspicuous hairless zone in front of fringe. *Pygidial plate usually narrow, the sides parallel,* but broad in *E. guillarmodi* and *flava.*

Male: Antenna short as in female, flagellum not thickened, first two flagellar segments both distinctly broader than long. Labrum with apical process short so that it is three to several times as broad as long.

Second hind tarsal segment about as long as third, base broader than base of third.

Gonocoxite not striate, with dorsolateral depressed area with lamella or flange on either side and often with one or more longitudinal ridges across depressed area. Gonostylus long, with basal setose lobe broad and directed mesobasad.

This genus ranges widely through sub-Saharan Africa, south as far as Cape Province; it also occurs in Madagascar, the Seychelles, and has recently been found in southern India. Baker (1974) has catalogued the described species. [He missed records of *E. sakalava* Blüthgen by Benoist, 1962, as well as a species, *E. constricta* (Benoist), new combination, described in the same paper as a *Sphecodes* and here transferred to *Eupetersia* on the basis of the description.] Keys to the species were given by Blüthgen (1928, 1935).

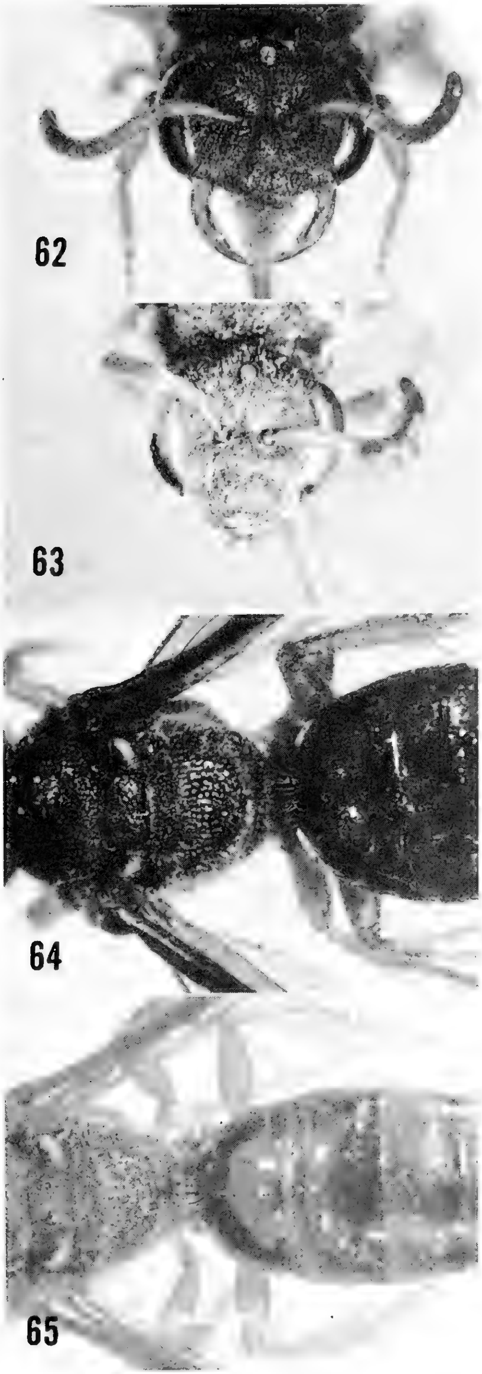
Compared to *Sphecodes,* the body form is rather elongate, about the same in the two sexes, with the antennae of the male short as in females. In species such as *E. bequaerti* (Meyer), the pitting of the mesoscutum, mesepisterna, and to a lesser degree the rest of the thorax is quite coarse, suggestive of *Sphecodes.* Also, the first metasomal tergum is not as elongate as in most species (length to breadth about as 9:10) and the part of the marginal cell subtended by submarginals extends well beyond the stigma. In these respects as well as coloration *E. bequaerti* resembles *Sphecodes.* Unfortunately, I have not seen males of this species, but it is a reasonable assumption that such *Sphecodes*-like forms were ancestral to the species typical of *Eupetersia.*

The existence in Africa of *Sphecodes*

species (unidentified, Karen, Nairobi, Kenya, Univ. of Kansas) with simple mandibles in the female, a strong preoccipital carina, and a narrow pygidial plate, nearly bridges the gap between *Sphecodes* and *Eupetersia* and supports the suggestion of Benoist (1962, p. 124) that *Eupetersia* is not generically distinct from *Sphecodes*. I have concluded, however, that *Eupetersia*, although an offshoot of *Sphecodes*, is different enough to receive generic status. The distinctive combination of characters is italicized in the above description, but it must be noted that few of these characters, by themselves, are diagnostic.

Most *Eupetersia* are distinguished from *Sphecodes* by the fine thoracic punctation, either rather dense or sparse, as well as the body form. The coloration is commonly unlike that typical of *Sphecodes*, ranging from entirely black or dark metallic blue [*E. coerulea* Blüthgen and allies, placed in *Calleupetersia* by Cockerell (1938) only because of the blue color] to specimens with the thorax red and the rest of the body black (some specimens of *E. paradoxa* Blüthgen) to the entirely reddish yellow *E. flava* described below.

Slender legs are diagnostic for females. The slender, parallel-sided pygidial plate occurs in some otherwise ordinary *Sphecodes*, such as *S. crassus* Thompson, *gibbus* (Linnaeus), *heraclei* Robertson, etc. The antennae of known males do not resemble those of any *Sphecodes* known to me. The flagellum is relatively short, not thickened as in *Sphecodes*, the middle segments slightly broader than long to longer than broad. The first two segments are both much broader than long. In *Sphecodes*, even species with relatively short male antennae, such as *S. cressonii* Robertson, *atlantis* Mitchell, and *costaricensis* Friese, the flagellum is longer and thicker than in the female and although the first segment is much broader than long, the second is nearly as long as broad or longer than



Figs. 62-65. *Eupetersia guillarmodi* Michener. Figs. 62, 63. Faces of holotype female and allotype male. Figs. 64, 65. Dorsal views of median parts of body, holotype female and allotype male.

broad. Unfortunately males of the most *Sphecodes*-like *Eupetersia,* such as *E. bequaerti,* are not known to me. For the same reason the genitalic characters listed above cannot with certainty be considered diagnostic of all species.

SUBGENUS EUPETERSIA BLÜTHGEN S. STR.

Eupetersia Blüthgen, 1928, Deutsche Ent. Zeitschr., 1928:p. 49. Type species: *Eupetersia neavei* Blüthgen, 1928, by original designation.

Calleupetersia Cockerell, 1938, Rev. Zool. Bot. Africaines, 30:329. Type species: *Halictus lasureus* Friese, 1910, by original designation.

Scutum more or less densely punctate. Scutellum with surface bigibbous, the two convexities not or sparsely punctate, punctures denser around them and on midline separating them. Recurrent veins both entering third submarginal cell or the first interstitial. Depressed area of male gonocoxite preapical.

This subgenus is limited to Africa and Madagascar. *Calleupetersia* is distinctive only in its metallic blue integumental coloration and does not warrant subgeneric status.

SUBGENUS NESOEUPETERSIA BLÜTHGEN

Nesoeupeterisa Blüthgen, 1935, Deutsche Ent. Zeitschr, 1935:182. Type species: *Sphecodes scotti* Cockerell, 1912, by original designation.

Scutal punctures scattered. Scutellum gently convex, not bigibbous, with scattered punctation similar to that of scutum. Second and third submarginal cells each receiving a recurrent vein, or the first vein interstitial. Depressed area of male gonocoxite extending much of length of gonocoxite, without carinae across it (examined only in *P. sakalava* Blüthgen).

This subgenus is known from Madagascar, the Seychelles, and south India, with a possibly incorrectly placed species from Zaire (see Baker, 1974).

GENUS SPHECODES LATREILLE

(Figs. 13, 14, 20-22, 27, 67-72)

Both sexes: Punctation of head and thorax usually coarse, but punctures, especially of mesoscutum, sometimes widely separated by shining ground. Head much wider than long (or scarcely so in *S. convergens* Michener), clypeus about two to usually more than three times as wide as long, often biconvex due to longitudinal median depression which is often reduced to a closely punctate zone or absent. Eyes usually nearly hairless, but with variably long hair in *S. biroi* Friese and in an unidentified Argentine species, and with scattered short hairs in various other species. Hairs of antennal flagellum all or nearly-all very short. Preoccipital carina usually absent in the holarctic region (occasionally present as in *S. scabricollis* Wesmael), but distinct in some groups from South America, south Asia to Australia, and Africa.

Pronotum with horizontal surface of collar almost absent medially, but forming lateral angles which are usually prominent (weak and rounded in *brachycephalus* Mitchell and some small Neotropical species) and below which a vertical ridge extends downward (ridge weak in forms with weak lateral angles and in *S. convergens* Michener, *persimilis* Lovell and Cockerell, etc.), vertical ridge approaching or merging with a more laterally directed ridge that extends toward coxal base, or laterally directed ridge weak or absent in many species; a carina from lateral angle across posterior lobe of pronotum. Anterior extremity of scutum strongly convex, vertical anterior surface nearly always with area that lacks punctures (or has them smaller and sparser than in adjacent areas

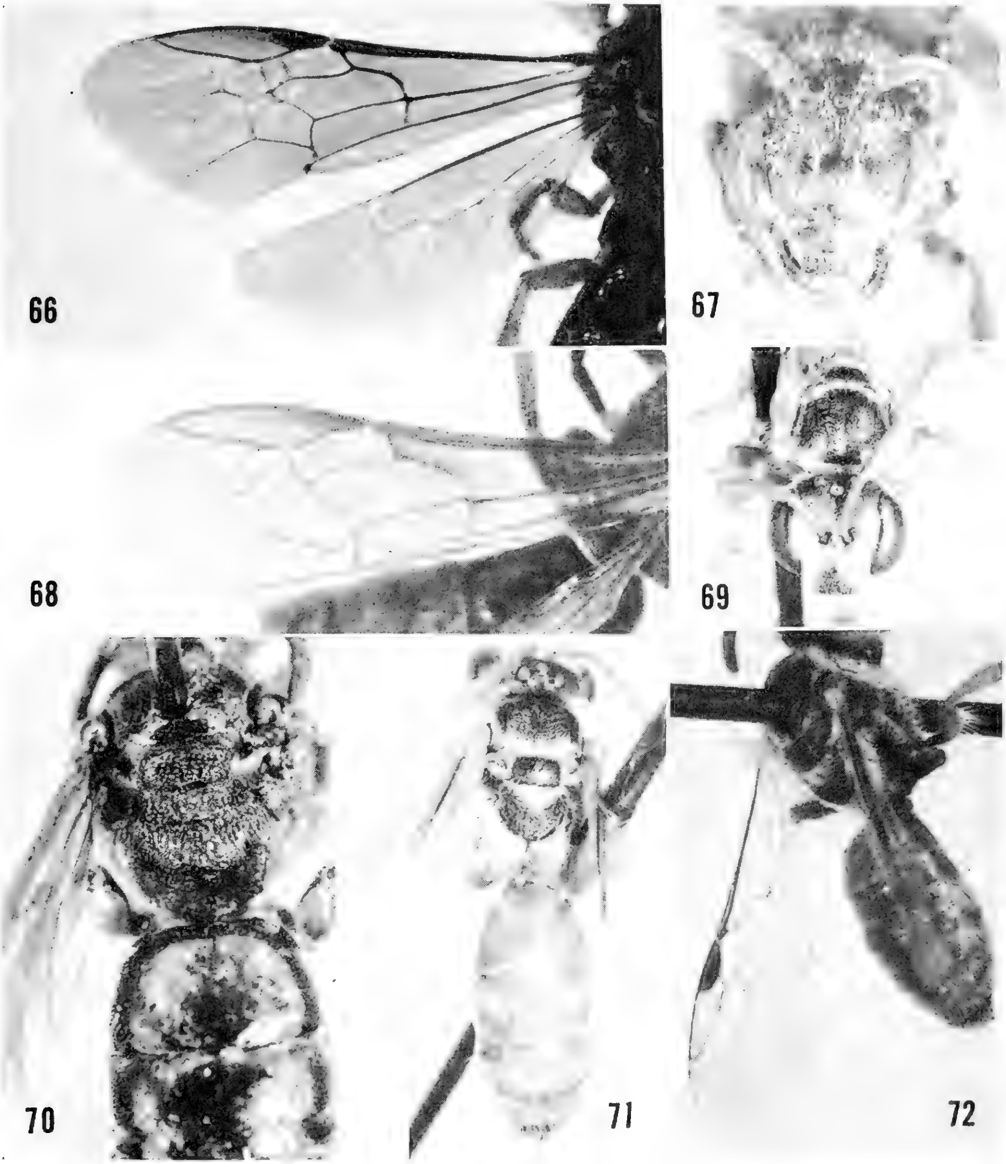


Fig. 66. *Eupetersia guillarmodi* Michener, wings of paratype female. Figs. 67, 68. *Sphecodes manskii* (Rayment), face and forewing of holotype female. Fig. 69. *Sphecodes convergens* Michener, face of holotype female. Fig. 70. *Sphecodes manskii,* dorsum of median part of body of holotype female. Figs. 71, 72. *Sphecodes convergens.*

in *S. convergens* Michener) and is therefore sharply different from rest of scutum. Scutellum gently convex or sometimes weakly biconvex due to feeble longitudinal median depression. Propodeum with dorsal area coarsely rugose, usually strongly areolate, usually about as long as scutellum, shorter than scutellum in a few species [e.g., *S. spinulosus* Hagens, *albilabris* (Kirby), and *ruficbelis* Strand], area broadly rounded posteriorly; posterior and lateral surfaces of propodeum usually without or with few short plumose hairs in addition to longer hairs, but such hairs sometimes rather conspicuous (e.g., in *S. heraclei* Robertson, *prosphorus* Lovell and Cockerell, *pulsatillae* Cockerell, *pecosensis* Cockerell, *rubicundus* Hagens, and in the subgenus *Austrosphecodes*).

Wings with hairs short and dense apically, somewhat longer and less dense toward bases [hairs rather long and dense throughout in *S. manskii* (Rayment)]; stigma of moderate size; marginal cell pointed to narrowly truncate at apex; free part of marginal cell beyond submarginal cells as long as to twice as long as part subtended by submarginal cells, which extend well beyond apex of stigma. Second and third submarginal cells each receiving a recurrent vein, or as occasional variants first recurrent and second transverse cubital interstitial, or in some species first transverse cubital absent so that there are only two submarginal cells.

First tergum usually broader than long, in various Neotropical *Austrosphecodes* species as wide as long or even longer than wide. In lateral view base of second tergum sometimes depressed so that there is a weak constriction between first and second terga. Posterior margins of terga 2-4 broadly depressed, hairless, commonly impunctate.

Female: Mandible with or without subapical tooth. Labrum with broad, flat apical process which is rounded, truncate, or bilobed and usually about twice as broad as long, but varies to nearly as long as broad [e.g., in *S. monilicornis* (Kirby)].

Legs commonly robust, hind femur little over twice as long as wide (*S. monilicornis* Kirby) to three or more times as long as wide, nearly always strongly convex on upper surface near base except in some *Austrosphecodes;* basitibial plate absent to demarked along posterior margin and at apex; long hairs on outer side of hind tibia plumose, barbed, or (rarely) mostly simple (*e.g.,* in *S. monilicornis* (Kirby), *profugus* Cockerell); upper margin of hind tibia with or without spine-like setae; hind tibial spine variable.

Fifth tergum, unlike preceding terga, with apical margin fringed except in *S. brachycephalus* Mitchell, often with dense prepygidial fimbria in front of apical fringe, fringe sometimes interrupted medially. Pygidial plate typically broader than in *Eupetersia,* but slender in various species [e.g., *S. gibbus* (Linnaeus), *pulsatillae* Cockerell].

Male: Antennae long to as short as in female, flagellum often thickened, first flagellar segment broader than long, second variable, but usually longer than first, the first and second never both very short as in *Eupetersia.* Labrum with apical process shorter than in female, usually several times as wide as long, but rarely (e.g., *S. chilensis* Spinola) little over twice as broad as long.

Second hind tarsal segment shorter than to longer than third, base broader than or equal to base of third.

Gonocoxite usually striate, sometimes with dorsal basal depression, but without dorsolateral margined depression as in *Eupetersia.* Gonostylus variable, commonly with basal setose lobe.

This genus consists of hundreds of species and is found on all continents, although it is nearly absent in Australia, being represented there by only two species found in the northern part of the continent. Major papers on the taxonomy of Old World species of the genus are by Blüthgen (1923b, 1924, 1927, 1928); comprehensive taxonomic treatment of New World species is limited to those of eastern North America by Mitchell (1960). Meyer (1919) listed and gave copies of descriptions of the species of all geographical regions.

The genus is quite variable and doubtless, with adequate study, could be divided into various subgenera. For the present, however, only two major groups are accorded subgeneric rank, the Neotropical *Austrosphecodes* and the rest of the genus, *Sphecodes* proper.

The mandible of the female usually has a subapical inner tooth. Sometimes it is reduced to a small tooth close to the main axis of the mandible (*e.g.,* in *S. brachycephalus* Mitchell, *costaricensis* Friese *sensu* Michener, 1954, and *pycnanthemi* Robertson). In various species the subapical tooth is absent so that the mandible is simple and sharply pointed. Such mandibles characterize *Austrosphecodes,* as well as species such as *S. antennariae* Robertson, *confertus* Say and *stygius* Robertson. The related genera *Eupetersia, Ptilocleptis,* and *Microsphecodes* also have simple mandibles. It seems likely that this feature has arisen independently in different species groups.

Male antennae are usually quite elongate, with most flagellar segments, including the second, much longer than broad, and with the first, by contrast, much shorter and broader than long. In various species, however [*e.g.,* most *Austrosphecodes* and *antennariae* Robertson, *atlantis* Mitchell, *costaricensis* Friese, *cressonii* Robertson, *illinoensis* (Robertson)], the first and second segments are not very different in length, each a little broader than long. The second antennal type is most common in small species. All intergrades between the two types exist (*e.g.,* in *heraclei* Robertson, *confertus* Say, and *chilensis* Spinola).

The legs of females are usually robust, the upper surface of the hind femur strongly convex basally, near the trochanter. To a variable extent this is not so in *Austrosphecodes* and in a few other species (*S. brachycephalus* Mitchell). The hind tibia of the female typically has some spinelike or even peglike setae, shorter than the nearby hairs, along the outer margin. At the apex, on the outer surface of the tibia, there is a strong tibial spine. These features are reduced in some, but not all, small species. In some small species like *S. brachycephalus* Mitchell, the spinelike setae are few in number and pale, hence difficult to see. The tibial spine is sometimes only a rounded prominence [*e.g.,* in *S. illinoensis* (Robertson)]. In *Austrosphecodes* the spinelike setae are absent or are as long as nearby hairs and sometimes with barbs or branches. The same is true of the very large *S. ruftchelis* Strand. The spinelike setae are usually absent in males, but are present in some species [e.g., *S. ruficrus* (Erichson), *spinulosus* Hagens].

The preoccipital carina is usually absent, the posterior surface of the head being rounded peripheral to its central concavity, but such a carina is present and very strong in *S. manskii* (Rayment), distinct in *S. chilensis* Spinola and some other *Austrosphecodes* as well as in *profugus* Cockerell, *scabricollis* Wesmael, and an unidentified African species (see discussion under *Eupetersia*).

The male gonocoxites are typically longitudinally striate over most of the upper and outer surfaces. Such striae are absent or weak and limited to certain areas in *Austrosphecodes.*

Subgenus SPHECODES
Latreille s. str.

Sphecodes Latreille, 1804, Nouvelle dictionnaire d'histoire naturelle [Deterville], Paris, Tableaux méthodiques, 24:182. Type species: *Sphex gibba* Linnaeus, 1758, monobasic.

Dichroa Illiger, 1806, Mag. Insektenk., 5:39. Type species: *Sphex gibba* Linnaeus, 1758, designation of Sandhouse, 1943, Proc. U. S. Nat. Mus., 92:545.

Sabulicola Verhoeff, 1890, Ent. Nachr., 16: 328. Type species: *Sabulicola cirsii* Verhoeff, 1890, = *Andrena albilabris* Kirby, 1802, monobasic.

Drepanium Robertson, 1903, Ent. News, 14: 103. Type species: *Sphecodes falcifer*

Patton, 1880, = *S. confertus* Say, 1837, monobasic.

Proteraner Robertson, 1903, Ent. News, 14: 103. Type species: *Sphecodes ranunculi* Robertson, 1897, monobasic.

Sphecodium Robertson, 1903, Ent. News, 14: 103. Type species: *Sphecodium cressonii* Robertson, 1903, by original designation.

Machaeris Robertson, 1903, Ent. News, 14: 104. Type species: *Sphecodes stygius* Robertson, 1893, by original designation.

Dialonia Robertson, 1903, Ent. News, 14: 104. Type species: *Sphecodes antennariae* Robertson, 1891, monobasic and original designation.

Callosphecodes Friese, 1909, Ann. Mus. Nat. Hungarici, 7:182. Type species: *Sphecodes (Callosphecodes) ralunensis* Friese, 1909, monobasic.

Mandible of female usually with subapical tooth. Labral process of male much shorter than in female, three or more times as wide as long. Preoccipital carina usually absent. *Legs almost always robust,* hind femur two to three times as long as broad, strongly convex on upper surface near base. *Hind tibia of female almost always with spinelike setae on outer margin; basitibial plate of female defined along posterior margin and sometimes also at apex.* Second hind tarsal segment of male shorter than or equal to, rarely longer than, third, *its base broader than base of third,* so that articulation to first is broader than articulation of third to second. Posterior surface of propodeum usually without short plumose hairs among long erect hairs. First metasomal tergum considerably broader than long. Male gonocoxites striate on most of outer and dorsal surfaces.

This subgenus is not known in South America, but is found on all other continents. As indicated by the discussion and descriptions above, it is quite diverse and may well be subdivided.

The status of the name *Callosphecodes* remains in doubt. It was described by Friese from a large, robust specimen with a metallic blue-black metasoma from New Britain in the Bismarck Archipelago. Unfortunately, Dr. Jeno Papp of the Hungarian Natural History Museum reports that the type (and only specimen) cannot be found. The blue color suggests some species of *Eupetersia* but it is not likely that *Callosphecodes* is a senior synonym of that name. The locality is far to the east of the known range of *Eupetersia,* and metallic species of that genus are known only in Africa. Moreover, the robust form (Friese says 3 mm wide, 9-9.5 mm long) does not suggest *Eupetersia.*

It seems likely that *Sphecodes (Callosphecodes) ralunensis* Friese is related to *S. manskii* (Rayment) from northern Australia, as suggested by Michener (1965). Rayment described this form as having a metallic purplish green abdomen, although the type entirely lacks such coloration at present, the metasoma being shining black. *S. manskii* is a very unusual *Sphecodes,* and if it is similar to *S. ralunensis,* the subgeneric name *Callosphecodes* may be used to unite the two species. Interesting features of *S. manskii* (Figs. 67, 68) include the unusually large subapical mandibular tooth of the female, the very strong preoccipital carina, the tooth at the posterior end of the hypostomal carina, and the unusually well defined, shining, slightly elevated basitibial plate of the female. The hind femur of the female is more slender (3 times as long as wide) and less convex on the dorsal surface near the base than usual for *Sphecodes s. str.,* especially for a large species with conspicuous spinelike setae on the outer margin of the hind tibia and a large, long tibial spine. The fifth tergum has a less dense prepygidial fimbria than most large species, the apical fringe being absent in the middle part of the margin, and a smooth shining hairless area being in front of this fringeless area. A unique feature of *S. manskii* among *Sphecodes* that I have seen is the vestiture of the wings, the hairs being long and dense as in *Eupetersia.* Unfortunately the species is known from only a single female specimen.

AUSTROSPHECODES New Subgenus

Type species: *Sphecodes chilensis* Spinola, 1851.

This subgenus includes the rather numerous South American species of the genus. I have studied unidentified specimens of many species, and identified specimens of *S. mutillaeformis* Schrottky, specimens of *S. chilensis* compared with Spinola's type by H. Toro, and of course *S. convergens* described below.

Mandible of female simple. Labral process of male two to three or more times as broad as long. Preoccipital carina often present. *Legs relatively slender,* hind femur not strongly convex on upper surface near base. Tegula usually larger than in *Sphecodes s. str. Hind tibia of female without spinelike setae on outer margin* or if present they are as long as the nearby hairs; *basitibial plate of female entirely absent.* Second hind tarsal segment of male as long as or longer than third, *narrowed at base like third* so that its articulation to first is similar to that of third to second. Posterior surface of propodeum with short plumose hairs among long erect hairs. First metasomal tergum variable but often as long as broad or longer than broad. Male gonocoxites without striae or striae fine, inconspicuous, and occurring only in limited areas.

In various features *Austrosphecodes* resembles *Eupetersia.* Both have simple mandibles and rather slender legs; some species of *Austrosphecodes* have the slender body and even a somewhat female-like body form in the male, suggestive of *Eupetersia;* some also have a preoccipital carina. *Austrosphecodes* also has short pale plumose hairs on the vertical surfaces of the propodeum, as does *Eupetersia. Austrosphecodes,* however, looks much more like *Sphecodes* than does *Eupetersia,* resembling *Sphecodes* in wing vestiture and venation, in basal flagellar segments of the male, and in lacking the margined depressed area of the male gonocoxite found in *Eupetersia.*

Presumably the similarities of *Austrosphecodes* and *Eupetersia* are convergences since the latter probably arose from African *Sphecodes* and not from South American forms.

The subgeneric name, meaning southern *Sphecodes,* refers to the South American range of the group.

APPENDIX

Descriptions of new species needed for inclusion in the preceding account, together with other taxonomic conclusions at the specific level, are presented here.

Moreover, a revision of the new genus *Ptilocleptis* is included.

Parathrincostoma seyrigi Blüthgen

Parathrincostoma seyrigi Blüthgen, 1933, Mitt. Zool. Mus. Berlin, 18:390, male.

New localities are as follows: Madagascar: District de Fanovana, Region orientale de forets humides, September-October, 1938 (C. Lamberton); east Madagascar, forest 600-1200 m, December-February, 1930-31 (C. Lamberton); Manombo s.l., Tulear Province, March 31, 1968 (K.M.G. and P.D.). The Lamberton material is in the American Museum of Natural History, New York; the other specimen is in the British Museum (Natural History).

The female (one specimen from "east Madagascar") has a strongly produced clypeus, almost as in the male; the anterolateral angles of the pronotum are produced to acute, almost spinelike angles; the punctation is relatively sparse, punctures of the frons below the ocelli being separated by much more than puncture widths; and metasomal segments 4-6 are brown, the rest of the body brownish black and the legs more noticeably reddish.

Parathrincostoma elongatum Benoist

Parathrincostoma elongatum Benoist, 1962, Verhandl. Naturf. Ges. Basel, 73:131.

This species, known only from the type female, has a less produced clypeus than *P. seyrigi;* the anterolateral angles of the pronotum are obtuse; the punctation is denser, punctures of the frons below the ocelli being separated by less than a puncture width, and metasomal segments 5 and 6 are brown, the rest of the body and legs being black.

Nomia ambrensis (Benoist) new combination

Parathrincostoma ambrense Benoist, 1962, Verhandl. Naturf. Ges. Basel, 73:130.

As indicated above, the remaining specific name proposed in *Parathrincostoma* is based on a specimen of *Nomia* in the broad sense. It is a slender black bee, with wings dark except for the clear bases, and thus is superficially extraordinarily similar to *Parathrincostoma.* However the lack of a preepisternal groove, the short pronotum without a transverse carina or lamella, the pale femoral scopa, the elongate third submarginal cell, and the short face clearly show the incorrect placement.

GENUS PTILOCLEPTIS

This genus, described above, is known from only seven specimens taken in the American tropics from Mexico to southern Brazil. Three species are easily recognizable, separated by the following key.

KEY TO THE SPECIES OF *PTILOCLEPTIS*

1. Terga 2-6 with extensive areas of dense, yellow brown, plumose hair; scutellum of male with an impunctate area on each side, but not strongly bigibbous .... *tomentosa*

.... Terga 2-6 with hairs mostly simple, not obscuring surface; scutellum of male strongly bigibbous, an elevation on either side of midline being impunctate at summit 2

2. Scutum with many plumose hairs although surface not entirely obscured; scutellum and metanotum yellow (female) .... *polybioides*

.... Scutal hairs mostly simple and surface not at all obscured; scutellum and metanotum black (male) .. *eickworti*

Ptilocleptis tomentosa new species (Figs. 11, 17, 28, 39-43, 47-50, 53, 54)

This middle American species is markedly larger than the other members of the genus, from which it also differs by having conspicuously hairy eyes and areas of dense, plumose, brown hair on the metasoma.

Female: Length 10 mm; forewing length 8 mm (7 mm in paratype). Black; the following parts red-brown: labrum, mandible, lower two-thirds of clypeus (entire clypeus in paratype), scape, pedicel, underside of flagellum (almost whole of two basal segments, red-brown coloration more restricted in area and darker in color toward apex), posterior pronotal lobe, tegula, axillary sclerites, tibiae (mid and hind with infuscated postmedian band in paratype), tarsi, apices of femora, apical half of sixth metasomal segment (the last blackish in paratype). Metasomal segments 2-5 with apical translucent brown bands, narrow on terga 2-3, progressively broader on 4-5. Wings light yellowish-brown, costal area of forewing from stigma to apex of wing (including entire marginal cell) dark brown; veins and stigma brown.

Pubescence yellow-brown to yellow-testaceous, on sixth metasomal segment dusky except laterally, that on venter of thorax and in paratype also on side of thorax and posterior surface of propodeum whitish. Hairs of head rather short, yellow-testaceous, plumose ones hiding most of paraocular area, frons, vertex, and genal area. Thorax with hairs rather short and simple, some long hairs on scutellum and metanotum, surface easily visible except for the following areas which have dense coverings of short, plumose, yellow-testaceous hairs obscuring the surface: dorsum of pronotal collar, margin of pronotal lobe and corresponding mesepisternal depression, pre-episternal groove (not entirely covered), line along mesepisternal-metaplural suture, rest of metapleuron (not entirely covered), line along scuto-scutellar suture, posterior margin of scutellum, disc of metanotum, posterior and posterolateral surfaces of propodeum. Metasoma with scattered, moderately long, erect, simple hairs, very sparse on disc of first tergum, longer and slanting posteriorly on apical terga dorsally, on all terga laterally, and on all sterna; second to fifth terga also with short hairs which are plumose, dense and form broad, yellow-testaceous basal band across tergum 2, basal half of tergum 3 similar, otherwise plumose hairs less dense and light brown; short, simple hairs on mid-dorsal convex part of tergum 2 and across posterior parts of terga 2-4; hairs on both terga and sterna extending almost to posterior margins, on terga 2-4 short hairs, more erect and laterally directed than the rest, forming weak, narrow, subapical, yellow-testaceous bands. Fifth tergum with hairs somewhat longer than on preceding terga, some arising almost to apex of tergum, but no recognizable subapical band and no dense prepygidial fimbria. Eye with rather abundant hairs about one-fourth as long as diameter of scape.

Head narrower than thorax, somewhat wider than long (100:88), upper and lower interorbital distances as 59:45, shorter than eye length (65). Clypeus convex, longer than clypeoantennal distance (27:20). Antennocular:interantennal:antennocellar:interocellar:ocellocular distances as 15:14.5:25:13.5:15. Labrum with broad, transverse, basal, elevated area covered with short hairs, apical process as long as basal area, about four times as wide as long, rounded at apex, margined with narrow band of slender hairs. Supraclypeal area gently elevated up to frontal tubercle, above which it is gently declivous to frons. Scape, pedicel, and upper surface of flagellum near base with rather conspicuous hairs, under surface of flagellum with only very short hairs; flagellum with first two segments broader than long, third longer than broad, middle segments slightly longer than broad. Dorsal area of propodeum slightly shorter than metanotum. Hamuli 8-10. First metasomal segment about as long as broad.

Head closely punctate, ground between punctures minutely roughened, anterior part of clypeus most coarsely punctate, rest of clypeus and lower supraclypeal area more coarsely so than frons and vertex, which are rather finely punctate except for area of coarser, sparser punctures above antennal base; genal area finely and rather sparsely punctate, lower genal area near foramen magnum striate. Mesoscutum closely punctate, punctures similar in size to largest clypeal punctures, anterior part rugose, punctate. Scutellum much more finely punctate than scutum, with some shining ground between punctures; metanotum closely and rather finely punctate; mesepisternum above scrobe somewhat more finely punctate than scutum, elsewhere coarsely reticulopunctate, strigose below; pre-episternal groove a series of pits separated by carinae; mesepisternal-metapleural suture marked by similar series of smaller pits; upper convexity of metapleuron with about four horizontal striae, rest of metapleuron with fine punctures and less conspicuous transverse striae, especially above. Basal area of propodeum with irregular, longitudinal carinae, seven or eight on each side, connected by a carina posteriorly and separating pits which middorsally are twice as long as wide, or more; posterior surface and posterior part of lateral surface of propodeum irregularly coarsely areolate. First metasomal tergum shining with only scattered minute punctures. Remaining terga with numerous small punctures, mostly separated by a puncture width or less, extending onto the slightly depressed brownish margins of terga 2-5, but punctures on these margins smaller and sparser than elsewhere; ground between punctures shining, but minutely lineolate, especially on more posterior terga; sterna shining, coarsely and sparsely punctate, apical margins of more anterior sterna broadly impunctate, surface between punctures minutely lineolate, progressively more strongly so on more posterior sterna.

Male: Similar to description of female, differing as follows: Forewing length 7 mm. Black, the following parts red-brown: scape, first flagellar segment, anterior tibia (darker brown along outer surface). Other parts described as red-brown in female are dark brown. Metasomal terga 1-2 without translucent margins, 3 with a rather narrow translucent brown margin, 4-6 with such margins broad.

Hairs of head as well as sides of thorax largely whitish, sparser than in female, partially obscuring surface only on paraocular area, scutoscutellar line and center of metanotum, fully hiding surface under dense plumose yellowish hair only on dorsum of pronotal collar. Basal band of plumose, yellowish hairs across tergum 2 supplemented by weaker preapical band, strongest dorsolaterally; similar, yellowish, plumose hairs occupying most of dorsum, anterior to translucent margins, of terga 3-6. Hair of eyes very short.

Structure, including facial proportions, about as in female. Second flagellar segment as long as broad, succeeding segments all longer than broad. Scutellum as in female.

Genal area somewhat more sparsely, but no more finely punctate than vertex. Upper part of metapleura with only two or three horizontal striae, rest of metapleuron areolate. First metasomal tergum shining with sparse large punctures and sparse smaller punctures intermixed.

Holotype female: 2 miles west of Palmares, Alajuela Province, Costa Rica, January 23, 1965 (D. H. Janzen), in the Snow Entomological Museum, University of Kansas. Allotype male: "Mex.," in the Academy of Natural Sciences of Philadelphia. Paratype female: Hacienda Capolinas, 5 km N.W. of Quezaltepeque, El Salvador, 450 m altitude, Dec. 26, 1964 (M. E. Irwin), in collection of the University of California at Riverside.

Ptilocleptis polybioides new species
(Figs. 25, 51, 52)

This Peruvian species differs from the other members of the genus in the yellow pronotum, scutellum, metanotum, and much of the first metasomal tergum, a pattern which enhances its wasplike aspect.

Female: Length 7 mm; forewing length 6 mm. Black, the following parts yellow (reddish-yellow in paratype): labrum, mandible (apex red-brown), clypeus, scape, pedicel, first two flagellar segments (reddish-yellow) (second dark brown in paratype), prothorax (lamella across front of collar dark), tegula (translucent), axillary sclerites, scutellum (reddish), metanotum, legs, basal two-thirds of first metasomal tergum, first sternum, and base of second sternum. Lower anterior part of mesepisternum with diffuse, yellow brown area (absent in paratype, which has sides of thorax dark brown). Metasomal terga and sterna with narrow, apical, dark, brownish bands; fifth and sixth segments more extensively brownish. Wings light yellowish brown, costal area of forewing from about level of vein cu-v to apex of marginal cell (including marginal cell except for narrow strip along its posterior border, or entire marginal cell in paratype) dark brown; stigma and veins proximal to it including basal vein dark brown, other veins yellow brown.

Pubescence yellowish-white (that of head and thorax more golden in paratype), that of posterior half of metasoma more brownish-white and of sixth segment dusky. Hair pattern of head and thorax as described for *P. tomentosa,* but scutum with abundant, plumose hair partly obscuring surface, plumose hairs (white) otherwise perhaps less dense and obscuring surface less than in *P. tomentosa,* conspicuously less abundant on scutellum. Hair pattern of metasoma as described for *P. tomentosa,* but short hairs are longer, and none are plumose. Eye with scattered, very short hairs.

Head about as wide as thorax, somewhat wider than long (75:63), upper and lower interorbital distances as 45:34.5, shorter than eye length (48.5). Clypeus convex, longer than clypeoantennal distance (18:12). Antennocular:interantennal: antennocellar:interocellar:ocellocular distances as 11:12:22.5:10.5:12. Labrum with broad, transverse, basal, elevated area covered with short hairs; apical process about twice as wide as long. Supraclypeal area and antennal pubescence as described for *P. tomentosa;* flagellum with first segment broader than long, second as long as broad or appearing longer than broad in paratype, the remainder all distinctly longer than broad. Scutellum biconvex, summits of convexities impunctate. Dorsal area of propodeum longer than metanotum. Hamuli 8. First metasomal tergum about as long as broad.

Punctation similar to that of *P. tomentosa,* differing from description of that species as follows: ground between punctures of clypeus and supraclypeal area smooth and shining, these areas similarly punctate; striae of lower genal area weak. Anterior part of mesoscutum punctate, but scarcely rugose; mesepisternum above scrobe as coarsely punctate as adjacent areas. Basal area of propodeum with more-regular longitudinal carinae, pits between median ones about three times as long as wide. Impunctate tergal margins broader. Sterna less coarsely punctate, less lineolate.

Holotype female: Tingo Maria, Peru, 620 m altitude, October 5-12, 1964 (H. C. Porter), in the Museum of Comparative Zoology, Harvard University. Paratype female: Monzon Valley, Tingo Maria, Peru, November 2, 1954 (E. I. Schlinger, E. S. Ross), in the California Academy of Sciences.

The specific name is based on the wasp genus *Polybia,* because of the bee's resemblance in general form and coloration to such polybiine wasps.

Unlike other known specimens of the genus, the paratype of *P. polybioides* has only two submarginal cells through loss of the second transverse cubital vein.

Ptilocleptis eickworti new species
(Figs. 44-46)

This species from southern Brazil is the smallest of the genus and also the darkest, having neither the rather extensive yellow markings of *P. polybioides,* nor the large areas of yellowish plumose hairs of *P. tomentosa.*

Male: Length 6 mm; forewing length 5 mm. Black, the following parts red-brown: scape, pedicel, first flagellar segment, tibiae, tarsi, and parts of femora; the following dark brown, sometimes blackish: labrum, mandible, clypeus, pronotal lobes and diffuse area on side of pronotum, tegula, axillary sclerites, coxae, trochanters, much of femora, and much of first tergum. Extreme base of first tergum yellow, this color continued middorsally to behind middle of tergum. Wings light brownish, marginal cell of forewing dark brown, dark color extending less intensely beyond apex of marginal cell as well as basal to stigma; veins and stigma brown.

Pubescence yellowish white, yellow on legs, brownish on metasoma, longer hairs of posterior segments dusky. Plumose hairs (white) less dense than in other species, not covering surface, most conspicuous on face and pronotal collar, present also on sides of thorax and sides and posterior surface of propodeum and surface clearly visible in these areas; plumose hairs largely absent on scutum so that surface is clearly visible. Hairs of metasoma and eyes as in *P. polybioides.*

Head about as wide as thorax, wider than long (64:57), upper and lower interorbital distances as 40:28, shorter than eye length (42). Clypeus convex, longer than clypeoantennal distance (15:11). Antenocular:interantennal:antennocellar:interocellar:ocellocular distances as 8:11:21:10:10.5. Labrum with broad, transverse, basal, elevated area with short hairs; apical process over twice as broad as long. Supraclypeal area and antennal pubescence as described for *P. tomentosa;* flagellar segments as described for *P. polybioides.* Scutellum bigibbous, with a strong elevation, impunctate at summit, on each side of midline. Dorsal area of propodeum longer than metanotum. Hamuli 7. First metasomal tergum distinctly longer than broad.

Punctation as described for *P. polybioides.*

Holotype male: Nova Teutonia, Santa Catarina, Brazil, March 24, 1966 (Fritz Plaumann) in the Museum of Comparative Zoology, Harvard University. Paratype male, same locality and collector (27° 11′ S, 52° 23′ W), no date, in the same collection.

This species is named for Dr. George C. Eickwort, who assembled most of the known specimens of *Ptilocleptis* and kindly permitted me to study them.

Eupetersia (*Eupetersia*) *guillarmodi*
new species
(Figs. 60-66)

This species differs from other species of the genus by the black body and red scape and legs; other species have the body partly red, yellow, or blue. The species is larger than other species except *E. neavei* Blüthgen, from which it differs in the black metasoma, the broad pygidial plate of the female, the largely black pubescence, and other characters.

Female: Length 10 mm (9.5 mm in one paratype); forewing length 8 mm. Black, the following parts red brown: labrum, mandible (except blackish apex which grades into the red basally), scape, pedicel, first two flagellar segments, legs including apices of coxae (but greater part of coxae black). Posterior lobe of pronotum, tegula, and axillary sclerites of wings slightly darker red-brown; third and following flagellar segments dark-brown. Wings fuliginous, veins and stigma dark brown.

Longer hairs black, those of labrum, mandible and lower clypeal margin reddish black, apical fringe of fifth tergum reddish. Anterior surface of front tibia and posterior surfaces of mid and hind tibiae with hair pale-red. Hairs of undersides of tarsi red. Short, white hair present among longer black hairs on much of head and thorax; most of hair of frons and metapleuron pale; short, pale hairs conspicuous among longer black hairs on pronotal collar, around hind wing base and on lateral and posterior faces of propodeum. Dense fringe on posterior pronotal lobe and dense hairs in corresponding depression of mesepisternum white.

Head as wide as thorax, much wider than long, upper and lower interorbital distances subequal (71:70.5), greater than eye length (60.5). Clypeus scarcely biconvex, higher than clypeoantennal distance (19.5:15). Antennocular:interantennal:antennocellar : interocellar : ocellocular distances as 22:12.5:27:16:20. Labrum with sharp, transverse, basal ridge with only a few short hairs on distal surface; process beyond ridge about twice as broad as long, rounded, margined with strong hairs, two or three irregularly placed preapical hairs. Supraclypeal area strongly elevated to frontal tubercle, then abruptly declivous upward between antennal bases. Flagellum with first two segments much broader than long, third longer than broad, middle segments slightly broader than long. Preoccipital carina continuous, but weak dorsally. Pronotal collar broader medially than in other species, anterolateral angles sharp although somewhat obtuse, a strong, high carina extending across pronotal lobe. Scutum with longitudinal median depression extending from anterior almost to posterior margin. Scutellum distinctly biconvex. Legs rather slender; basitibial plate with posterior margin indicated by distinct smooth line which curves anteriorly at apex and indicates end of plate; hairs along upper margin of hind tibia with branches along convex surfaces, spinelike setae absent, but there are some simple bristles especially near base and apex; hairs of outer surface of hind tibia appearing simple in lateral view, but with a few short branches on convex sides visible from above. Apex of marginal cell narrowly subtruncate with appendage. Hamuli seven. Pygidial plate rather broad, but lateral margins converging somewhat anteriorly so that plate is nearly round.

Head dull, coarsely and closely punctate, transversely rugose-punctate on vertex between ocelli and preoccipital carina, punctures finer and arranged to suggest weak striae on genal area; hypostomal area shining, with widely scattered, coarse punctures, surface between them minutely shallowly punctulate. Scutum and metanotum dull, closely punctate, more coarsely so than head, transversely rugose anteriorly on scutum. Scutellum more finely, closely punctate except for the two large, shining, convexities with scattered punctures. Mesepisternum coarsely rugose-punctate, becoming more coarsely reticulate below and ventrally; preepisternal groove consisting of a series of pits separated by carinae, a similar series of pits along anterior margin of metapleuron; upper convexity of metapleuron with about four horizontal striae, rest of metapleuron rugose-punctate, more finely so below. Dorsal surface of propodeum shining, longitudinal carinae irregular and connected by numerous transverse carinae, so that surface is areolate, at margins areolae of similar size extending down on lateral and posterior surfaces of propodeum, except that anterior, lateral surface is finely punctate. First metasomal tergum polished, at first glance impunctate, but with scattered small punctures laterally and even less conspicuously extending across tergum middorsally. Terga 2-5 with punctures densest laterally, quite fine on 2, progressively coarser on 3-5; posterior marginal zones of terga 2-5 broadly shining, impunctate, hairless; marginal zones as well as surface between punctures nearly smooth on 2, progressively more distinctly lineolate on 3-5; marginal zones slightly depressed, most noticeably so sublaterally because of gently elevated, less closely punctate convexities of punctate areas in front of marginal zones; marginal zone of tergum 2 occupies one third exposed length of tergum, the zones being progressively broader on terga 3-5, occupying most of exposed length of 5. Anterior sterna with only scattered coarse punctures and large median impunctate areas; sterna progressively more closely and more finely punctate posteriorly.

Male: Length 10 mm (to 8 mm in one paratype); forewing length 8 mm (to 7 mm in one paratype). Coloration as in female, but posterior lobe of pronotum black; tegular and axillary sclerites brownish black.

Pubescence colored as in female, but hairs of sixth and seventh terga black or dusky.

Upper interocular distance somewhat longer than lower (64:58), subequal to eye length (60). Clypeal length to clypeoantennal distance as 20:15. Antennocular:interantennal:antennocellar:interocellar:ocellocular distances as 19:13:26:16.5:18.5. Labral process shorter than in female, about three times as broad as long. Third as well as middle flagellar segments about as broad as long. Longitudinal scutal depression weaker than in female and not noticeable behind middle of scutum. Hairs of hind tibia with fewer and shorter branches, those of outer surface simple. Apex of pygidial plate broadly rounded with margin slightly raised. Gonocoxite with depressed area about as broad as long with several longitudinal carinae across it; gonostylus over half length of gonocoxite, broad, rounded, with broad basal ventral lobe.

Terga much as described for female, but 5 should read 6 throughout; second tergum with punctures sparse dorsally and surface between them not or scarcely lineolate.

Holotype female: Mamathes, Lesotho (= Basutoland), March 8, 1953 (C. Jacot-Guillarmod). Allotype male, same data but January 2, 1960. Two female and five male paratypes, all from same locality, females taken January 12, 1947 (L. Bevis) and February 18, 1945 (A. Jacot-Guillarmod), the males on November 19 and 22, 1945 (L. Bevis), January 12, 1947 (L. Bevis), February, 1940 (C. Jacot-Guillarmod), and February 11, 1945 (C. Jacot-Guillarmod).

The holotype and allotype are in the British Museum (Natural History), paratypes in the Albany Museum in Grahamstown and the Snow Entomological Museum, University of Kansas.

This species is named for one of its collectors, Charles Jacot-Guillarmod, Director of The Albany Museum, Grahamstown, South Africa.

Eupetersia (*Nesoeupetersia*) *flava*
new species
(Figs. 58, 59)

This species differs from other members of the genus by the uniformly reddish-yellow color, so that the insect is suggestive of various nocturnal Hymenoptera. *E. scotti* (Cockerell) and *madagasca* Blüthgen are species of *Nesoeupetersia* with partly red head and thorax, but no others have the wholly reddish yellow body of *E. flava.*

Female: Length 6 mm; forewing length 5.5 mm. Reddish yellow, apices of mandibles red, upper surface of flagellum brown; wings nearly clear, veins and stigma brown.

Hairs yellowish white, longer hairs of lower part of face dusky yellow, hairs of tarsi yellow, longer hairs of posterior sterna and sides of posterior terga dusky in certain lights.

Head slightly wider than thorax, much wider than long, upper and lower interorbital distances as 35:34, about equal to eye length (36). Clypeus uniformly convex, upper margin concave medially, height of clypeus greater than clypeoantennal distance (8:6). Antennocular:interantennal:antennocellar:interocellar:ocellocular distances as 11:5:23:7.5:11. Labrum with sharp transverse basal ridge with a few hairs on distal surface; labral process over twice as broad as long, margined with strong hairs and without premarginal hairs. Supraclypeal area weakly elevated to frontal tubercle, then gently descending above, between antennal bases. Flagellum with first three segments all much broader than long, middle segments broader than long. Preoccipital carina continuous, but weak dorsally. Anterolateral angles of pronotum nearly right angular, a weak carina extending across pronotal lobe. Scutum without longitudinal depression. Legs slender, basitibial plate slightly elevated and short; hairs along upper margin of hind tibia with branches along convex surfaces, these intermixed with some coarse, simple, curved, pointed bristles about half as long as longest hairs or longer; hairs of outer surface of tibia as described for *E. guillarmodi*. Apex of marginal cell pointed almost on wing margin. Hamuli six. Pygidial plate rather broad, sides diverging anteriorly.

Body shining, with scattered minute punctures, lower half of face and entire genal area minutely roughened between punctures, upper part of frons smooth between punctures separated by several puncture widths, vertex almost impunctate; thorax with punctures coarser than those of head, punctures of scutum separated by one to two puncture widths, scutellum with similar sized punctures separated by three of four puncture widths, space between punctures minutely roughened, more conspicuously so on scutum than scutellum; sides and venter of thorax smooth, with scattered small punctures, about two horizontal striae on upper convex part of metapleuron. Dorsal surface of propodeum with longitudinal, slightly irregular carinae, terminating at posterior margin; posterior and lateral surfaces of propodeum finely roughened and punctate, not areolate except for a few, large, incomplete areolae just above attachment of metasoma, carinae delimiting them extending only about half way up from metasomal attachment to summit of posterior face of propodeum. Metasomal terga entirely shining and nearly impunctate, minutely lineolate except on first tergum, weakly so on second; dorsal hairs almost absent except on fifth and sixth terga; basal parts of terga and apical marginal zones not differentiated except sublaterally on terga 1-4, which have distinct sublateral swellings in front of marginal zones. Sterna 1-2 nearly impunctate, 3-6 with coarse punctures posteriorly and laterally, interspaces conspicuously lineolate.

Holotype female: East Madagascar, Forest 600-1200 meters altitude, December to February, 1930-31 (C. H. Lamberton, collector), in the American Museum of Natural History, New York.

The specific name refers to the uniformly yellow color of the body.

Sphecodes (*Austrosphecodes*) *convergens* new species

(Figs. 69, 71, 72)

This species differs from other *Sphecodes* known to me by the relatively narrow face, with eyes strongly converging below. In this and other respects it resembles the genus *Ptilocelptis* and suggests the origin of that group from *Austrosphecodes*. The abundant, snow white hair is unusual, and the areas of dense, white hair at the sides of the terga probably distinguish it from other species such as *S. cordillerensis* Jörgensen.

Female: Length 7 mm; forewing length 5.5 mm. Black, the following parts light red: labrum, mandible (apex red-brown), antenna (upper surface red-brown, basal half of scape brown in some paratypes), pronotal lobe, legs (coxae and in some paratypes trochanters infuscated, front coxa essentially black; hind tarsal segments 1-3 infuscated in some paratypes), metasomal terga 1-3 and basal half of 4, sterna (fifth and sixth brownish). Clypeus dark brown. Tegula and basal wing sclerites translucent testaceous. Wings transparent, veins and stigma dark brown.

Hairs snowy-white, those of apex of abdomen yellowish; shorter hairs largely densely plumose, obscuring paraocular area and extreme sides of clypeus, slightly less dense on frons and supraclypeal area, most of clypeus with only scattered sparse simple hairs; genal area hidden by dense hair. Thoracic surface largely hidden by plumose hairs in the following areas: posterior margin of pronotum and outer surface of pronotal lobe, anterolateral, lateral and posterior margins of mesoscutum, lateral part of scutellum, metanotum, lateral and ventral surface of thorax, posterior and lateral surfaces of propodeum. Hair of legs rather abundant, longer hairs of hind tibia longer than tibial diameter, mostly branched, none thickened or spinelike; hairs of under surfaces of tarsi pale-yellowish. Lateral parts of terga 1-5 with diffuse areas of white hairs, mostly not quite dense enough to hide surface, these areas extending mesally toward midline on middle parts of terga 2 and 3 as areas of laterally directed hairs, conspicuous from some angles. Apical fringe of fifth tergum broadly interrupted medially so that medially this tergum has broad, hairless margin like preceding terga; prepygidial fimbria rather weak, nowhere fully obscuring surface of fifth tergum. Eye with scattered short hairs.

Head as wide as thorax, broader than long (about 80:70); eyes strongly converging below, upper and lower interorbital distances as 48:38, both less than eye length (50). Clypeus slightly biconvex, only slightly more than twice as wide as long (37:16), longer than subantennal distance (16:14). Antennocular:interantennal:antennocellar:interocellar:ocellocular distances as 14:6.5:19.5:14.5:11. Mandible simple. Labrum with transverse basal elevated area about four times as wide as long, summit of this area feebly emarginate medially, distal surface of this area with short hairs; process beyond elevated area rounded, about twice as broad as long, hairs of marginal row slender, not bristles. Supraclypeal area gently convex, frontal carina not steeply declivous above frontal tubercle. Flagellum with first segment almost twice as broad as midventral length, segments 2-9 subequal in length, slightly longer than broad (3-5 most distinctly so) to about as broad as long. Preoccipital carina absent dorsally, distinct laterally and extending to posterior end of hypostomal carina where the two form a posteriorly directed acute angle. Anterolateral angle of pronotum with dorsal, transverse, horizontal carina, angle about right-angular seen from above, no strong ridge, but only a rounded surface extending downward from angle, but ventrolaterally directed ridge extending toward coxal base distinct. Scutum with vertical, anterior surface convex, with punctures and therefore less sharply differentiated from rest of scutum than usual. Scutellum feebly biconvex. Legs slender, hind femur width to length as 12.5:47. Hind tibia without basitibial plate, apical spine, or spinelike setae; hairs of outer surface of hind tibia with branches along convex sides. Apex of marginal cell narrowly truncate with short appendage. Hamuli five. First metasomal tergum nearly as broad as long. Pygidial plate rather broad, margins diverging anteriorly.

Head closely and rather finely punctate, dull because of punctation except clypeus, which is shining with coarser round punctures separated by about a puncture width, and hypostomal area which has only very scattered punctures, but whose surface is minutely roughened, dull. Scutum with punctures nearly as large as those of clypeus, separated by about one-third puncture width or almost contiguous anteriorly; scutellum more finely punctate; metanotum finely reticulate; sides of thorax reticulate punctate, finely so above, weakly and finely so on metapleuron and anterior part of propodeum; upper part of metapleuron with about three horizontal striae. Dorsal surface of propodeum rather finely reticulate, nearly smooth around the arcuate posterior margin; posterior and posterior lateral surfaces of propodeum more coarsely reticulate-areolate. First metasomal tergum shining, with small punctures mostly separated by three or four puncture widths, except laterally in some areas where they are coarser and closer and posteromiddorsally, where they are finer and sparser. Second tergum similarly punctured, depressed apical margin not differently punctured, coarsest punctures widely separated and on elevation anterior to depressed margin. Remaining terga with punctures closer, surface between them somewhat less shining, marginal areas impunctate posteriorly but basal parts with punctures. Sterna with surface rather dull, finely-lineolate.

Holotype female and three female paratypes (one headless): Zapala, Prov. Neuquén, Argentina (Juan Foerster). One paratype is dated March, the others have no dates. One female paratype: Tornquist, 500 m altitude, Sierra de la Ventana, Prov. Buenos Aires, Argentina, December, 1954 (F. H. Walz). The holotype is in the Snow Entomological Museum, University of Kansas. Paratypes are in that collection, the American Museum of Natural History, and the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia."

The specific name refers to the inner ocular margins which are strongly convergent below, unlike other *Sphecodes*.

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THE MECOPTERA OF INDONESIA: GENUS *NEOPANORPA*

By

Helen Chwei-Sia Chau
and
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The Mecoptera of Indonesia: Genus *Neopanorpa*

Helen Chwei-Sia Chau and George W. Byers

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The Mecoptera of Indonesia: Genus *Neopanorpa*[1]

ABSTRACT

The Mecoptera (scorpion flies) of Indonesia are limited to species of the genera *Leptopanorpa* and *Neopanorpa* of the family Panorpidae. Our detailed examination of all available museum specimens of Indonesian *Neopanorpa* indicates they form four groups: A *Neopanorpa muelleri* group, including *N. muelleri, N. hyalinata, N. fuscicauda* n. sp., and *N. umbonata* n. sp.; a *Neopanorpa angustiapicula* group, including *N. angustiapicula* n. sp., and *N. diloba* n. sp.; a *Neopanorpa fractura* group, including *N. fractura* n. sp., *N. crinita* n. sp. and *N. sumatrana* n. sp.; a *Neopanorpa borneensis* group, including *N. borneensis, N. flavicauda* and *N. spicata.* One other species, *Neopanorpa lieftincki* n. sp., cannot be placed with any of the groups. Established species are redescribed and new species described. The genera *Neopanorpa* and *Leptopanorpa* are compared and distinguished.

INTRODUCTION

Indonesian insects of the order Mecoptera, commonly known as scorpion-flies, have been studied by van der Weele (1909) and Lieftinck (1936), and incidentally by a few others. Mecoptera of some other areas of southeastern Asia have also been examined in detail: Japan (Miyake, 1913; Issiki, 1933), China (Cheng, 1957), and Indo-China (Byers, 1965).

The Mecoptera are represented in Indonesia only by the family Panorpidae and by only two of its three genera, *Leptopanorpa* and *Neopanorpa.* Weele's work concerned only three forms of *Neopanorpa* (which we think are all of a single species) and four species now assigned to *Leptopanorpa.* Lieftinck later dealt in detail with *Leptopanorpa* only. The primary objectives of this study are to describe the Indonesian species of *Neopanorpa* and to attempt to show how they are related to one another and to the mainland species of the genus. Another purpose is to evaluate the characters used to differentiate *Neopanorpa* and *Leptopanorpa* to determine whether these nominal genera are distinct.

Weele (1909) first proposed *Neopanorpa* as a subgenus of *Panorpa.* Westwood (1842) described its type species, *Panorpa angustipennis,* from either Java or Tenasserim (peninsular Burma), not explaining why he was uncertain of the locality. The female holotype is labeled, "Java." In revising *Panorpa* (1846), Westwood reversed the order of possible type localities as "Tenasserim, India, *vel* Java." Others, however, have regarded *angustipennis* as a Javanese species (Weele, 1909; Enderlein, 1912; Esben-Petersen, 1913; Roepke, 1916), but the Javanese species they described was actually *Neopanorpa muelleri,* as Banks (1931a) supposed. Byers (1965) judged that *angustipennis* is an Indo-Chinese (mainland) species, rather than Indonesian. He showed that the thoracic markings and the genital plates of the holotype of *angustipennis* are characteristic of mainland species, and the wing markings, while very similar to those of *muelleri,* are also like those of some other Indo-Chinese species. He also found that one of two female Malayan specimens matched the type, and judged that those and associated males were conspecific with the holotype.

Weele (1909) separated the Indonesian

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Mecoptera into two genera, *Panorpa* Linnaeus and *Leptopanorpa* MacLachlan. Because he assigned to the genus *Leptopanorpa* those males with length of the abdomen about twice that of the wings, he placed in *Panorpa* four species currently considered as *Leptopanorpa.* Weele differentiated subgenus *Neopanorpa* from typical *Panorpa* because the notal organ of males of the Indonesian species is conspicuous, whereas that structure is but slightly developed in the European species of *Panorpa* with which he was familiar. He also separated from *Panorpa* (*Neopanorpa*) *muelleri* a new, smaller subspecies, *ungaranensis,* that has the pterostigmal band divided into two spots in the hind wings. Karny (1923) said that those characters had no taxonomic significance and he could not tell typical *muelleri* and *m. ungaranensis* apart, for some smaller individuals do not have the pterostigmal band of the hind wing broken into two spots and some larger ones do.

Enderlein (1910) erected the genus *Campodotecnum* for *Panorpa angustipennis* Westwood and the genus *Himanturella* for *Leptopanorpa tubifera* Enderlein and *L. nematogaster* MacLachlan. In 1912, he retained *angustipennis* (actually *muelleri*) in *Campodotecnum* and described two new species, *Campodotecnum lemniscatum* and *C. cingulatum.* He raised *Neopanorpa* to generic status, but designated as its type species *Panorpa nematogaster* MacLachlan (now in *Leptopanorpa*), not knowing that the type species, *angustipennis,* had been fixed by Weele. These errors were noted by Esben-Petersen (1913) and Roepke (1916).

Esben-Petersen (1913) described a new species, *hyalinata,* from Java and transferred *Panorpa jacobsoni* Weele, *P. javanica* Westwood and *P. pi* Weele to the genus *Leptopanorpa.* He also synonymized *Campodotecnum* with *Neopanorpa,* and *Himanturella* with *Leptopanorpa.*

Navás (1913) accepted *Campodotecnum* as the generic name for his new species *falcatum* from Java and added to that genus the species *effusum* Navás, from Sikkim.

In 1915 Esben-Petersen transferred *Panorpa nematogaster* MacLachlan and *Neopanorpa linguata* Navás to the genus *Leptopanorpa,* both as synonyms of *Leptopanorpa charpentieri* Burmeister. Later, in 1921, he reviewed the Javanese species of *Neopanorpa,* including as valid species *angustipennis* Westwood, *hyalinata* Esben-Petersen, *muelleri* Weele, *lemniscata* Enderlein and *cingulata* Enderlein. He synonymized *Campodotecnum falcatum* Navás with *hyalinata* and *muelleri ungaranensis* with *muelleri.* Variation, especially of color, in the latter pair was earlier discussed by Roepke (1916), who presumed that they were the same species.

Banks (1931b) described *Neopanorpa flavicauda,* the first mecopteran recorded from Borneo, and suggested (1931a) for the first time, that Weele's *angustipennis* is only a form of *muelleri.*

Lieftinck (1936) accepted the new status of some *Leptopanorpa* species transferred from *Panorpa* by Esben-Petersen (1913) and described six new species as *L. erythrura, L. filicauda, L. inconspicua, L. peterseni, L. robusta,* and *L. sarangana,* and one new subspecies, *L. pi decorata,* adding some morphological and biological observations. He judged that *Leptopanorpa charpentieri,* regarded by Esben-Petersen (1915) as synonymous with *L. nematogaster* MacLachlan, was from Bengal, not from Java. Burmeister, 1839, had said that he would describe a new species from Bengal, but in his description of *charpentieri,* supposedly that new species, he gave the locality as "Ostindien." Since *charpentieri* was unknown to Lieftinck, he thought it was distinct from *nematogaster.* He also suggested that *Campodotecnum lemniscatum* Enderlein was a *Neopanorpa* and that *C. cingulatum* Enderlein might be identical with his *L. erythrura.* The former is a synonym of *Leptopanorpa pi* Weele and the latter, the senior synonym of *L. erythrura* (Byers, 1967).

Lieftinck made the following statement about synonymy of *Leptopanorpa* and *Neopanorpa:*

"Enderlein, in the Zool. Anzeiger, 35, 1910, p. 192, has erected the generic name *Himanturella,* with *tubifera* Enderlein as genotype, but since *tubifera* End. 1910 is the same species as *longicauda* Weele 1909, which is a true *Leptopanorpa,* Enderlein's unfortunate selection is invalidated. Moreover, Enderlein created a second invalid name in making *Panorpa javanica* Westwood the type of his new genus *Campodotecnum,* a species belonging undoubtedly to *Leptopanorpa.* In 1912, Enderlein adds further to the confusion in placing his *Himanturella* as a synonym of *Neopanorpa,* while *nematogaster* is erroneously fixed as the type of *Hinanturella* End. Thus, as has been clearly ascertained by Esben-Petersen in his 'Synonymic List of the order Mecoptera' (Entom. Meddelelser, 10, 1915), *Neopanorpa* Weele 1909 (type: *P. angustipennis* Westwood) is of earlier date than *Campodotecnum* Enderlein 1910, and should be used as the name of this genus, while *Himanturella* becomes an absolute synonym of *Leptopanorpa* MacLachan 1875, of which *ritsemae* is the type."

Byers (1966) described two additional species of *Neopanorpa* from Borneo and redescribed *N. flavicauda* Banks.

The only key for Indonesian *Neopanorpa* (Weele, 1909) concerned primarily those species now assigned to *Leptopanorpa.*

ACKNOWLEDGEMENTS

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METHODS AND MATERIALS

We examined 395 dried, pinned specimens, nearly all from the Rijksmuseum van Natuurlijke Historie, Leiden. Most type specimens of older species were examined and drawn (by camera lucida) by Byers in 1964. The lectotypes of *muelleri* and *ungaranensis* were reexamined in 1972 and that of *muelleri* dissected.

Terminology for wing venation is that of Comstock and Needham; for wing markings, that of Esben-Petersen (1921); for male and female genitalia, by Byers (1965).

The genital bulb was removed from the male (sometimes also the 7th and 8th abdominal segments), and the 8th and following abdominal segments from the female. These were boiled in water for one or two minutes to soften them and to prevent breakage during dissection. For the male, the ninth sternum (including hypovalves) and ninth tergum were removed together from the genital bulb. For detailed examination of genitalia the aedeagus was excised by cutting along the inner bases of the basistyles. Dissected parts were preserved in glycerin in microvials, these being attached to the individual specimen's pin. For the female, the terminal segments were boiled, the subgenital plate of the 8th sternum cut off, and the exposed genital plate was removed. These were preserved on an insect mounting point in a drop of polyvinyl alcohol, which is water soluble, so that the dissected parts can be washed off when reexamination is desired.

Line drawings were made with the aid of a camera lucida. For wing photographs, specimens were relaxed for two days before removal of the wings.

Measurements of antennae, wings and body length were made with dividers and a millimeter scale. Body length was measured as the distance from the front of the head to the end of the dististyles for the male, from front of head to tips of cerci for the female. Wing length is the straight-line distance from point of the wing's attachment to its apex. This is adequate, since precise measurements are not significant in taxonomy of Mecoptera and the method gives a general impression of the insects' sizes.

MORPHOLOGY

GENERAL DESCRIPTION:

Adults of *Neopanorpa* (Fig. 1) are medium-sized insects. The body length is about 14 to 19 mm for males and 11 to 16 mm for females, depending on the species. Wing length is about 12 to 14 mm, variable among species.

Head: Elongation of the clypeus, subgenae and certain mouthparts produces the characteristic beak-like rostrum. The compound eyes are large and black; three large, transparent, brown ocelli are close together on a raised triangle. The term "dorsum of head" used here descriptively refers to the top of the head, from the antennal sockets to the post-occipital margin. Chewing mouthparts are at the end of the rostrum. The small labrum is not separated by a distinct suture from the greatly elongated clypeus. The mandibles cross each other on preserved specimens. The stipites of the maxillae are greatly elongated and the submentum is elongated and membranous. Tips of maxillary and labial palps are usually darkened.

The antennae are long (about 12 mm) and slender, each composed of a thickened scape, a nearly spherical pedicel and a flagellum, slightly tapered from the base to the apex, consisting of 40 to 46 cylindrical segments or flagellomeres (number varies with species and individuals).

Thorax: The wide pronotum bears bristles or hairs along its anterior margin. Below the pronotum are an undivided pleuron and the front coxae. At each side, between the propleuron and the posterior margin of the head, is a large cervical sclerite. The mesonotum is clearly divided into scutum, scutellum and postnotum, the first two separated by the scutoscutellar suture, and the scutellum from the postnotum by a membranous, intersegmental conjunctiva. The pleural suture is distinct, dividing the pleuron into episternum and epimeron. The metathorax is about the same size and form as the mesothorax. The mesothoracic spiracle is in a membraneous area between the pronotum and mesepisternum, and the metathoracic spiracle is between the mesepimeron and metepisternum.

Legs: The coxae and mera are well developed, especially on the mesothorax and metathorax. The femora and tibiae are long and each is of rather uniform diameter throughout. At the apex of each tibia are two large, tibial spurs. There are five tarsomeres, basitarsus much longer than the others. The two pretarsal claws bear five pectinations each.

Wings: There are two pairs of long, narrow wings. Wing shape and venation are useful in generic diagnosis. For *Leptopanorpa,* the wing is narrower than for *Neopanorpa,* especially the wing

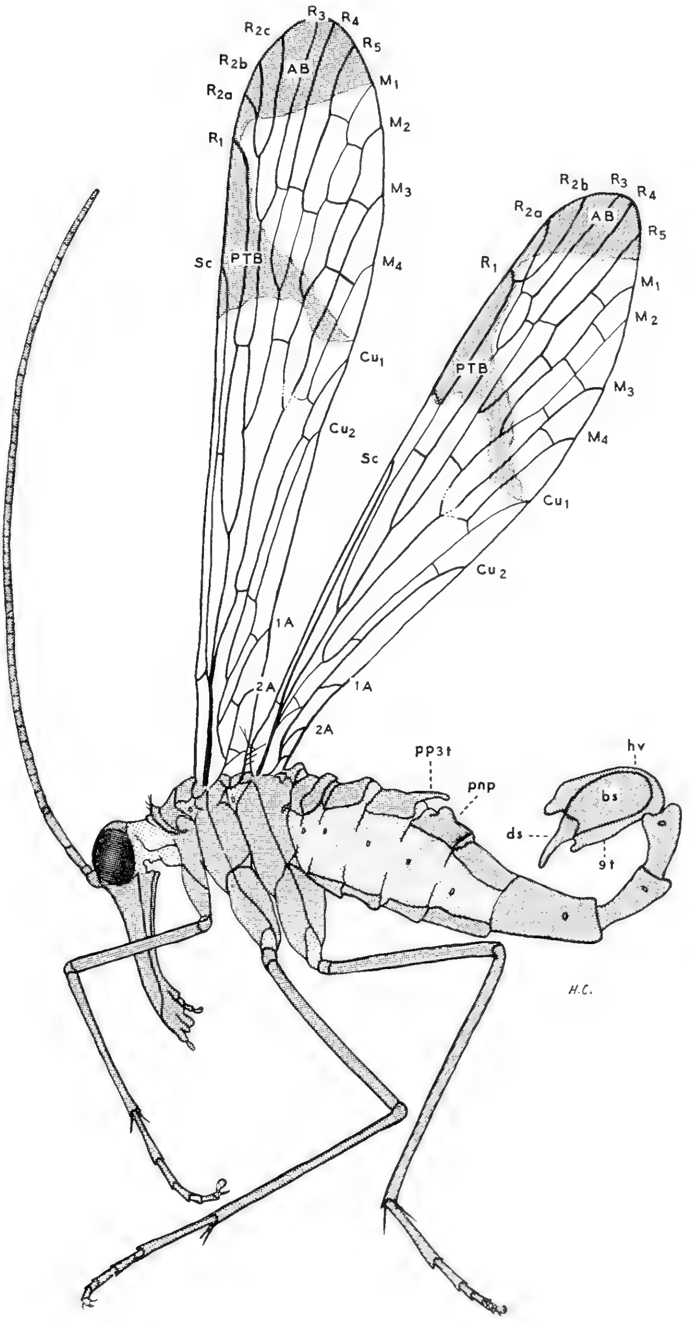


FIG. 1. *Neopanorpa muelleri* (Weele), male, left lateral aspect; wings elevated to show venation; right legs and most of antennal flagella omitted. Abbreviations: A—anal veins; AB—apical band; bs—basistyle, Cu—cubitus; ds—dististyle; hv—hypovalve (abdominal sternum 9); M—media; pnp—posterior notal process; pp3t—posterior process of abdominal tergum 3; PTB—pterostigmal band; R—radius; Sc—subcosta; 9t—abdominal tergum 9.

base. *Neopanorpa* differs from *Panorpa* in the length of vein 1A, which reaches the wing margin before the level of the origin of the radial sector in the former, well beyond it in the latter (Esben-Petersen, 1921). The wing markings (Fig. 1) are smoky dark brown to faint brown, depending on the species. They include: An apical band (AB) extending from anterior to posterior margin at the apex of the wing; a pterostigmal band (PTB), which usually extends from anterior to posterior margin and may or may not fork at mid-length into a proximal (basal) branch and a distal (apical) branch, but which may be reduced to a pterostigma only (*hyalinata, angustiapicula*); a marginal spot extending generally from C to near R_{4+5}; a basal band from C to 1A or Cu_2, sometimes broken into two spots; and a basal spot near the base of Cu_1 and Cu_2. The wing markings help in primary identification, varying from the most complete pattern (presence of all the markings, as in typical *muelleri*) to the most reduced, obscure one (*diloba*). They may vary much within one species (*muelleri*); or the same pattern may occur in different species (*umbonata, muelleri* and *sumatrana*). The hind wings are usually slightly smaller than the fore wings and have less extensive markings.

Abdomen of the male: There are nine, readily visible abdominal segments. The first tergum is divided into an anterior sclerite joined to the metathorax and a separate posterior sclerite. The median posterior process of tergum 3 (upper part of the notal organ) projects backward from the usually shallowly emarginate tergum and rests on a small elevation on anterior tergum 4. Weele (1909) used this to differentiate *Neopanorpa* as a subgenus from typical *Panorpa*. It varies from species to species, sometimes enough to be used in species diagnosis. The tergum and sternum are fused and the pleura obliterated in segments 6-8. Paired spiracles are present on the first eight segments.

The enlarged ninth segment (genital bulb) is connected to the eighth by a short pedicel. The ninth tergum (epiandrium, or preëpiproct; Fig. 1, 9t) bears two subapical processes that extend ventrally around the tenth segment. In *Neopanorpa,* the apex of tergum 9 has a shape that distinguishes this genus from *Leptopanorpa,* but it does not vary sufficiently within the genus to be useful in species recognition. The ninth sternum (hypandrium) is divided apically into two hypovalves, the length, shape and curvature of which are useful as specific taxonomic characters.

Between the ninth tergum and hypovalves are the stout, paired basistyles (gonocoxites, or coxopodites; Fig. 1, bs). At the apex of each is a chelate dististyle (stylus, or harpagone; Fig. 1, ds), the usually slender, apical half of which is curved mesad and tapers to a sharp point. Projecting from the inner margin of the dististyle near its attachment is the basal lobe (basituberculus of Tjeder, 1970), which varies in size and shape according to the species. For most species, such as *muelleri* or those of the *fractura* group, the basal lobes are knob-like, but for a few (the *angustiapicula* group) they are flattened (Figs. 83, 87). Two to four long, stout, curved, black spines project mesad from the dorsal surface of the basal lobe in the *muelleri* group (Fig. 26), but are absent in other Indonesian species. Smaller, curved, black spines (4 to 25 in number) may also occur in a group on the anterodorsal surface of the basal lobe.

The structure of the aedeagus assists specific diagnosis but has not been used in earlier taxonomic treatments of Indonesian *Neopanorpa*. Most of the aedeagus is only weakly sclerotized, but certain parts are firm and darkly pigmented. The aedeagus (Figs. 17, 27) consists of a pair of blunt ventral valves (penis) slightly divergent at their apices, a usually somewhat smaller pair of dorsal valves, and associated appendages. It is braced between the basistyles by the lateral processes. These processes are simple for nearly all Indonesian species, but in the *angustiapicula* group they are complexly divided into two lamellae enclosing a deep pocket. Ventral parameres are not present on Indonesian *Neopanorpa* except in the *angustiapicula* group, where they are large, project ventrally from the genital bulb and are partly visible, laterally (Fig. 71). The dorsal parameres (penunci of Tjeder, 1970) are ordinarily small, vertically oriented blades of varying shape, above the dorsal valves of the aedeagus. They are, however, complicated for *fuscicauda* and the *fractura* group, extending ventrally alongside the ventral valves of the former and bearing a small, flattened, dorsal appendage, projecting dorsad, on the latter.

Segments 10 and 11 comprise the proctiger. They are small and ordinarily telescoped beneath tergum 9. The single-segmented cerci arise between segments 10 and 11.

Abdomen of the female: The abdomen of the female of *Neopanorpa* is very similar to that of *Leptopanorpa*. Ten clearly recognizable segments taper gradually to the rear, and paired spiracles are present on the first seven. No laterotergites are present on the seventh and eighth segments as on some *Panorpa*. Part of segment 8 is modified as the subgenital plate, and the tergum and sternum are fused on segment 10. The two-segmented cerci arise from the so-called cercifer (cercal bases, in Ferris, 1939) of the tenth segment.

The eighth and ninth segments include external female genitalia. The subgenital plate (subgenitale) of sternum 8 is broad, usually notched and whitish apically (except in *angustiapicula*), and bears long setae on each posterior lobe and along the apical, outer margin of some species (Fig. 28). Above the subgenital plate are the so-called genital plates (internal skeleton, in Miyake, 1913; medigynium, in Tjeder, 1970). These provide the best specific characters for the female. Each (Fig. 29) is composed of an axial portion (gonoclavi of Tjeder, 1970) above and behind which are two blade-like arms (distal plate or lamnae), twisted somewhat at their bases. The axial portion is usually elongate in Indonesian species, but is short and oval for a few (*fractura* group, *fuscicauda, angustiapicula* group and *borneensis* group).

The taxonomic characters used by most authors who have dealt with Indonesian Mecoptera, such as differences of size, of wing markings and body color, and overall shape of the genital bulb in males, are not sufficient for species distinction. For example, Weele (1909) separated a new subspecies, *Neopanorpa muelleri ungaranensis,* from his new species *muelleri* by its smaller size and the division of the pterostigmal wing band into two spots in the hind wing, but he ignored the identical structure of the genitalia of the two forms. Some authors later regarded certain individuals of *muelleri* as Javanese specimens of *N. angustipennis* Westwood because of their general appearance, especially wing pattern; but they ignored the absence of thoracic markings on *muelleri* and its distinctive genitalia. Wing pattern and body color have taxonomic value only when associated with genitalic and other characters. Accurate distinction of species requires comparison of the combination of all available characters.

TOPOGRAPHY, CLIMATE AND VEGETATION

Indonesia now includes Sumatra, Java, Sulawesi (Celebes), Kalimantan (Indonesian Borneo), Nusa Tenggara (the Lesser

Sunda Islands), Maluku (the Moluccas, including Ceram and Halmahera), Flores, Sumbawa, part of Timor, West Irian (approximately the western half of New Guinea) and some 3000 smaller islands. In the past, the name Indonesia was applied to various combinations of these and adjacent territories. Most of these islands belong to young, Tertiary mountain systems that lie completely in the tropics and within the Indo-Australian monsoon region. Indonesia therefore has a climate with high temperatures, high humidity and abundant rains. The mean annual temperature at sea level is about 27° C (80° F) and the mean humidity 80%. The montane climate is more temperate. There is a decrease of temperature between 5.5 and 6° C (10-11°F) for each rise of 1000 m, e.g., the average temperature is 22.1° C (71.8° F) at Bandung, 730 m above sea level, and only 15.9° C (60.8° F) at Tosari, 1734 m in altitude (Bemmelen, 1949).

Since Mecoptera are known only from Sumatra, Java, Borneo and possibly Halmahera, the following geographical comments pertain only to these islands.

Sumatra (Fig. 5), located southwest of the Malay Peninsula, has an area of 435,000 sq. km. It is 1650 km long by 100-200 km wide in the northern part and about 350 km wide in the southern part. It lies between latitude 5°45′ N and 6° S and longitude 95°20′ E and 106° E. The Barisan Mountains extend along the entire southwestern coast and separate the northeastern and southwestern coastal lowlands. The slope toward the Indian Ocean is generally steep. The eastern and southeastern parts of the island are jungle lowlands traversed by five major rivers. The southwestern coastal range (Barisan Mountains) contains many peaks from 2000 m to 4000 m high, often of volcanic origin, some still active.

With the equator crossing Sumatra near its center, the climate is equatorial. The average, annual, lowland temperature is about 27° C (80° F); rainfall is heavy. The slopes, exposed to a continual southwestern wind, receive more than 300 cm of rainfall, annually, that is distributed fairly evenly over the island (Robequain, 1954). The warm, moist air favors growth of dense forests (myrtaceous and ficaceous trees, oaks, guttapercha, camphor, teak, pine, etc.) that cover about 90% of the island.

In the forests, the Sumatran Neopanorpas flourish. Hesse (1937) believed endemic animal species of Sumatra were primarily found south of the mountains; but most of the six endemic Sumatran species of *Neopanorpa* are distributed on both the southwestern and northeastern slopes of the moutains. Hesse (1937) also thought faunal differences between the two coastal lowlands of Sumatra exceed the differences between the northeastern slopes and the Malay Peninsula; but, again, this is not the case with the Sumatran species of *Neopanorpa.* The species of Sumatra have not been found in nearby Malaya.

Java (Figs. 2-4), located southeast of Sumatra and south of Borneo, between the Java Sea and the Indian Ocean, has an area of 127,000 sq. km. It is 975 km long by 206 km wide at its widest part and lies between 5°52′ and 8°47′ S and 105°13′ and 114°37′ E. Three physiographic provinces can be distinguished: 1. West Java (west of the longitude of Tjeribon) (Fig. 2). 2. Central Java (between Tjeribon and Semarang) (Fig. 3). 3. East Java (east of Semarang and Jogjakarta) (Fig. 4).

The west-to-east mountain chain includes 112 major volcanoes, 35 still active. The northern coast is lowland, of volcanic deposits or marine sand and clay, but the southern coast has limestone ridges. In East Java, the mountains are generally near the southern coast. These include Java's highest volcanic peak, Mahameru

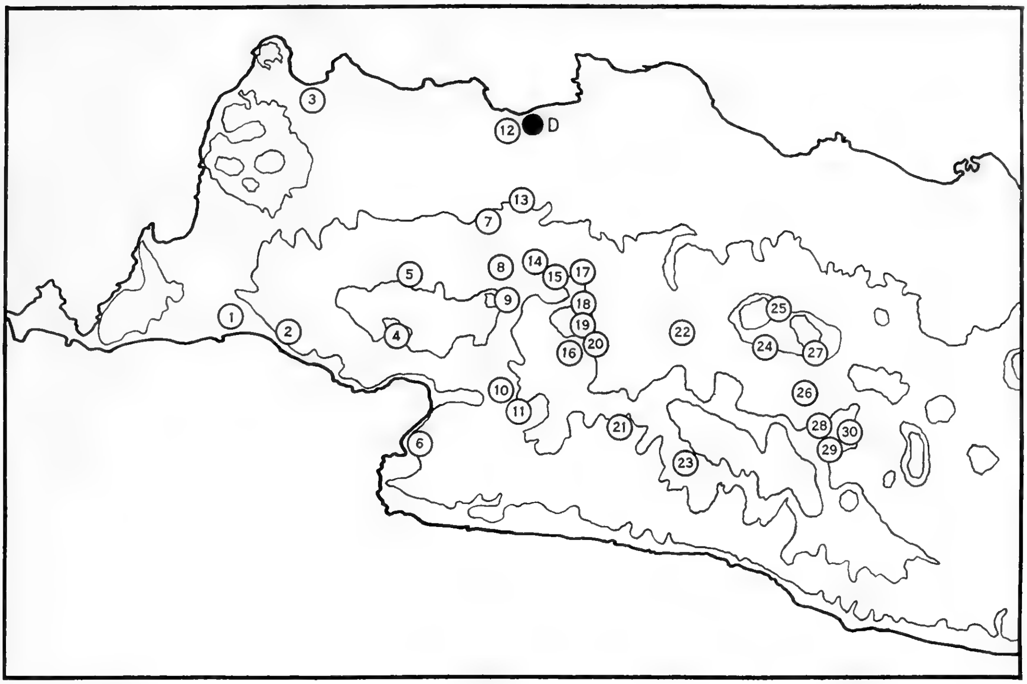


FIG. 2. MAP OF WESTERN JAVA. Circles indicate localities where Mecoptera have been collected. Numbers, in sequence from left to right, correspond to locality numbers appearing in the alphabetical gazetteer. Black spots indicate major cities; D—Djakarta. Contour lines at 100 m, 1000 m, and 2000 m, to indicate coastal lowlands, intermediate elevations, and high mountains.

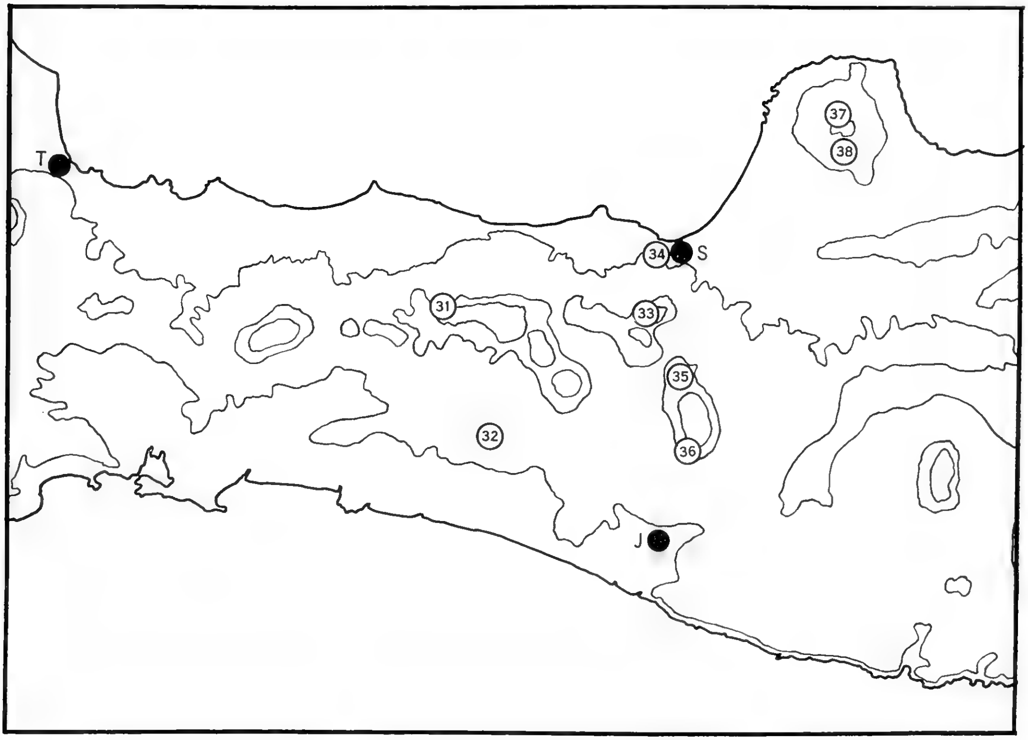


FIG. 3. MAP OF CENTRAL JAVA. See Fig. 2 for explanation. J—Jogjakarta, S—Semarang, T—Tjeribon.

(3711 m; 12,060 ft), and the volcanic Tengger, Ijang and Ijen highlands, which form a wide peninsula extending eastward toward Bali. In Central Java, the mountains are more central and the main watershed is toward the south. Here, the volcano Slamet reaches 3472 m. The Preanger Mountains in southeastern West Java are lower (the major peak less than 3000 m) and include extensive upland basins. Further westward the summits are lower, but rise again in the northwest to nearly 2000 m. There are four major rivers, draining generally northward.

The coastal temperature of Java averages 26-27° C (78-80° F), while temperate conditions occur above about 700 m. In general, humidity is high (75%-90%). The Asiatic (northwest) monsoon, from November to April, brings much rain, especially in the north. From May to October, the southeast monsoon season brings some rain to the southern coast but in general is drier than the northwest monsoon. Western Java (except northwest Java) and the entire southern coast have high annual rainfall (more than 200 cm), quantity depending largely on the altitude and situation of the mountains. Bogor (Buitenzorg), 290 m above sea level, has more than 406 cm of rain per year; Bandung, at 730 m, 195 cm. Maximal rain falls in the Djampangs, on Mt. Tangkuban Prahu, Mt. Malabar, various mountains of East Priangan, and Mt. Tjerimai (Tjaréme) in Tjeribon. In Central Java, annual rainfall is 665 cm on the upper northern slopes of the mountains, but only 215 cm at Semarang on the northern coast. The rainfall is not so evenly distributed as in West Java. There is an obvious dry season from June to September. Semarang receives only 13% of its total rainfall during the four-month dry season. In Central Java, the maxima of rainfall are found on Mt. Slamat and the range east of it, including Mt. Ungaran, the Merbabu and Merapi volcanoes. East Java is drier than Central Java. The foehn-like, southeastern, moonsoon winds from the Australian deserts are generally warm and relatively dry. They bring less rainfall to the eastern end of the island than to the central part, eastern volcanic peaks becoming islands of heavier rainfall. The northeastern coastal lowlands get only 150-200 cm of rain, annually, the months of July to October being practically dry (Bemmelen, 1949). In East Java, regions of maximal rainfall are on Mt. Lawu, the Tengger Mountains, the southern slopes of Mt. Raung and Idjen Plateau.

Rainfall decreases from western Java to eastern Java, and because the southern mountain slopes force the monsoon winds to rise, there is also a decrease from south to north. This pattern of rainfall coincides with the distribution of Javanese *Neopanorpa* (Figs. 2-4), just as it does with that of *Leptopanorpa* (Lieftinck, 1936). The genus *Neopanorpa* requires high atmospheric humidity. The distribution and mode of life of Indonesian scorpion flies are closely related both to the total amount of rain and the seasonal rainfall pattern.

Java's many volcanoes and its heavy equatorial rainfall contribute to the fertility of the soil and the abundant plant and animal life. The moist mountain slopes have an extensive evergreen forest with the tall timber tree, rasamala, common in the west, but absent in the east where mountain *Casuarina* is plentiful. Teak is more frequent and the evergreen rain forest less robust in Central Java than in West Java. Many species of scorpion flies are apparently restricted to the luxuriant forest in the mountains of western Java. Mayr (1944) called the fauna of Java impoverished, compared to that of Sumatra (or Borneo). However, collections of scorpion flies suggest the opposite. Mayr thought the volcanic lava and ashes during the Pleistocene may have exterminated

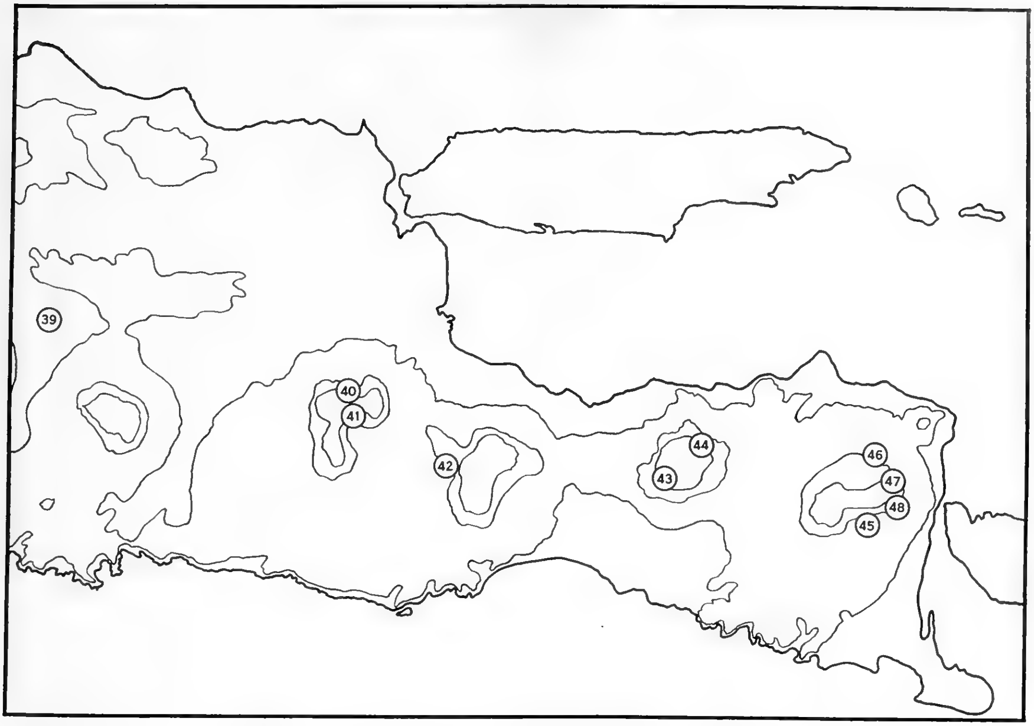


FIG. 4. MAP OF EASTERN JAVA. See Fig. 2 for explanation.

many local species and that Java is less humid and poorer in habitats than Sumatra, more peripheral and less accessible to colonizing species. We suggest that human depletion of forests in Java (20-30% of the surface covered with forests, as contrasted with 90% in Sumatra), destroying much of the shaded habitat of scorpion flies, must have had a profound effect upon the present fauna.

Borneo, the second largest island of the Malay Archipelago (736,000 sq. km), is roughly triangular, with two small peninsulas at its eastern side, and lies between latitude 7°3′ N and 4°20′ S and longitude 108°50′ E and 119°20′ E. Its northern and central parts are hilly and mountainous, but mostly under 1500 m. The chief ranges extend northeast to southwest, with western, southwestern and eastern branches. The highest point is Mt. Kinabalu, 4485 m (13,456 ft), in Sabah, the northernmost part of the island. Alluvial plains between ranges are often swampy near the ocean because of tidal flows. Most of Borneo has evergreen rain forest of rich and varied vegetation. Coastal temperatures usually range from 28-34° C (82-93° F). The rainfall is often violent; mean, annual rainfall is about 310 cm at Sandakan. The few records of Mecoptera from Borneo are from highlands around Mt. Kinabalu.

Since Panorpidae usually frequent moist, northern, continental, temperate forests, their penetration into Indonesian tropics requires explanation. Perhaps panorpids migrated there from the Asiatic mainland when Indonesia was much cooler than now. As the climate warmed, the panorpids moved to suitably cool and forested habitats on mountain slopes, where they survive today.

Some of the species appear to us to have narrow vertical limits. *N. angustiapicula* is found only above 2000 m; *N. lieftincki* at approximately 1900 m; *N.*

fractura at 1400 m; *N. diloba* and *N. fuscicauda* around 1000 m; *N. sumatrana* between 920 and 1200 m; *N. crinita* between 500 and 1000 m. Those species having narrow vertical limits are also often limited to one area only: *N. angustiapicula, N. diloba* and *N. fuscicauda* have been found only in East Java; *N. lieftincki* and the *fractura* group in Sumatra only. Some other species have a much broader vertical distribution: *N. muelleri* can be found from low country (at 100 m, 500 m and 1000 m) to above 2000 m altitude; *N. umbonata* ranges from the coast to 920 m; and *N. hyalinata* is found from 300 to 1850 m. Other species tend to have wider horizontal or overlapping distributions: *N. muelleri* occurs throughout the islands of Java and Sumatra; *N. hyalinata* occurs both in West Java and East Java but as yet is unknown in Central Java. *N. muelleri* is the only species known from both Java and Sumatra (and possibly Halmahera). *N. muelleri* might have developed before these two islands became separated.

The doubtful record of *N. muelleri* from Halmahera is discussed elsewhere in this paper (see Zoogeography).

ZOOGEOGRAPHY

Neopanorpa occurs only in southeastern Asia, where 83 species (including 8 new species from Indonesia) are known. Thirty are in nine provinces of southern and southeastern China, including Sikang, Szechwan, Yunnan, Kweichow, Anhwei, Kiangsu, Kiangsi, Fukien, Kwangtung (Cheng, 1957); 17 are found in southern India, southern Nepal, Sikkim, Assam and Burma (Rust and Byers, 1976); 14, in Indo-China (Byers, 1965); 9, in Taiwan and 13 (including the 8 new species) in Indonesia. There appears to be no overlap of specific ranges from one of these regions to another. This may be due to restricted ranges, but more probably to insufficient collecting.

The 13 Indonesian species of *Neopanorpa* are restricted to Java, Sumatra, and Borneo (and perhaps Halmahera); one occurs in Java and Sumatra (possibly also Halmahera), 4 others on Java, 5 others only on Sumatra and 3 others only on Borneo. There is as yet no record of Mecoptera from Celebes, Lesser Sunda Islands (Lombok, Sumbawa, Flores, Timor, etc.) or New Guinea. Lack of records of *Neopanorpa* and other Mecoptera from these islands may be due to inadequate collection or to physical barriers, or both.

In early Miocene or late Oligocene, the earth's crust buckled downward along the western Sumatran islands (Simeulue, Nias, Kepulauan, Batu, Siberut, Sipura, etc.), Timor, Kai, Ceram and Halmahera (Earle, 1845, in Mayr, 1944). In late Miocene, a second folding formed parts of Sumatra and Java. At first most of this fold was under water, some islands not emerging until mid-Pleistocene. The Pleistocene ice-age lowered the sea level to about 100 m lower than now, establishing several land connections between present islands (map, pp. 16, 17, Townes and Chiu, 1970). Sumatra, Java, Bali and Borneo and the Malay Peninsula formed "Sundaland," an extension of the Asiatic mainland. Lombok, however, remained separated by the 312 m depth of Lombok Strait (Mayr, 1944). We presume that Mecoptera from mainland Asia migrated across these land connections to Sumatra, Java, Borneo and the Philippines during the cool Pleistocene.

The Indonesian Mecoptera (all in the family Panorpidae) have no taxonomic familial connections with Mecoptra of Australia (families Bittacidae, Choristidae, Nannochoristidae, Apteropanorpidae and Meropeidae). Instead, the Mecoptera of Australia show connection with those of South America, e.g., the genus *Nannochorista,* occurring also in Chile and Argentina (Riek, 1954). Many elements in

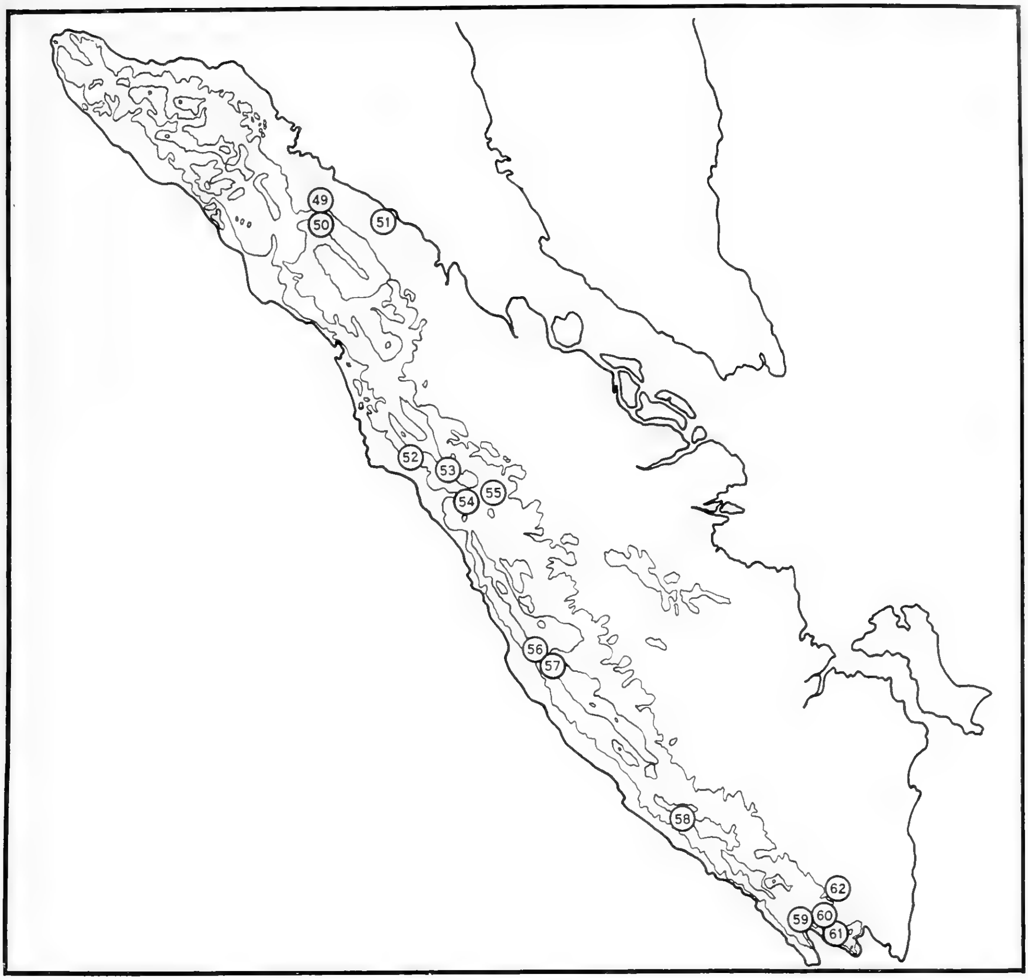


FIG. 5. MAP OF SUMATRA. See Fig. 2 for explanation of symbols. Contour lines at 200 m, 1000 m, and 3000 m, to indicate coastal lowlands, intermediate elevations, and high mountains.

other groups of insects (Edmunds, 1957, and Hardy, 1951, in Gressitt, 1958), in vertebrates and plants are common to Australia, southern South America and, in some cases, Africa (Gressitt, 1958). This tends to support the existence of an original southern supercontinent ("Gondwanaland") which may have existed some 150 million years ago, of which an Australian fragment broke off and moved northward, joining Asia. Geological changes (sea level, orogenic forces, coral formation, etc.), later broke the connection between Asia and Australia, re-established it and broke it again (Robequain, 1954). Animals and plants originating in Asia developed, in Australia, as unique life forms, due to the long period of isolation.

As pointed out by Lieftinck (1936), all the Indonesian Mecoptera are endemic; even the species of Sumatra are not known from nearby Malaya. Of the two Indonesian genera, *Neopanorpa* and *Leptopanorpa,* only the former occurs on mainland Asia. *Leptopanorpa,* as we have limited the genus, is known only from Java, but possibly occurs on Sumatra as well. We have examined the syntypes (1 male now without abdomen and 1 female) of *L. charpentieri* (Burmeister), described from "Ostindien." They bear no locality labels. Lieftinck, in 1936, assumed the species was from Bengal as indicated in the Introduction above. Esben-Petersen (1921) correctly synonymized *charpentieri* and *nematogaster;* Lieftinck did not agree. We believe that *nematogaster* is a synonym of *charpentieri,* and we conclude that *L. charpentieri* is from Indonesia, not from India. The other two supposed Himalayan Leptopanorpas, *L. furcata* and *L. effusa,* are large *Neopanorpa* species (Byers, 1971).

Endemicity of Indonesian Mecoptera is probably due to evolution in the present ranges following migration of ancestral species from mainland Asia. These migrants were isolated by water barriers resulting from the melting of the glaciers during and at the end of the Pleistocene.

Warming lowland temperatures probably further isolated these Mecoptera, driving them up into their somewhat isolated ranges on mountains. Mecoptera are not strong fliers; their low vagility intensifies spatial isolation, inbreeding and species formation, giving rise to endemic species or even endemic genera in the particular environments of the isolated tropical islands. We now find no species common to Malaya and Sumatra, and only one, *N. muelleri,* occurring both on Java and Sumatra.

Two specimens of *N. muelleri* in the Canadian National Collection are labeled as from Halmahera. How did these Java-Sumatran species cross approximately 1450 km (900 mi) from Java to Halmahera? Perhaps the specimens are mislabeled. Townes and Chiu (1970: 234) doubted the supposed occurrence of the ichneumonid wasp, *Xanthopimpla f. fastigiata,* on Halmahera, the specimens thereof in question having been collected by the same collector whose label appears on the supposed Halmahera *N. muelleri.* Wallace's Line may hold its validity for such weakly flying insects as Mecoptera, if the labels are correct, for both flying and flightless Indo-Malayan elements have been found even in Timor (Rensch, 1936, in Mayr, 1944); and the straits separating the Indonesian islands have not been absolutely insuperable obstacles to the migration of animal and plant species (Robequain, 1954). Mayr (1944) states that each of the straits in the Lesser Sunda Islands is to some extent a zoogeographic barrier, with the Lombok Strait more effective than any of the others, because of its depth and its persistence through periods of low sea level during the Pleistocene.

TAXONOMY

We divide the Indonesian Mecoptera into four groups, as follows, primarily on the basis of genitalial structure of the males and to a lesser degree on the basis of genitalial characters of the female and wing pattern. One species (*lieftincki,* n. sp.) must be placed alone.

Neopanorpa muelleri group:
- *muelleri* van der Weele
- *hyalinata* Esben-Petersen
- *fuscicauda,* new species
- *umbonata,* new species

Neopanorpa angustiapicula group:
- *angustiapicula,* new species
- *diloba,* new species

Neopanorpa fractura group:
- *fractura,* new species
- *crinita,* new species
- *sumatrana,* new species

Neopanorpa borneensis group:
- *borneensis* Byers
- *flavicauda* Banks
- *spicata* Byers

Ungrouped species:
- *lieftincki,* new species

KEY TO MALES OF *NEOPANORPA* IN INDONESIA

This key is based mainly on readily visible characters, not requiring dissection for visibility. Identifications may be verified by reference to structural details of genital bulb, etc., in the species descriptions.

1. Hypovalves of sternum 9 each bearing a lightly sclerotized projection from dorsal surface near mid-length (seen in lateral aspect) 2

   Hypovalves of sternum 9 without such projections 6

2. Hypovalves expanded basally and attenuate toward apex 3

   Hypovalves not expanded basally or not attenuate toward apex 4

3. Basal lobe of diststyle conspicuously divided into a proximal and a slightly larger distal protuberance (fig. 134) .... *flavicauda*

   Basal lobe of diststyle divided into a ventral portion and a more thickened dorsal portion (fig. 127) .... *borneensis*

4. Dorsal surface of hypovalves bearing long hairs (fig. 104) .... *crinita*

   Dorsal surface of hypovalves without long hairs 5

5. Apical band and pterostigmal band entire; dorsal sclerotized projections of hypovalves small, forming about a 25° angle with hypovalves (fig. 114) .... *sumatrana*

   Apical band almost absent, or reduced to spots; pterostigmal band much constricted near mid-length; dorsal sclerotized projections of hypovalves expanded, forming about a 35° angle with hypovalves (fig. 93) .... *fractura*

6. Hypovalves acuminate in apical half or abruptly narrowed in apical one-third 7

   Hypovalves gradually narrowed, rounded at apex 8

7. Posterior process of abdominal tergum 3 extending across about two-thirds length of tergum 4; hypovalves overlapped mesally near mid-length (fig. 67); pterostigmal band much reduced, with only conspicuous stigma remaining (fig. 66); general body color reddish brown; occurring in Java .... *angustiapicula*

   Posterior process of abdominal tergum 3 long, extending to mid-length of segment 6 (fig. 138); hypovalves separated throughout their length (fig. 139); pterostigmal band complete; general body color dark brown to brownish black; occurring in Borneo .... *spicata*

8. Wing markings almost obliterated, very faint smoky brown; basal lobe of diststyle without stout, black dorsal spines 9

   Wing markings conspicuous, dark smoky brown, even if only pterostigma remains; basal lobe of diststyle bearing stout, black dorsal spines (fig. 26) 10

9. Outer edges of hypovalves greatly infolded, the folded margins subparallel in ventral aspect (fig. 142); basal lobe of diststyle concave mesally, not flattened (fig. 145) .... *lieftincki*

   Outer edges of hypovalves slightly infolded, the folded margins not subparallel in ventral aspect (fig. 81); basal lobe of diststyle flattened, divided into ventral and dorsal parts (figs. 83, 87) .... *diloba*

10. Wings almost clear, hyaline, with only conspicuous pterostigma darkened (figs. 30-32) .... *hyalinata*

    Wing markings more complete, usually including apical and pterostigmal bands 11

11. Ventral and dorsal portions of basal lobe of diststyle distinctly separated, ventral portion flattened, rounded, directed ventrocaudad, not concealed by hypovalves (fig. 56); dorsal sur-

face of dorsal portion of lobe bearing three sizes of spines in three proximate groups (fig. 62) .... *umbonata*

Ventral and dorsal portions of basal lobe of dististyle either not clearly separated or not far apart, both usually concealed by tips of hypovalves, directed mesad; dorsal surface of lobe bearing two sizes of spines in two separated groups 12

12. Genital bulb uniformly dark brown to blackish brown; basal lobe of dististyle about as wide as long (fig. 47) .... *fuscicauda*

Genital bulb mostly yellowish brown to brown (brown throughout in a few individuals); basal lobe of dististyle much less wide than long (figs. 25, 26) .... *muelleri*

KEY TO FEMALES OF *NEOPANORPA* IN INDONESIA

Specific identification of females usually requires examination of the subgenital plate and the genital plate, the latter visible by simple dissection described earlier. The female of *diloba* is unknown; that of *flavicauda* has not been examined in detail.

1. Wing markings much reduced or nearly obliterated; markings may be only faint brown, or apical band may be reduced to a few spots, pterostigmal band either entire or interrupted near mid-length; or wings may be almost clear and hyaline, with only pterostigma remaining 2

Wing markings dark smoky brown, usually including entire apical band and pterostigmal band (includes *flavicauda* and probably *diloba*) 6

2. Pterostigmal band reduced to pterostigma only, or with only a small triangular extension behind stigma .. 3

Pterostigmal band faintly indicated, or entire or interrupted near midlength 4

3. General body color reddish brown; apical band usually present but not entire; axial portion of genital plate ovoid (figs. 66, 77) .... *angustiapicula*

General body color dark brown to blackish brown; apical band absent, wings almost clear-hyaline except for conspicuously darkened stigma; axial portion of genital plate forked anteriorly (figs. 30, 43) .... *hyalinata*

4. Wing markings faint brown, much reduced and almost obliterated; axial portion of genital plate forked anteriorly, without lateral lobes (figs. 141, 150) .... *lieftincki*

Wing markings dark smoky brown, distinct; apical band reduced to spots, pterostigmal band either entire or interrupted near mid-length; axial portion of genital plate ovoid with rounded lateral lobes 5

5. Pterostigmal band entire, with conspicuous proximal branch, distal branch obliterated or represented by a spot; subgenital plate narrowed smoothly to apex; lateral lobes of genital plate conspicuous, darkly sclerotized (figs. 101, 110) .... *crinita*

Pterostigmal band interrupted or greatly constricted near mid-length, proximal branch usually reduced to a spot; subgenital plate narrowed abruptly near mid-length; lateral lobes of genital plate inconspicuous, visible only by transmitted light (figs. 89, 99) .... *fractura*

6. Axial portion of genital plate forked anteriorly 7

Axial portion of genital plate not forked anteriorly 8

7. Tips of anterior branches (apodemes) of axial portion of genital plate thick, bent sharply laterad (fig. 64) .... *umbonata*

Tips of anterior branches of axial portion of genital plate slightly thickened, not bent (fig. 29) .... *muelleri*

8\. Axial portion of genital plate short, conical; bases of arms of plate expanded to form a darkly sclerotized, subquadrate plate cleft medially above apex of axial portion (fig. 51) .... *fuscicauda*

Axial portion of genital plate short but ovoid; bases of arms of plate not forming a subquadrate plate 9

9\. Genital plate without rounded lateral lobes (fig. 140) .... *spicata*

Genital plate with rounded lateral lobes 10

10\. Subgenital plate narrowed from near mid-length to apex, with pale median streak or zone (fig. 130) .... *borneensis*

Subgenital plate narrowed in posterior one-third, without pale median zone but with pale area just before apical notch (fig. 120) .... *sumatrana*

DESCRIPTIONS OF SPECIES

NEOPANORPA MUELLERI Group

Neopanorpa muelleri Weele, 1909

Panorpa müller i Weele, 1909.
Panorpa mülleri ungaranensis Weele, 1909.
Panorpa angustipennis; Weele, 1909 (misidentification).

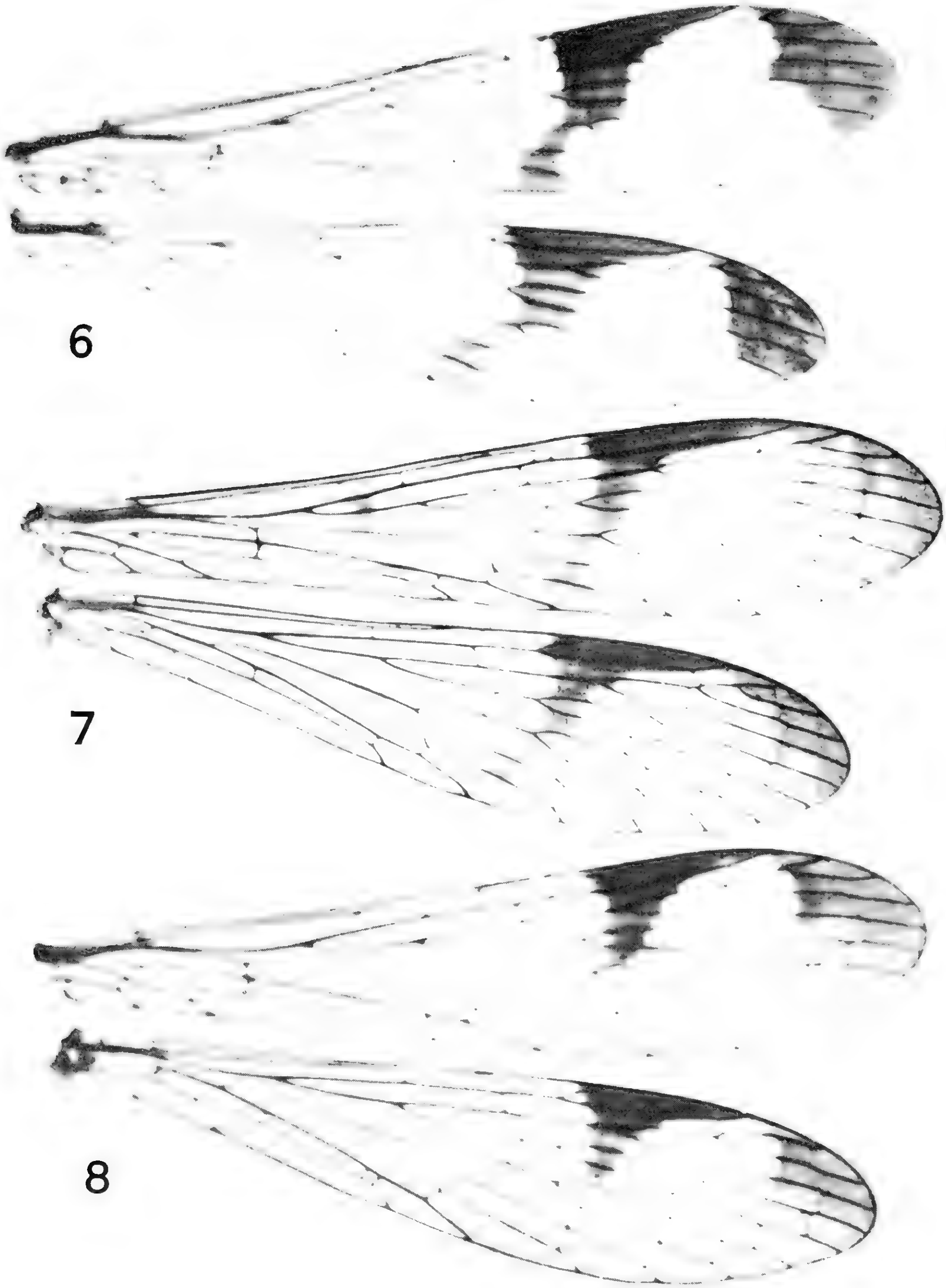
Van der Weele based his description of *muelleri* on one male and five females and that of *muelleri ungaranensis* on one male and four females. The male specimen of each of these is hereby designated as respective lectotype.

Head: Dorsum glossy blackish brown to black; frons below antennal sockets dark brown to blackish brown; rostrum reddish brown to dark brown anteriorly, yellowish brown to brown laterally or laterobasally; mouthparts reddish brown to dark brown, black on tips of palps in some specimens. Antennal scape yellowish brown (lectotype) to brown, pedicel brown (lectotype) to dark brown; flagellum dull dark brown basally, remainder dull blackish brown to black; 41 flagellomeres.

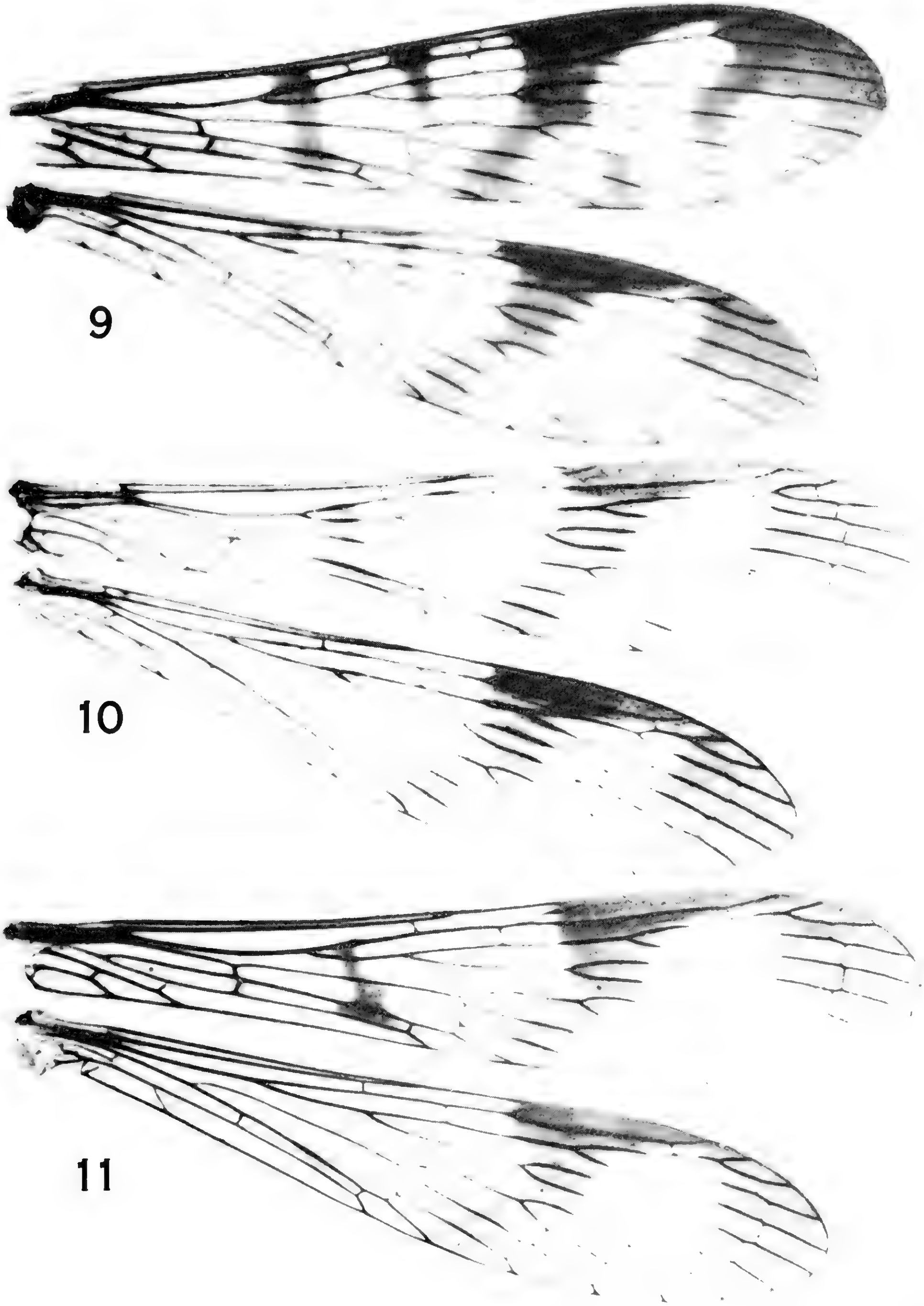
Thorax: Pronotum black, with 2-5 bristles at each side along anterior margin. Mesonotum and metanotum black, with small dark brown areas near wing bases in most specimens; paler on scutellum in some specimens. Pleura and coxae dingy yellowish brown, dark brown near wing bases in a few specimens, to dull dark brown throughout; femora yellowish brown to dark brown; tibiae and tarsi dark brown.

Wings (Figs. 6-14): Almost colorless, slightly iridescent, with smoky dark brown bands and spots. Apical band usually complete, with variously shaped proximal prominence in both fore and hind wings, or reduced to narrow darkened zone along apical margin and one or two other slender spots, usually along crossveins (six specimens). Pterostigmal band usually complete, narrowly joining apical band along costal margin, not forked in most specimens. Marginal spot conspicuous to small or absent. Basal band entire, of variable width, or reduced to one or two spots, or absent. Basal spot present or absent.

Abdomen of male: Terga 1-6 blackish brown to nearly black; sterna 2-5 yellowish brown to dull dark brown; segment 6 paler ventrally than dorsally. Segments 7-8 yellowish brown, reddish brown or dull dark brown. Posterior process of tergum 3 narrowly triangular, extending about half-way across tergum 4. Hypovalves of sternum 9 darkened or not (dark brown at least basally, where they are separated by a nearly circular space, below which is a semicircular, pale membranous area), widened at mid-length, often overlapping, paler and covered with long hairs apically (Fig. 15). Ninth tergum yellowish brown to dark brown, paler and shallowly emarginate apically. Cerci pale at base, dark brown at apex. Basistyles mostly dark



FIGS. 6-8. *Neopanorpa muelleri* (Weele), wings, showing variation in degree of pigmentation. 6, specimen from Central Java; 7, from West Java; 8, from East Java. See also FIGS. 9-14.



Figs. 9-11. *Neopanorpa muelleri* (Weele), wings, showing variation in degree of pigmentation. 9, specimen from Sumatra; 10, 11, specimens from West Java. See also Figs. 6-8, 12-14.

brown, lighter brown where concealed by hypovalves. Dististyles darkened basally, paler apically, or of uniform color throughout, outer margin slightly concave near base, abruptly curved near apex. Ventromesal concavity of basal lobes of dististyles medium (lectotype) to large, with pendant mesal and lower margins (Figs. 22, 24); 2-4 large, apically curved, black spines projecting from dorsal surface of basal lobes (Fig. 26); cluster of 8-25 apically curved smaller spines projecting from anterodorsal surface of basal lobes; inner pendant margins of basal lobes bearing hairs (Fig. 25). Aedeagus lightly sclerotized, reddish brown; ventral valves blunt, slightly divergent at apex, projecting a little beyond dorsal valves; lateral processes broad; dorsal parameres compressed, blade-like, projecting dorsad; ventral parameres absent (Figs. 17, 27).

Abdomen of female: Terga 1-6 dark brown to black, corresponding sterna sordid yellowish brown to dark brown. Segments 7-10 dark brown. Cerci black. Subgenital plate of sternum 8 (Fig. 28) yellowish brown to dark brown, notched and whitened apically, bearing setae on each side of notch and along outer margin, with or without laterobasal translucent, membranous areas. Axial portion of genital plate of variable length, anterior apodemes straight, only slightly divergent; arms of distal plate long, twisted basally (Fig. 29).

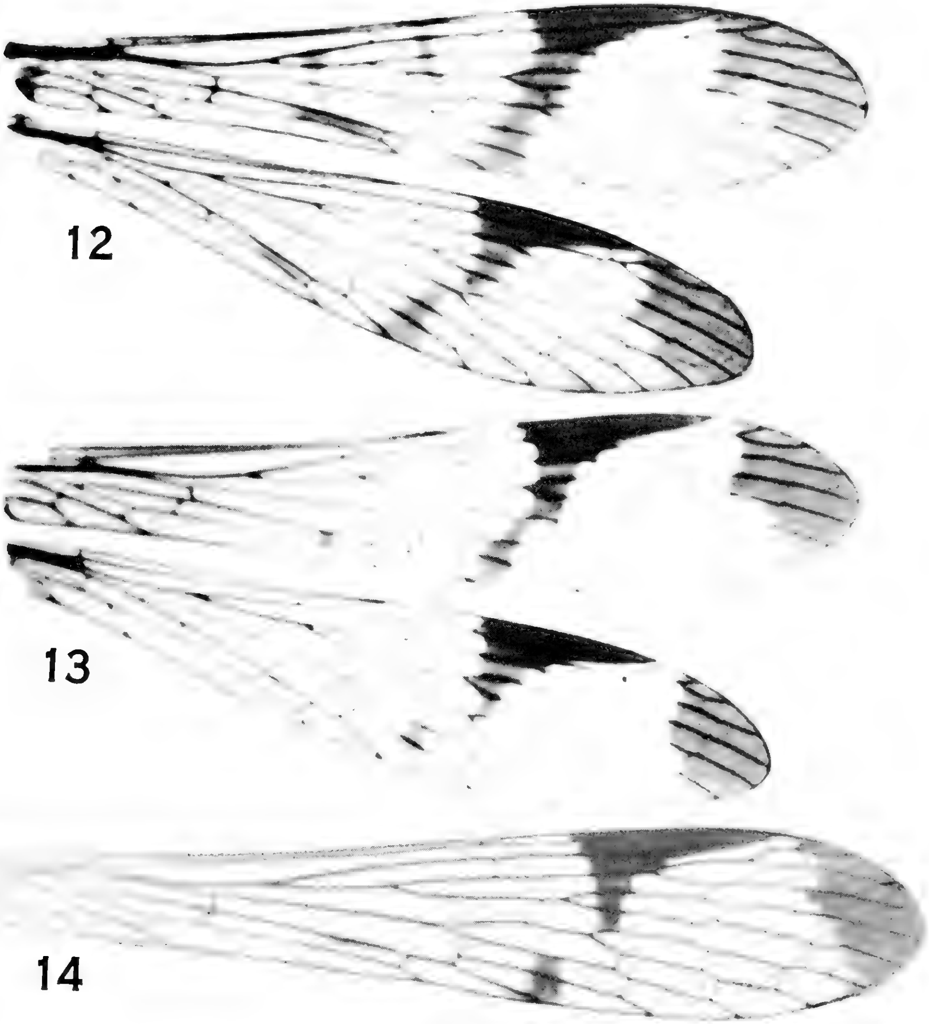
Body length: Male, 12.3-15.6 mm; female, 9.0-14.5 mm. *Length of fore wing:* Male, 12-13.6 mm; female, 7.9-14 mm.

Holotype: Male, collected at Bahia, Java (no date recorded), by S. Müller.

Additional specimens examined: West Java: 1 ♂, Mt. Malang, Tengeh, Djampangs, 200-800 m, Jan. 1940, Walsh; 2 ♂♂, the same data as above, except Dec. 1937, Walsh and 1931, Betrem; 13 ♂♂, 14 ♀♀, Omg. Sukanegara, Djampangs, 700-1000 m, 23 and 28 Dec. 1931, Lieftinck; 2 ♂♂, the same data as above, except 700 m, 19 April 1935, Toxopeus; 1 ♂, 1 ♀, Bibidjilan, Banten (district) south coast, low country, 1937, Walsh; 1 ♂, 2 ♀♀, Mt. Bunder, Salak, 6 April 1931, Lieftinck; 2 ♂♂, Depok, Karang, 26 Dec. 1920 and 17 Feb. 1924; 2 ♀♀, Preanger, 1500 m, Oct. 1937, Jacobson; 1 ♂, 1 ♀, Mt. Gedeh, 1200-1700 m, Dec. 1912 and 12 Dec. 1929, Jacobson; 17 ♂♂, 18 ♀♀, Mt. Gedeh, Tapos, 700-800 m, 1 Nov., Apr. 1933 and Aug. 1936, Kalshoven; 1 ♀, same data as above, except 16 Oct. 1932, Lieftinck; 3 ♂♂, 6 ♀♀, Mt. Gedeh, Tapos, 1200 m, without date, Kalshoven; 4 ♂♂, 4 ♀♀, Mt. Guntur, Kamodjang, 1400 m, May 1935 and Sept. 1938, Overbeck; 3 ♂♂, 5 ♀♀, Mt. Karang, Bantam, 800 m, 27 May 1931, Lieftinck; 1 ♀, the same data as above, except 1000 m, Oct. 1930, Paine; 8 ♂♂, Kawa Kamodjan, near Garut, Mt. Guntur, 1450 m, May 1935, Overbeck; 1 ♀, Mt. Madiun, Java, 1200 m, 10 Jan. 1930, Leeuven; 1 ♀, Mt. Manglajang, Preanger, 1400 m, 11 May 1931, Toxopeus; 2 ♂♂, 1 ♀, Mt. Megamendung, 800-1000 m, 27 March and 25 Sept. 1932, Lieftinck; 1 ♂, Pangerango, Oct. 1908, Jacobson; 1 ♀, Pateungteum, 1300 m, 24 Nov. 1935, Toxopeus; 1 ♂, 2 ♀♀, Patjet, Mt. Bésér, 1300 m, 30 Sept. 1934 and 10 March 1940, Lieftinck; 1 ♂, 1 ♀, Pelabuanratu (Wynkoops Bay), southern West Java, low country, Nov. 1935; 1 ♀, Pantjar Mts., Mt. Gedeh, 1500 m, 8 July 1931, Tutbing; 1 ♂, Preanger, Piepers; 1 ♀, Radjamandala, 335 m, June 1935, Jacobson; 2 ♂♂, Selabintana, near Sukabumi, Mt. Gedeh, 1000 m, Dec. 1938, Walsh; 5 ♂♂, 15 ♀♀, Sukabumi; 1 ♂, 3 ♀♀, Mt. Tangkubanprahu (Tangkuban Prahu), Preanger, 1333-1700 m, 4 Jan. 1924 and Jan. 1936, Drescher; 4 ♂♂, 5 ♀♀, the same data as above, except 1400 m, 3 Nov. 1940, Olthof; 2 ♂♂, 3 ♀♀, Tjibodas, Mt. Gedeh, 1400 m, 22 May 1935, Vecht; 3 ♀♀, the same data as above, except 1550-1700 m, 27 July 1930 and 28 March 1932, Lieftinck; 1 ♀, Tjiomas, Warung Loa, Salak, 9 Nov. 1932, Lieftinck; 1 ♂, 2 ♀♀, Tjipeundeng, Leuwibiang, 900 m, 22 July 1934, Lieftinck; 5 ♂♂, 1 ♀, Tjisarua, Mt. Gedeh-complex, 1050 m, 6 July 1930, Lieftinck; 9 ♂♂, 1 ♀, Tjisarua, Mt. Panggerango, Mt. Gedeh, 1000-1400 m, 27-30 Aug. 1931, 2 Jan. 1936, 30 May 1937, and 16 April 1950, Lieftinck; 3 ♂♂, Mt. Tjisura, Tengah, Djampangs, 500 m, Sept. 1932, Walsh; 2 ♀♀, Ungaran Gunung, 800-1200 m, Oct. 1909, Jacobson.

Central and North Java: 2 ♂♂, 3 ♀♀, Kaliurang, Djokjakarta, C. J., low country, Nov. 1936, Overbeck; 2 ♂♂, Mt. Muria, Macrodjambangan, N. J., 1000 m, 14 and 17 Dec. 1935, Walsh; 3 ♂♂, 10 ♀♀, Mt. Raung, Bajukidael, C. J., 500-800 m, 8 May, Sept. and Dec. 1932, Lucht; 4 ♂♂, 4 ♀♀, Mt. Telamojo, res. Kedu, C. J., 1200-1400 m, 29 Oct. 1939, Lieftinck; 2 ♂♂, 4 ♀♀, Tjolo, Muria Mts., C. N. J., 800 m, 20 and 24 Oct. 1939, Lieftinck.

East Java: 6 ♂♂, 9 ♀♀, Blawan, Idjen Plateau, 950 m, 12 Dec. 1934, 15 March and 26 Dec. 1935, 5 May and 13 Dec. 1936, Lucht; 1 ♂, 1 ♀, Mt. Kendeng, 2000 m, 13 Nov. 1933, Lucht; 2 ♂♂,



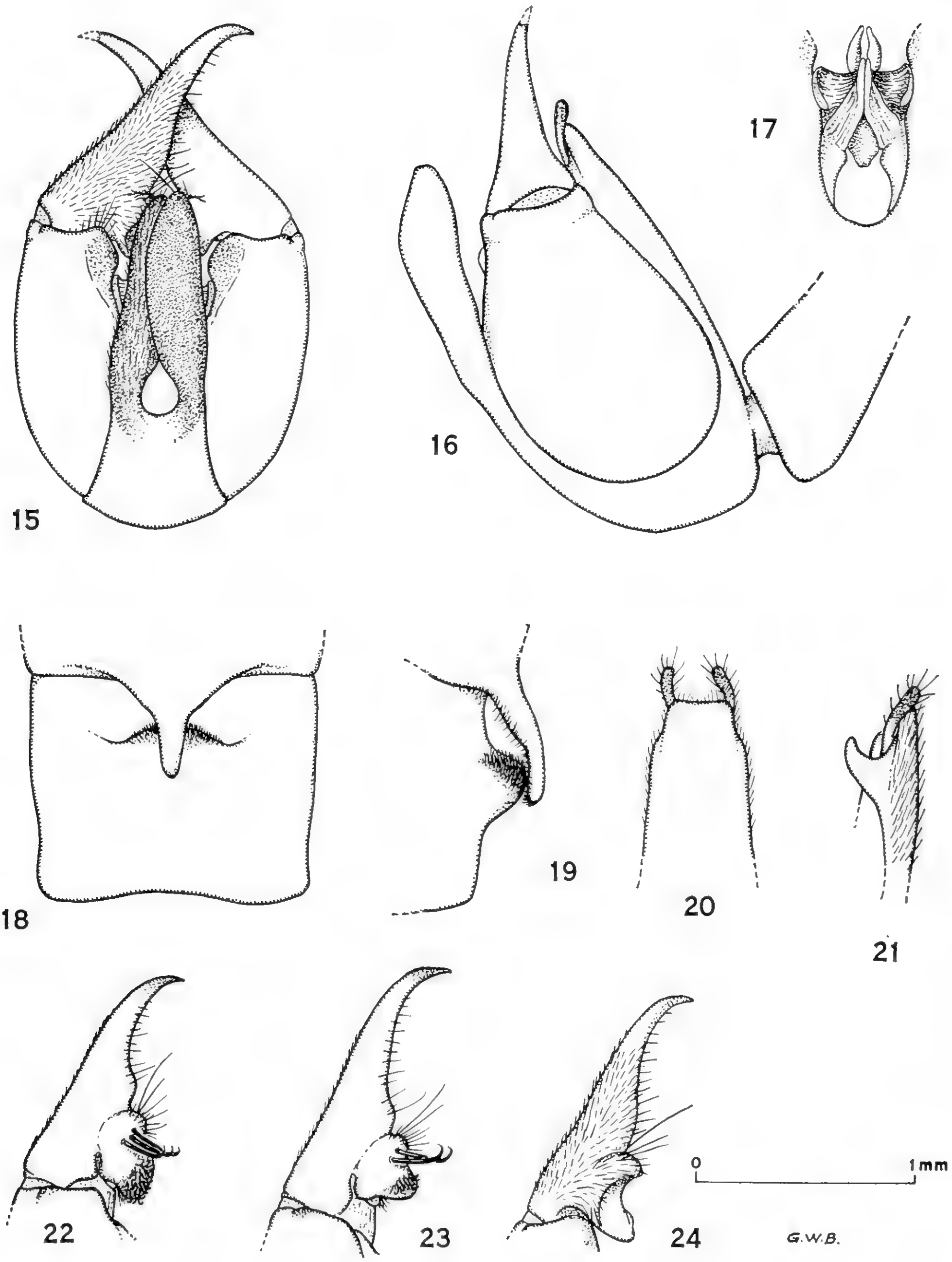
FIGS. 12-14. *Neopanorpa muelleri* (Weele), wings, showing variation in degree of pigmentation. 12, specimen from West Java. 13, specimen from Central Java; note broken pterostigmal band in hind wing, a character used by Weele in differentiating subspecies *ungaranensis* from typical *muelleri*. 14, fore wing only of specimen showing broken pterostigmal band. See also FIGS. 6-11.

1 ♀, Ongop-ongop, Idjen Mts., 1600-1850 m, May 1924, Dammerman and 27 Dec. 1935, Toxopeus.

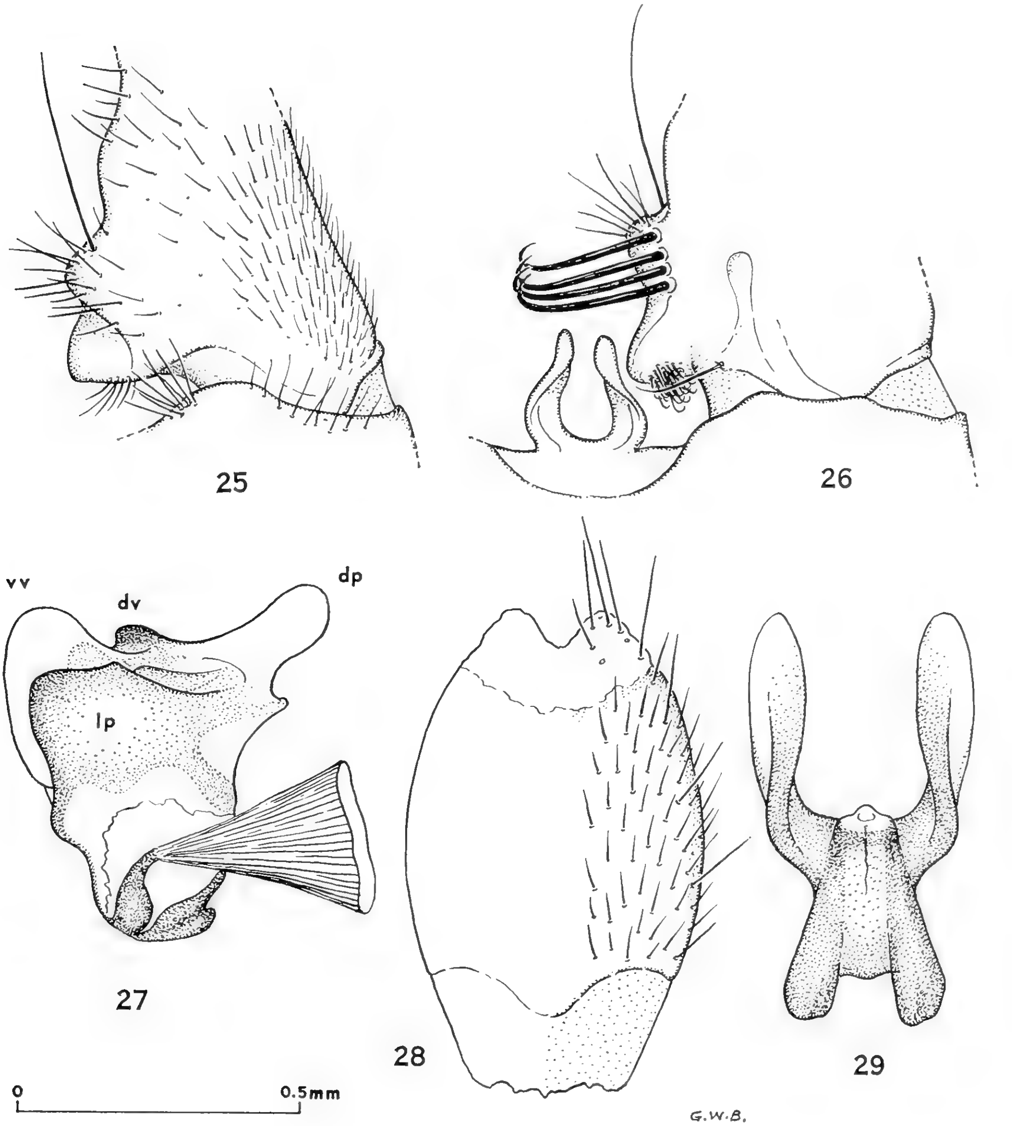
Sumatra: 1 ♂, Air Tarbis, Dec. 1913, Jacobson; 4 ♀♀, Brastagi, northeastern Sumatra, 950-1400 m, 12 Nov. 1950, Lieftinck; 1 ♂, 4 ♀♀, Giesting, Mt. Tanggamus, southwestern Lampongs, southern Sumatra, 800 m, 27 Dec. 1934, Lieftinck; 1 ♂, 2 ♀♀, Serapai Kur., July 1915, Jacobson; 2 ♂♂, Suban Ajam, July 1916, Jacobson; 4 ♂♂, 3 ♀♀, Tandjunggadang (west coast), 1000-1200 m, Oct. 1925 and Feb. 1926, Jacobson.

Neopanorpa muelleri is the commonest Indonesian *Neopanorpa,* with the broadest range of habitats and of vertical or horizontal distribution. It ranges from low country to above 2000 m, throughout the islands of Java and Sumatra, and possibly on Halmahera. This relatively great range probably has helped produce some of the complicated variation within this species.

The wing markings vary (Figs. 6-14) from clear except for the pterostigmal band and reduced apical band to a complete pattern including apical band, pterostigmal



FIGS. 15-24. *Neopanorpa muelleri* (Weele), structural details of male. 15, genital bulb of lectotype, ventral aspect. 16, same, right lateral aspect. 17, aedeagus, lectotype, ventral aspect. 18, abdominal terga 3 and 4, showing notal organ, dorsal aspect, reconstructed from lectotype. 19, same, left lateral aspect. 20, ninth abdominal tergum, lectotype, dorsal aspect. 21, same, right lateral aspect. 22, right dististyle, specimen from Sumatra, dorsal aspect, showing only three large spines and many smaller spines on elongate basal lobe. 23, right dististyle, specimen from Sumatra, dorsal aspect, showing only two large spines and smaller group of small spines on shorter basal lobe. 24, left dististyle, male lectotype of subspecies *ungaranensis* (Weele), ventral aspect, showing prolonged anterior (ventral) portion of basal lobe.



FIGS. 25-29. *Neopanorpa muelleri* (Weele), deatils of male and female genitalia. 25, base of right dististyle, male lectotype, ventral aspect. 26, base of left dististyle and dorsal parameres, male lectotype, dorsal aspect. 27, aedeagus, male from Ongop-ongop, East Java, right lateral aspect. 28, subgenital plate of female, ventral aspect. 29, genital plate of female, ventral aspect.

band, marginal spot, basal band and basal spot. The apical band varies from a reduced, incomplete type to large with conspicuous proximal prominence or enclosing a small posterior pale spot. The pterostigmal band may be either complete or incomplete, broad or narrow, forked posteriorly or not. The distal branch may be complete or isolated as a spot. The basal band may be entire, reduced to one or two spots, or absent. Marginal and basal spots are either present or absent. Color variation in *N. muelleri* is not affected by altitude (*i.e.,* the dark form both in body and wings is found both in the mountains and in the lowlands). Hypovalves and dististyles may be darkened or not. The basal lobe of the dististyle has a medium-sized concavity (or cup) on all Javanese forms of *muelleri,* but bears a larger cup in all Sumatran specimens. The number of smaller, curved spines on the anterior dorsum of the basal lobe varies from as few as 8 on most Javanese forms to 25 on most Sumatran forms (Fig. 22).

Weele (1909) and some other authors thought certain of these variants were different species, *Neopanorpa muelleri* and *N. angustipennis.* We found no specimens from Indonesia having the same structure and coloration as the holotype of *angustipennis,* supporting the view (Byers, 1965) that the type of *angustipennis* is from Tenasserim (peninsular Burma), not Java. Weele (1909) also described *ungaranensis* as a subspecies of *muelleri,* based on the smaller size of the former and its more reduced wing pattern, but Karny (1923) dissented. As Karny did, we find that variation in body size and color and wing markings occurs in a distribution that cannot sensibly be geographically subdivided, and we judge the nominal subspecies *ungaranensis* to be a variant of *muelleri.* Once, we thought these might be a group of very similar species (and initially sorted these specimens into four "species"), but we prefer the more conservative view that these variant forms represent instead one widespread, variable species.

Neopanorpa hyalinata Esben-Petersen, 1913

Neopanorpa hyalinata Esben-Petersen, 1913: 227-228.

Campodotecnum falcatum Navás, 1914.

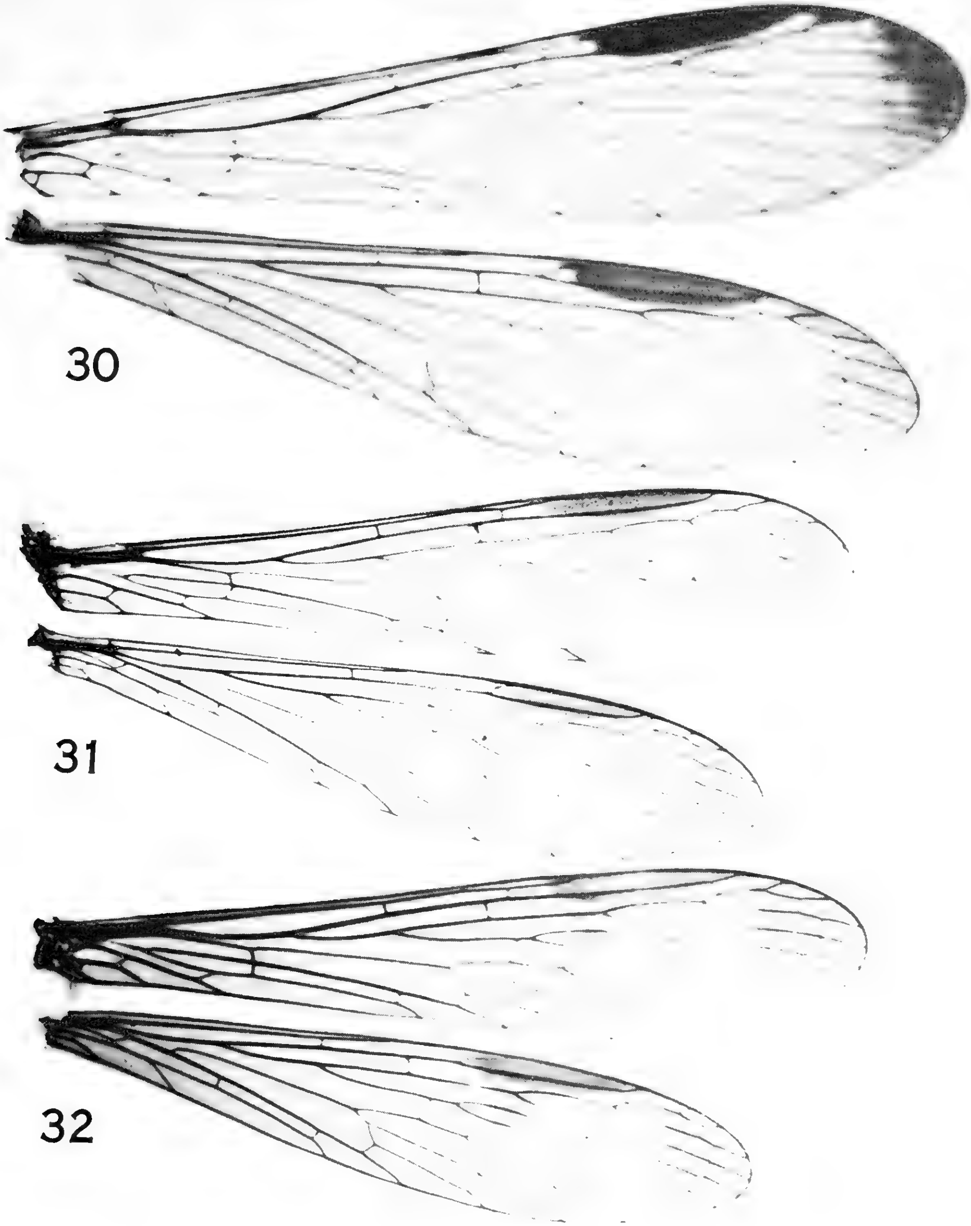
Esben-Petersen based his description of *hyalinata* on the male holotype, female allotype, and one male, one female paratypes.

Head: Dorsum glossy black; frons below antennal sockets dark brown; rostrum reddish brown anteriorly, yellowish brown laterally and brown apically; mouthparts brown with tips of palps dark brown. Antennal scape brown, pedicel dark brown, basal flagellomeres dull brown, others dull dark brown, flagellum with 44 segments (extreme apex broken in holotype).

Thorax: Pronotum brownish black to black (holotype), bearing 3-4 bristles at each side along anterior margin. Mesonotum and metanotum black. Pleura and coxae pale yellowish brown to sordid brown (holotype). Femora sordid yellowish brown (holotype) to dull dark brown; tibiae brown; tarsi dark brown.

Wings: (Figs. 30-32): Almost colorless, slightly iridescent, with spots dark smoky brown. Apical band greatly reduced, from almost absent to slightly tinged with light brown on distal margin of wing. Pterostigmal band usually absent, pterostigma conspicuous, long and very dark. Behind inner end of pterostigma a small, dark brown spot connected to pterostigma in some specimens. Marginal spot, basal band and basal spot absent.

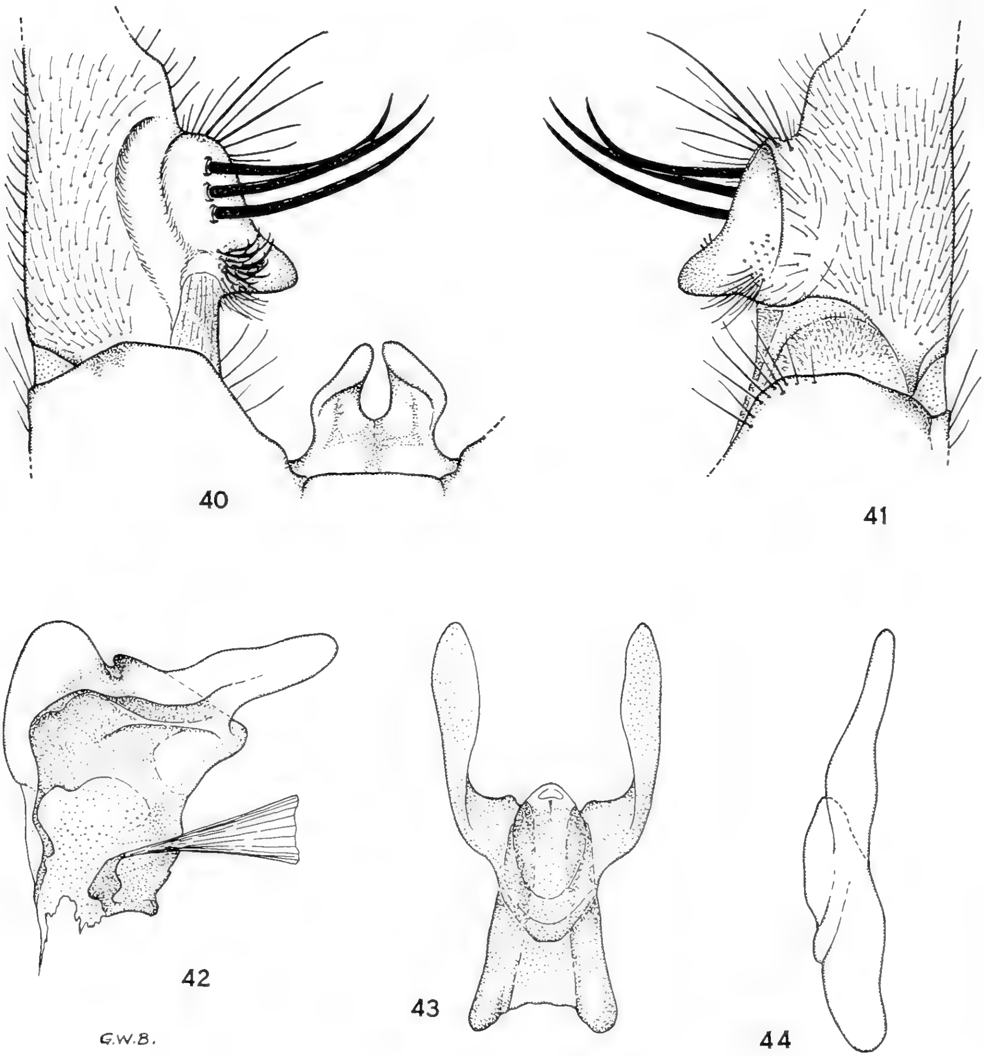
Abdomen of male: Terga 1-5 brownish black, corresponding sterna yellowish brown to dark brown. Segment 6 black dorsally, blackish brown ventrally. Segments 7-9 brownish black. Posterior process of tergum 3 narrowly triangular (Fig. 36). Hypovalves of sternum 9 widened and overlapping near mid-length, bearing a few long hairs, darkest near base, paler in apical half, narrowed to pointed apex. Tergum 9 pale and emarginate apically. Dististyles slender, dark brown basally, reddish brown distally, outer margins slightly concave near mid-length, abruptly curved near tips. Basal lobes of dististyles concave ventrally, bearing long pale hairs on distal margin and short pale hairs on anterior margin; each with 3-4 long, apically curved, stout, black spines on mesodorsal surface (4 in male syntype), about



FIGS. 30-32. *Neopanorpa hyalinata* Esben-Petersen, wings, showing variation in wing pattern. 30, typical pattern; note long, dark pterostigma; male, from East Java. 31, male, from East Java. 32, female, from East Java; this pattern also occurs in males.

6 smaller, apically curved spines on anterodorsal surface (Fig. 40). Ventral valves of aedeagus broad, extending a little beyond dorsal valves (Figs. 33, 42); lateral processes broad; ventral parameres absent, possibly represented by sclerotized bands in membrane below lateral processes (Figs. 33, 42); dorsal parameres conspicuous, blade-like, apices directed dorsomesad (Fig. 42).

Abdomen of female: Terga 1-6 black, terga 7-10 blackish brown; sterna



FIGS. 40-44. *Neopanorpa hyalinata* Esben-Petersen, details of male and female genitalia. 40, base of right dististyle and dorsal parameres, dorsal aspect; male from Malang, Java. 41, same as 40 except ventral aspect without parameres. 42, aedeagus, right lateral aspect. 43, genital plate, ventral aspect; female from East Java. 44, same as 43, right lateral aspect.

male, Nongkodjadjar, Java, Jan. 1911, Jacobson, in Rijksmuseum van Natuurlijke Historie, Leiden; 1 ♂, 1 ♀, (type specimens of *Campodotecnum falcatum* Navás), Java, 1891, Fruhstorfer, in Naturhistorisches Museum, Wien. Additional specimens: 5 ♂♂, 4 ♀♀, Tengger Mts., Nongkodjadjar, East Java, 1200 m, 2 May 1938, Walsh; 2 ♂♂, 1 ♀, Djunggo, Malang, Java, 22 Dec. 1931, Betrem; 1 ♂, 1 ♀, Ongop-ongop, Idjen, Java, 1850 m, May 1924, Dammerman; 2 ♀♀, Sumberbrantas, Mt. Ardjuno, East Java, 1500 m, Jan. 1936, Overbeck; 2 ♀♀, Bodjongkalong, Djampangs, West Java, 300 m, June 1938, Walsh.

We place this species in the *muelleri* group because of the large spines on the basal lobes of the dististyles and other significant details of the male and female genitalia. It is easily recognized by the hyaline, slightly marked wings, for which the species is named, by its conspicuous pterostigma, and by the somewhat more blackish body color than that seen in other species. We find that the small spot below the inner end of the pterostigma is also present in some females (absent according to Esben-Petersen, 1913).

Neopanorpa fuscicauda, new species

Description based on 2 males, 5 females, pinned.

Head: Dorsum glossy black; frons below antennal sockets dark brown; rostrum brown anteriorly, yellowish brown laterally; mouthparts brown. Antennal scape and pedicel brown, flagellum dull dark brown with 41 segments (both antennae missing from holotype).

Thorax: Pronotum black, bearing 5 bristles at each side along anterior margin. Mesonotum and metanotum black. Pleura and coxae yellowish brown (holotype) to reddish brown or blackish brown (2 females). Femora yellowish brown; tibiae and tarsi brown (holotype) to dark brown.

Wings (Fig. 45): Almost colorless, slightly iridescent, with markings dark smoky brown. Apical band incomplete posteriorly, with small proximal prominence in one female. Pterostigmal band complete but not forked posteriorly, narrowly joined to apical band along anterior margin, narrow in males, broader in females. Marginal spot, basal band and basal spot usually absent (marginal spot present and basal band represented by a spot between end of Cu_1 and Cu_2 in one female).

Abdomen of male: Terga 1-5 brownish black; sterna 2-5 sordid yellowish brown. Segment 6 brownish black. Segments 7-8 brown basally, dark brown distally. Segment 9 blackish brown (holotype) to dark brown. Posterior process of tergum 3 narrowly triangular (as in *muelleri*), extending about half-way across tergum 4. Hypovalves of sternum 9 blackish brown (holotype) to dark brown at base, remainder grayish brown, with inner margins separated or slightly overlapping near mid-length, outer margins infolded dorsally, the folded edges subparallel in ventral aspect (Fig. 48). Tergum 9 slightly emarginate apically (Fig. 49). Basistyles blackish brown (holotype) to dark brown; dististyles blackish brown (holotype) to dark brown basally, brown apically. Basal

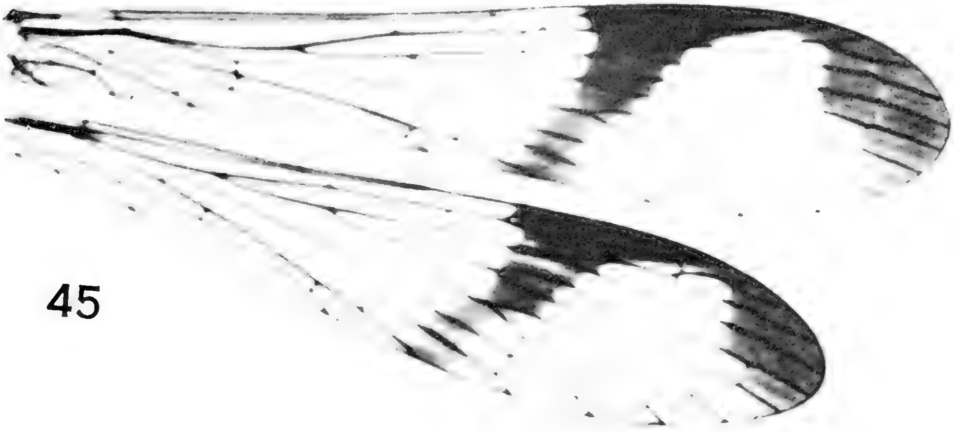
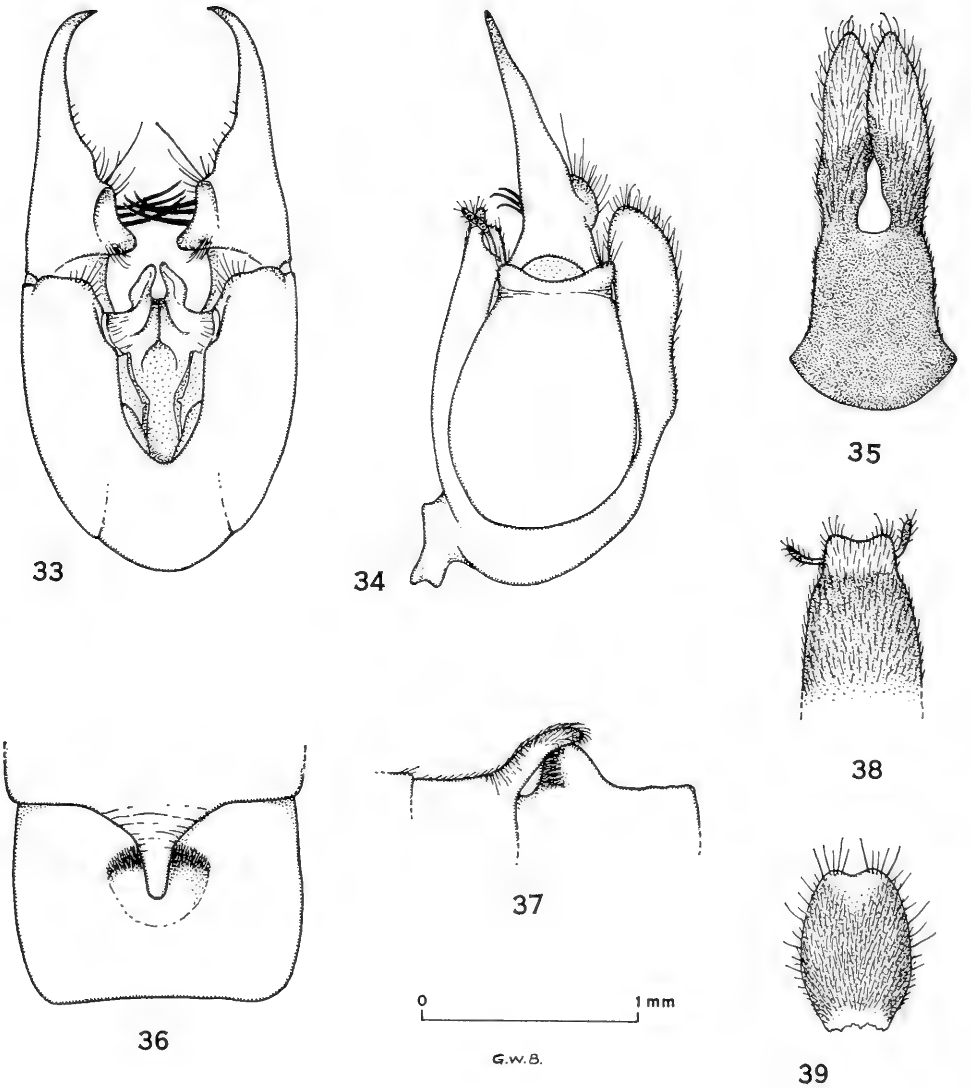


FIG. 45. *Neopanorpa fuscicauda,* new species, wings of female paratype.

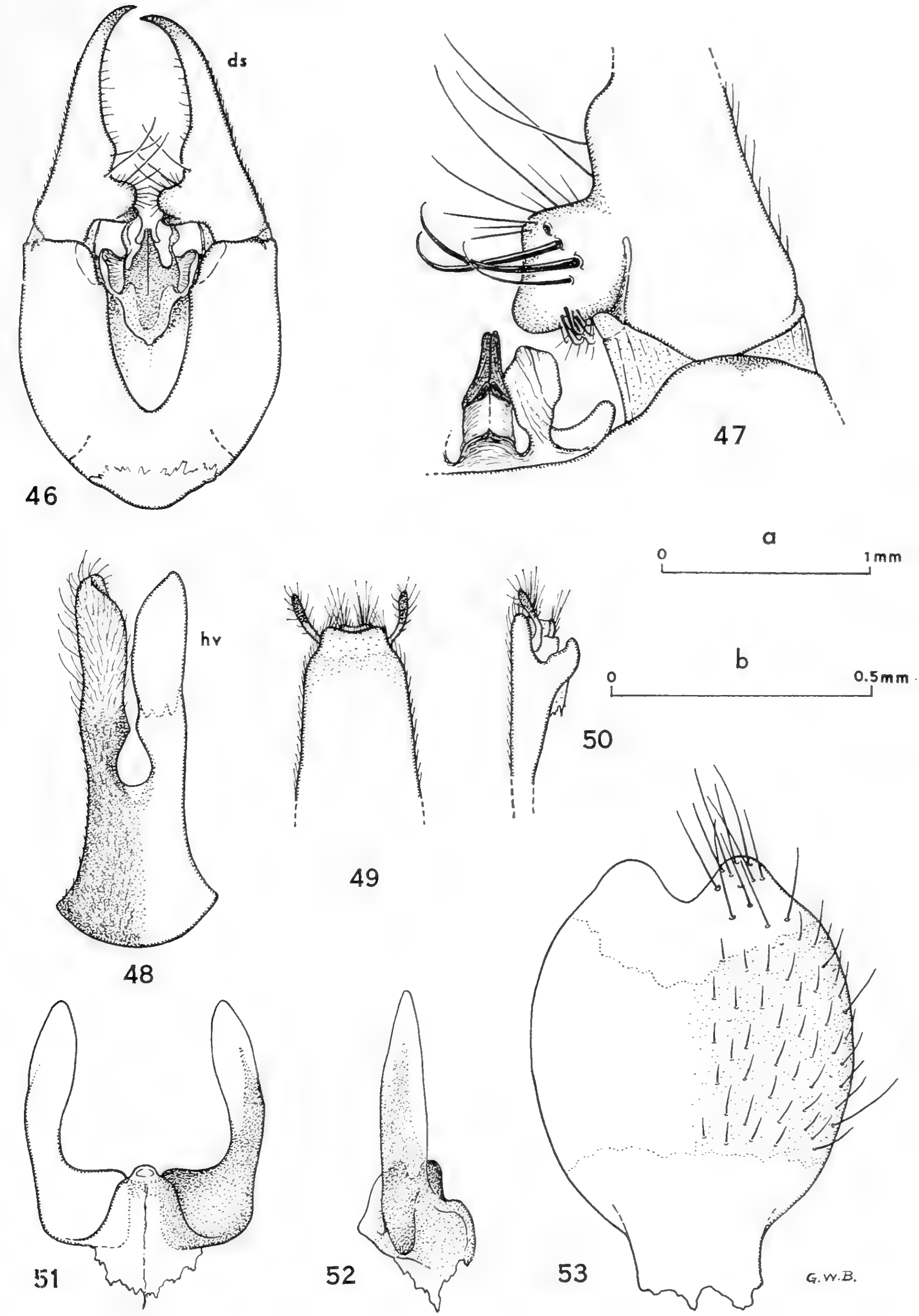


FIGS. 33-39. *Neopanorpa hyalinata* Esben-Petersen, structural details. 33, genital bulb, ventral aspect, ninth sternum removed to show aedeagus; male from Malang, Java. 34, same as 33, left lateral aspect, ninth sternum in place. 35, ninth abdominal sternum and hypovalves, ventral aspect, shaded to indicate color pattern; male from Malang, Java. 36, reconstruction of abdominal terga 3 and 4, showing notal organ, dorsal aspect; male holotype. 37, same as 36, left lateral aspect. 38, ninth abdominal tergum, dorsal aspect; male from Malang. 39, subgenital plate, ventral aspect; female from East Java.

1-5 light brown (allotype) to sordid brown, sterna 6-7 brown to dark brown. Subgenital plate of sternum 8 dark brown, slightly notched and whitish apically (Fig. 39), bearing long setae at each side of notch and on lateral margins, membranous basally. Axial portion of genital plate elongate, arms broad and twisted basally (Fig. 43).

Body length: Male, about 13-15 mm; female, about 10-12 mm. *Length of fore wing:* Male, 12.8-13.5 mm (holotype 13.2 mm); female, 12.1-12.9 mm.

Holotype: Male, and allotype, fe-



FIGS. 46-53. *Neopanorpa fuscicauda,* new species, details of male and female paratypes. 46, genital bulb, ventral aspect, with sternum 9 removed to show aedeagus; ds—dististyle. 47, base of left dististyle and dorsal parameres, dorsal aspect. 48, ninth abdominal sternum and hypovalves (hv), ventral aspect, partly shaded to indicate color pattern. 49, ninth abdominal tergum, dorsal aspect. 50, same as 49, left lateral aspect. 51, genital plate of female, ventral aspect. 52, same as 51, right lateral aspect. 53, subgenital plate, ventral aspect, partly shaded to indicate color pattern. Scale a—FIGS. 46, 48-50; scale b—FIGS. 47, 51-53.

lobes of dististyles subrectangular, with long hairs on posterior surface, 2-3 stout, black, apically curved spines projecting from mesodorsal surface, and about 8 smaller, apically curved spines on anterodorsal surface; some pale hairs arising on anterior margin (Fig. 47). Ventral valves of aedeagus long and slender, projecting beyond dorsal valves in dorsal aspect (Fig. 47); lateral processes deeply concave; ventral parameres absent; dorsal parameres well developed, broadly triangular, mesally concave blades, projecting somewhat dorsad and connecting ventrally to sides of ventral valves (Fig. 46). (Note that entire aedeagus as shown in Fig. 46 may be atypically displaced upward, or caudad).

Abdomen of female: Terga 1-6 black; sterna 2-5 yellowish brown to dark brown (allotype), sternum 6 dark brown. Terga 7-9 brownish black, corresponding sterna dark brown. Cerci dark brown. Subgenital plate of sternum 8 short and broad, mostly dark brown, notched and with large whitish area apically, bearing several setae at each side of notch, otherwise sparsely hairy; basal portion slender, pale, membranous. Axial portion of genital plate very short, conical; arms slender, sclerotized on outer basal margins, translucent on inner margins (Fig. 51); base of each arm expanded to form a subquadrate plate, the two plates separated by a median cleft above apex of axial portion and each darkly sclerotized adjacent to axial portion (Fig. 51).

Body Length: Male, about 12-15 mm (holotype 15 mm); female, about 9-15 mm (allotype 11 mm). *Length of fore wing:* Male, 12.2-13 mm (holotype 13 mm); female, 12.3-13.3 mm (allotype 13 mm).

Holotype: Male, Tengger Mts., Nongkodjadjar, East Java, 1200 m, 5 May 1938, Walsh. Allotype, 1 ♂ and 4 ♀ paratypes, same data as holotype; 1 ♀, same data as holotype, except Jan. 1911, Jacobson. Holotype, allotype and 3 ♀ paratypes in the Rijksmuseum van Natuurlijke Historie, Leiden; 1 ♂, 1 ♀ paratypes in the Snow Entomological Museum, The University of Kansas.

We place this species in the *muelleri* group because of its wing pattern and the spiniferous basal lobes of the male dististyles. It can be easily recognized by its dark brown to blackish brown genital bulb, from which the species is named (also found in some *muelleri* but not as uniformly as *fuscicauda*) and the characteristic dorsal parameres of the aedeagus (extending ventrally alongside the ventral valves). Females can be identified by the unique structure of the genital plate (base of each arm expanded to form a subquadrate plate).

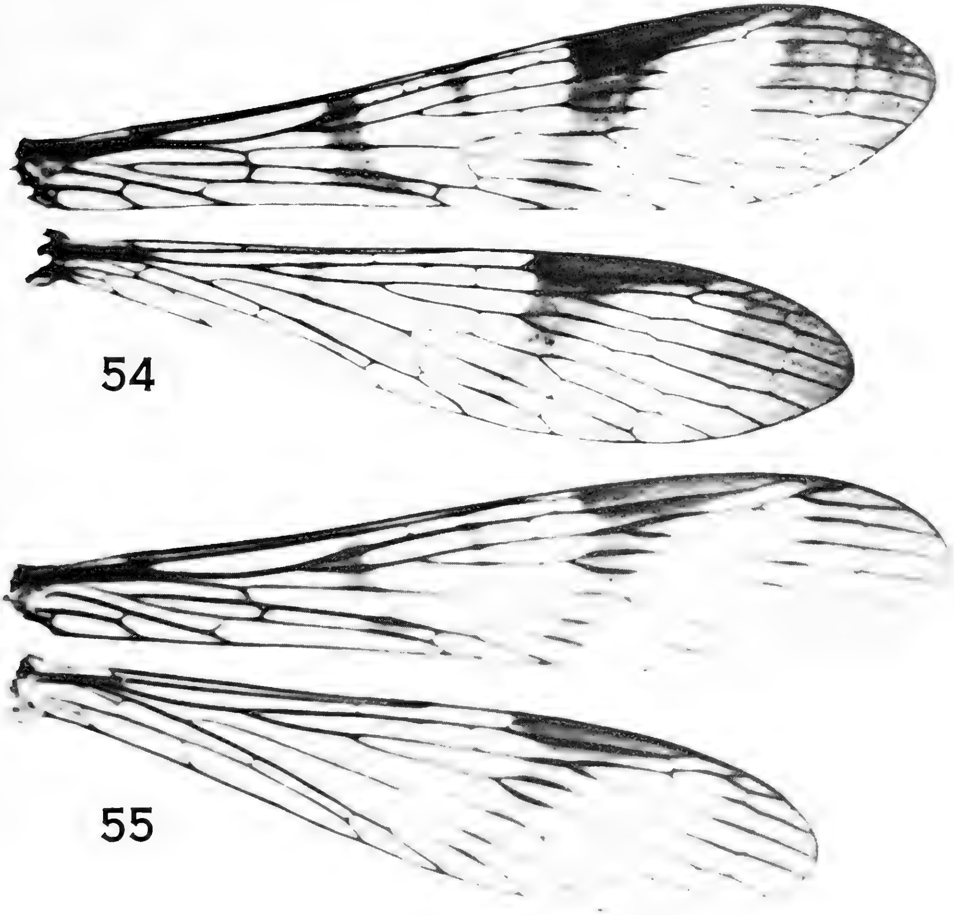
Neopanorpa umbonata, new species

Description based on 15 males, 21 females, pinned.

Head: Dorsum glossy brownish black (holotype) to black; frons below antennal sockets dark brown; rostrum brown with yellowish brown median and lateral stripes; mouthparts brown except tips of palps dark brown. Antennal scape yellowish brown, pedicel brown, flagellum mostly dull dark brown, brown at base, with 42 flagellomeres.

Thorax: Pronotum brownish black, with 3-4 bristles at each side along anterior margin. Mesonotum and metanotum brownish black. Pleura mostly yellowish brown (holotype) to reddish brown, dark brown on episternum near wing base. Coxae yellowish brown (holotype) to reddish brown. Femora yellowish brown; tibiae and tarsi dark brown.

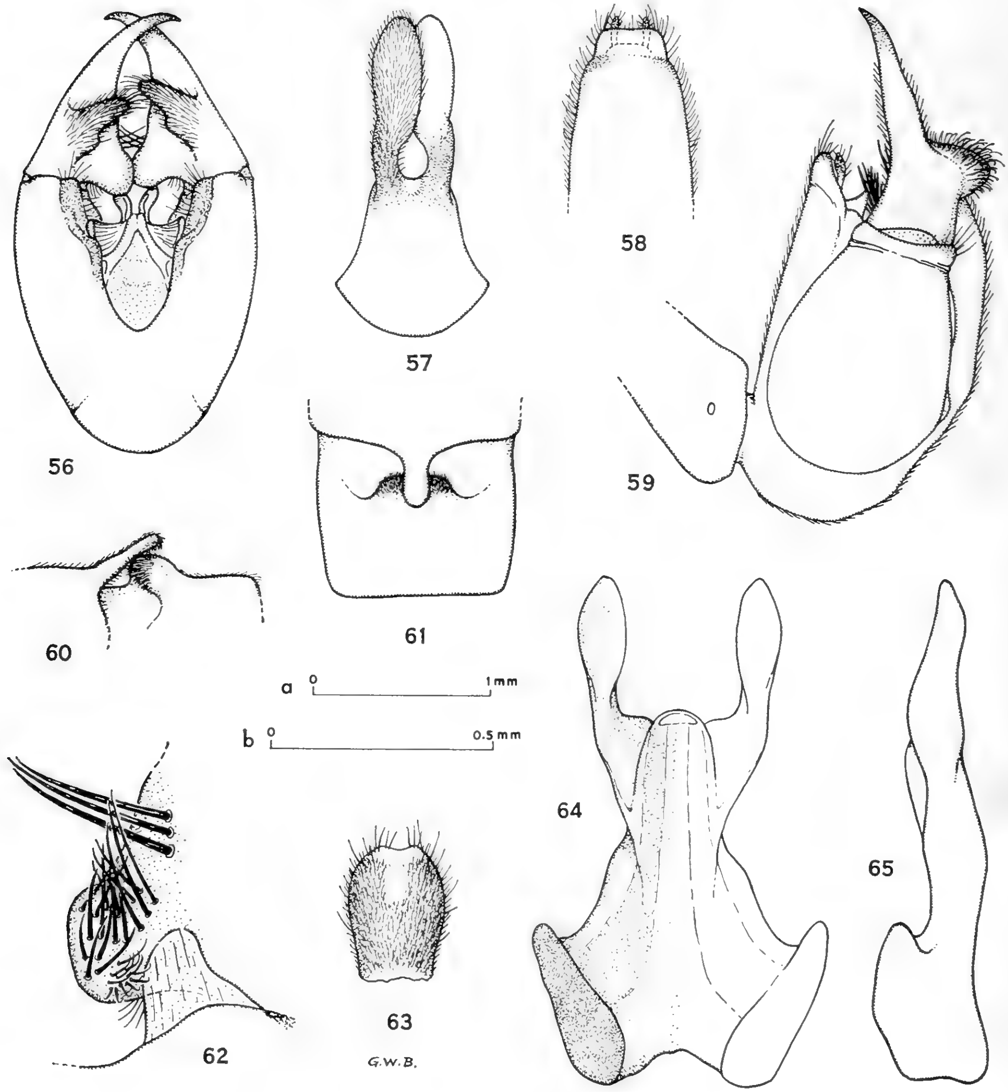
Wings (Figs. 54, 55): Nearly colorless, slightly iridescent, with bands and spots smoky dark brown. Apical band interrupted posteriorly or including variously shaped clear areas. Pterostigmal band with complete proximal branch, dis-



FIGS. 54-55. *Neopanorpa umbonata,* new species, wings of male paratypes from two localities in southern Sumatra, showing variation in pigmentation. 54, male from Tandjong Sakti. 55, male from Wai Lima, Lampongs.

tal branch reduced to spot on posterior wing margin. Marginal spot small (holotype) to conspicuous. Basal band slender, usually interrupted in cell M (holotype), complete in some paratypes. Basal spot absent.

Abdomen of male: Terga 1-3 brownish black, terga 4-5 dark brown; sterna 2-5 usually yellowish brown. Segment 6 dark brown. Segments 7-9 brownish yellow. Posterior process of tergum 3 (Fig. 61) narrow with subparallel sides, extending about half-way across tergum 4. Hypovalves of sternum 9 dark brown at base to brown at tip, inner margins overlapped near mid-length, tips usually concealed by basal lobes of dististyles. Tergum 9 (Fig. 58) narrowed just before truncate apex, elongate, nearly concealing cerci. Basistyles slender, glabrous and darkly sclerotized mesally. Dististyles dark brown, their outer margins generally straight in basal two-thirds, then smoothly curved toward tips (Fig. 56). Basal lobes of dististyles divided into thin, expanded posteroventral and anterodorsal portions together forming a large cup-like recess (Fig. 56); posteroventral portion directed ventrocaudad, usually covering tips of hypovalves, covered with long hairs; more



FIGS. 56-65. *Neopanorpa umbonata,* new species, structural details of holotype and male and female paratypes. 56, genital bulb of male, ventral aspect, ninth sternum removed to show aedeagus. 57, ninth abdominal sternum and hypovalves, ventral aspect, partly shaded. 58, ninth abdominal tergum, dorsal aspect, most hairs omitted. 59, genital bulb, left lateral aspect; holotype. 60, abdominal segments 3 and 4, left lateral aspect, showing notal organ; holotype. 61, same as 60, dorsal aspect. 62, basal lobe of left dististyle, dorsal aspect. 63, subgenital plate of female, ventral aspect. 64, genital plate of female, ventral aspect. 65, same as 64, right lateral aspect. Scale a—FIGS. 56-61, 63; scale b—FIGS. 62, 64-65.

Wings (Fig. 66): Tinged with yellow and slightly iridescent, markings smoky brown. Apical band incomplete, bearing variously shaped proximal prominence in some paratypes, reduced almost to a light, small spot in one (teneral) paratype. Pterostigmal band incomplete, reduced to a small spot (holotype), or only stigma pigmented (two paratypes), triangular and including stigma in females. Marginal spot absent in all males, present in females. Basal band absent.

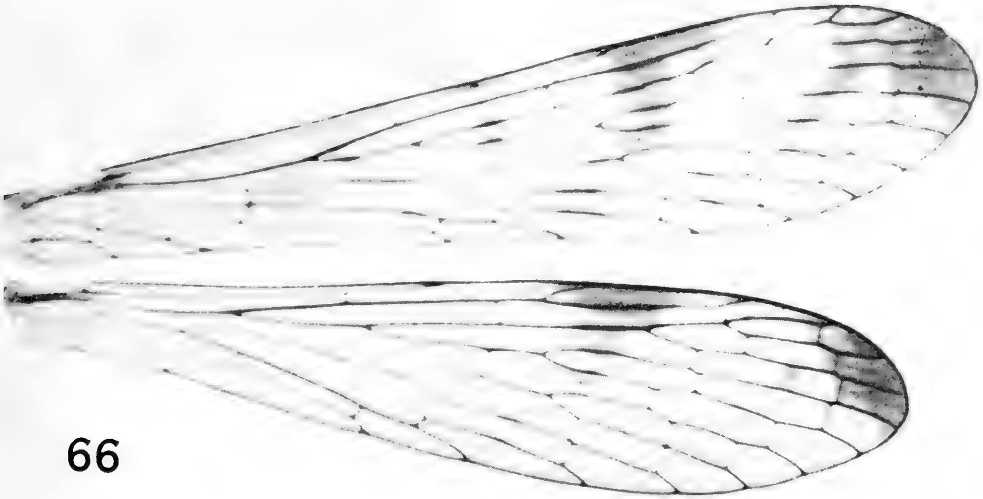


FIG. 66. *Neopanorpa angustiapicula,* new species, right wings of female paratype.

Abdomen of male: Terga 1-3 blackish brown, terga 4-5 dark brown (holotype) or dark brown in the middle, grading into light to yellowish brown at margins (paratypes); sterna 2-5 yellowish brown to light brown (holotype). Segment 6 brown dorsally, reddish brown ventrally; dark brown in one paratype. Segments 7-9 reddish brown, 7-8 much longer than in any other Javanese *Neopanorpa* (Fig. 71). Posterior process of tergum 3 elongate, stout, fringed with hairs at base, extending across about two-thirds length of tergum 4 (Figs. 69, 70). Elevated process on tergum 4 bifurcate. Smooth, shiny area on tergum 4 beneath posterior process of 3. Male genitalia (based mainly on dissected paratype): Hypovalves of sternum 9 apically and mesally darkened, long, expanded and overlapping at mid-length, narrowed and bearing sparse long hairs on apical one-third (Fig. 67). Ninth tergum (Fig. 72) broad, reddish brown (holotype) to yellowish brown, paler and almost squarely truncate apically. Cerci pale basally, dark brown apically. Genital bulb short and stout. Dististyles short, their outer margins generally straight or slightly concave but abruptly curved at tips (Fig. 67). Basal lobes of dististyles large, subrectangular in posterior mesal aspect, flattened, darkened, bearing many long yellowish hairs (Figs. 68, 73). Mesal margins of dististyles above basal lobes also somewhat pointed, bearing a long setae dorsally (Fig. 73). Aedeagus complex, with conspicuously projecting ventral parameres (Figs. 71, 74-76). Ventral valves small, projecting caudad only about as far as dorsal valves; dorsal valves concealed between dorsal parameres. Ventral parameres thick, darkly sclerotized, strongly curved ventrad and caudad, abruptly narrowed to mucronate tip (Figs. 74, 76). Dorsal parameres thickened, bluntly rounded, each continued dorsocephalad as a thin, slightly hooked blade (Figs. 74, 75). Lateral processes complexly divided into two parts separated by a deep, sclerotized pocket (Fig. 74).

Abdomen of female: Terga 1-6 dark brown (allotype) to blackish brown, corresponding sterna dull brown to light brown (allotype). Segments 7-8 brown basally, reddish brown apically (allotype) or entirely reddish brown. Segments 9-10 blackish brown (allotype) to reddish brown basally, dark brown apically. Cerci black. Subgenital plate yellowish, broadly dorsal portion of lobe with 2-3 long, stout, black spines projecting from its posterodorsal surface, about 12 smaller black spines on mesodorsal surface and about 9 small apically curved spines on anterodorsal surface (Fig. 62). Ventral valves of aedeagus divergent basally, extending slightly beyond dorsal valves and lateral processes; ventral parameres absent; dorsal parameres conspicuous, tongue-shaped blades, close together basally but with apices divergent (Fig. 56).

Abdomen of female: Terga 1-6 brownish black, corresponding sterna dull yellowish brown (allotype) to dull brown. Terga 7-10 dark brown; sternum 7 brown; cerci black. Subgenital plate of sternum 8 (Fig. 63) brown, whitish and notched apically, bearing long setae at each side of notch, weakly sclerotized anterolaterally. Axial portion of genital plate, greatly enlarged anteriorly (Fig. 64), bearing conspicuously protruding, ventral processes (Fig. 65). Arms broad, slightly twisted near base.

Body length: Male, about 13-15 mm (holotype 14 mm); female, about 9-11 mm (allotype 11 mm). *Length of fore wing:* Male, 11.9-14 mm (holotype 11.9 mm); female, 12.2-13.3 mm (allotype 12.6 mm).

Holotype: Male, Giesting, Mt. Tanggamus, southwestern Lampongs, southern Sumatra, 500-800 m, 24 and 27 Dec. 1934, Lieftinck. Allotype, 10 ♂♂, 15 ♀♀, same data as holotype; 1 ♂, 3 ♀♀, same data as holotype, except 500-1000 m, 29 June and Sept. 1933-34, Toxopeus; 1 ♂, 1 ♀, Lampongs, Wai Lima, southern Sumatra, 11 Dec. 1921, Karny; 1 ♂, Muara, Sako, Sumatra, Oct. 1915, Jacobson; 1 ♀, Fort de Kock (Bukittingi), Sumatra, 920 m, 1924, Jacobson; 1 ♂, Tanduong Sakti, Benkulen, southern Sumatra, 650 m, June 1935, Walsh. Holotype, allotype and most paratypes in the Rijksmuseum van Naturrlijke Historie, Leiden; 2 ♂, 1 ♀ paratypes in the Snow Entomological Museum, The University of Kansas.

We place this species in the *muelleri* group because of its wing pattern, the large spines on the dorsal surface of the basal lobes of the dististyles and the structure of the aedeagus in males. It can be easily recognized by the prominent, rounded components of the basal lobe of the dististyle, from which the species is named. Especially, the entirely exposed, ventrocaudally directed part is conspicuous and characteristic. For the female, the peculiar structure of the genital plate (protruding processes on anteroventral axial portion) is diagnostic.

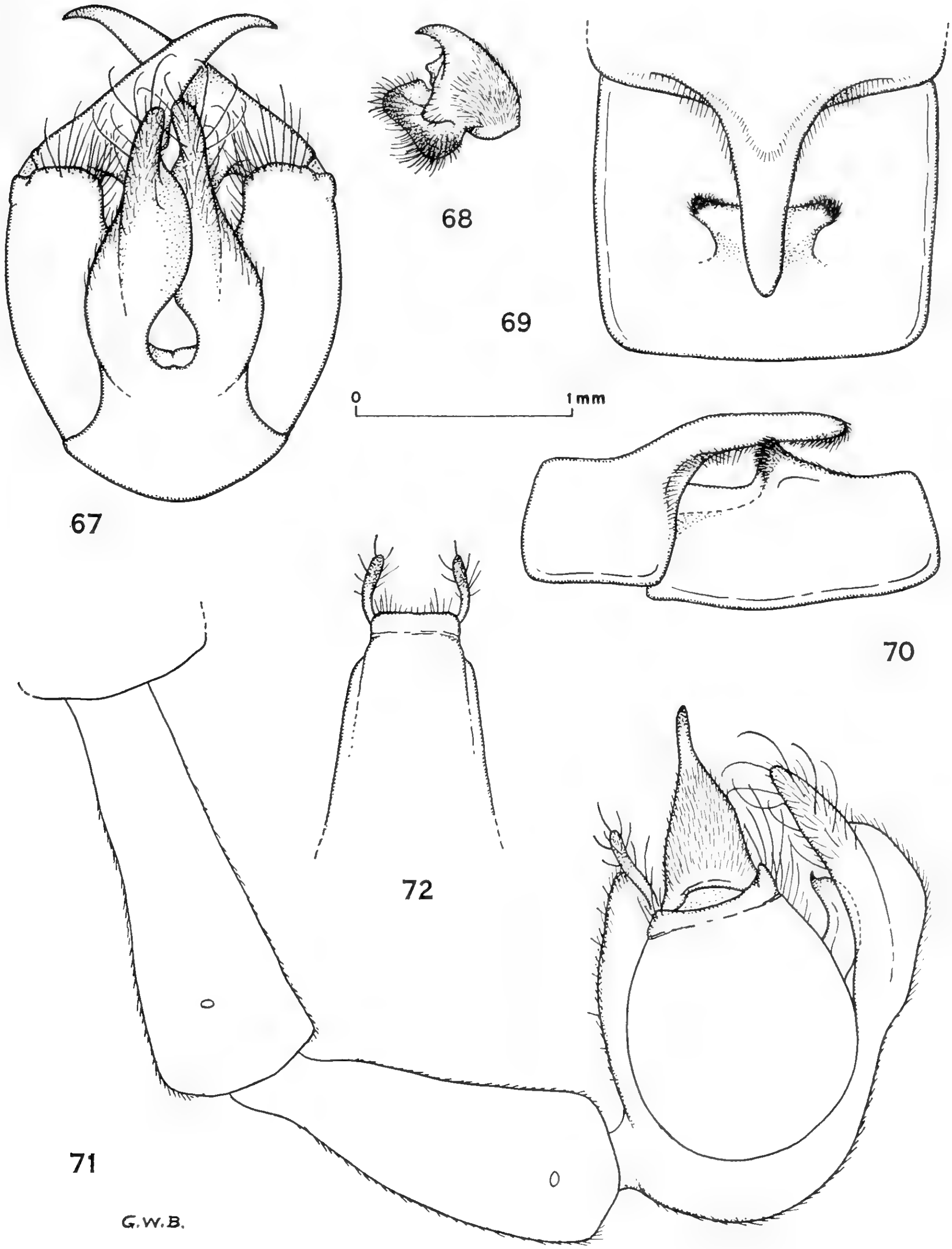
NEOPANORPA ANGUSTIAPICULA Group

Neopanorpa angustiapicula, new species

Description based on 4 males, 7 females, pinned.

Head: Dorsum of head glossy brownish black except brown bordering eyes; frons below antennal sockets dark brown to brown (two paratypes); rostrum in males reddish brown anteriorly, bright yellowish brown laterally, dark brown in most females; mouthparts dark brown. Antennal scape light brown, brown or reddish brown (holotype), pedicel dark brown, basal flagellomeres dull dark brown, others dull blackish brown; flagellum with 46 segments (paratypes; both antennae broken in holotype).

Thorax: Pronotum blackish brown to black (holotype), bearing many short, dark hairs but usually no bristles along anterior margin (three short bristles at each side in some females). Mesonotal and metanotal scuta blackish brown to black (holotype) with elongate, diffuse, yellowish brown spots at each side, above bases of wings. Mesonotal and metanotal scutella dark brown. Pleura and coxae yellowish brown to reddish brown (holotype). Femora yellowish brown; tibiae brown; tarsi dark brown.



FIGS. 67-71. *Neopanorpa angustiapicula,* new species, structural details. 67, genital bulb, ventral aspect; male holotype. 68, right dististyle, posteromesal (dorsomesal) aspect, to show shape of basal lobe; paratype. 69, abdominal terga 3 and 4, dorsal aspect, showing notal organ; holotype. 70, same as 69, left lateral aspect. 71, terminal abdominal segments, left lateral aspect, holotype. 72, ninth abdominal tergum, dorsal aspect; paratype; most hairs omitted.

oval, notched apically between two rounded lobes bearing long setae (Fig. 79), lightly sclerotized and translucent laterobasally. Genital plate small (compared to that of other species), axial portion ovoid, transparent basally (Fig. 77); arms short, not twisted mesal edges translucent, lateral edges darkened.

Body length: Male, 16.7-18.7 mm (holotype 18.7 mm); female, 10.9-16.6 mm (allotype 16.6 mm). *Length of fore wing:* Male, 12.9-13.1 mm (holotype 13 mm); female, 12.2-13.0 mm (allotype 13 mm).

Holotype: Male, Sumberbrantas, Mt. Ardjuno-Mt. Andjasmoro, East Java, about 1900 m, Jan. 1936, M. E. Walsh. Allotype, female, and 2 ♀ paratypes, same data as for holotype; 3 ♂ ♂, 3 ♀ ♀, same data as for holotype except altitude about 2000-2300 m. This species is known from East Java only. Holotype, allotype and most paratypes in the Rijksmuseum van Natuurlijke Historie, Leiden; 1 ♂, 1 ♀ paratypes in the Snow Entomological Museum, The University of Kansas.

Neopanorpa angustiapicula appears closely related to *N. diloba,* forming with it the *angustiapicula* group on the basis of the aedeagal structure. Both species have well developed ventral parameres (absent in most other Indonesian species, except *spicata* and *borneensis*); both have shorter, thicker dorsal parameres than other species; the lateral processes are large and complicated; and both species have large, flattened basal lobes on the dististyles and lack the long, thick, black spines present in the *muelleri* group.

Neopanorpa angustiapicula can be easily distinguished from *diloba* and other species by its reduced wing pattern, generally reddish brown body color, and for males by the elongated process of abdominal tergum 3, the notched process of tergum 4, the long segments 7-8 (more than 1.5 times longer than in other species), the robust genital bulb and the narrowed tips of the hypovalves, from which the species is named. The female differs from other species in the ovoid axis of the genital plate and in having no apical pale or hairless areas on the subgenital plate.

Neopanorpa diloba, new species

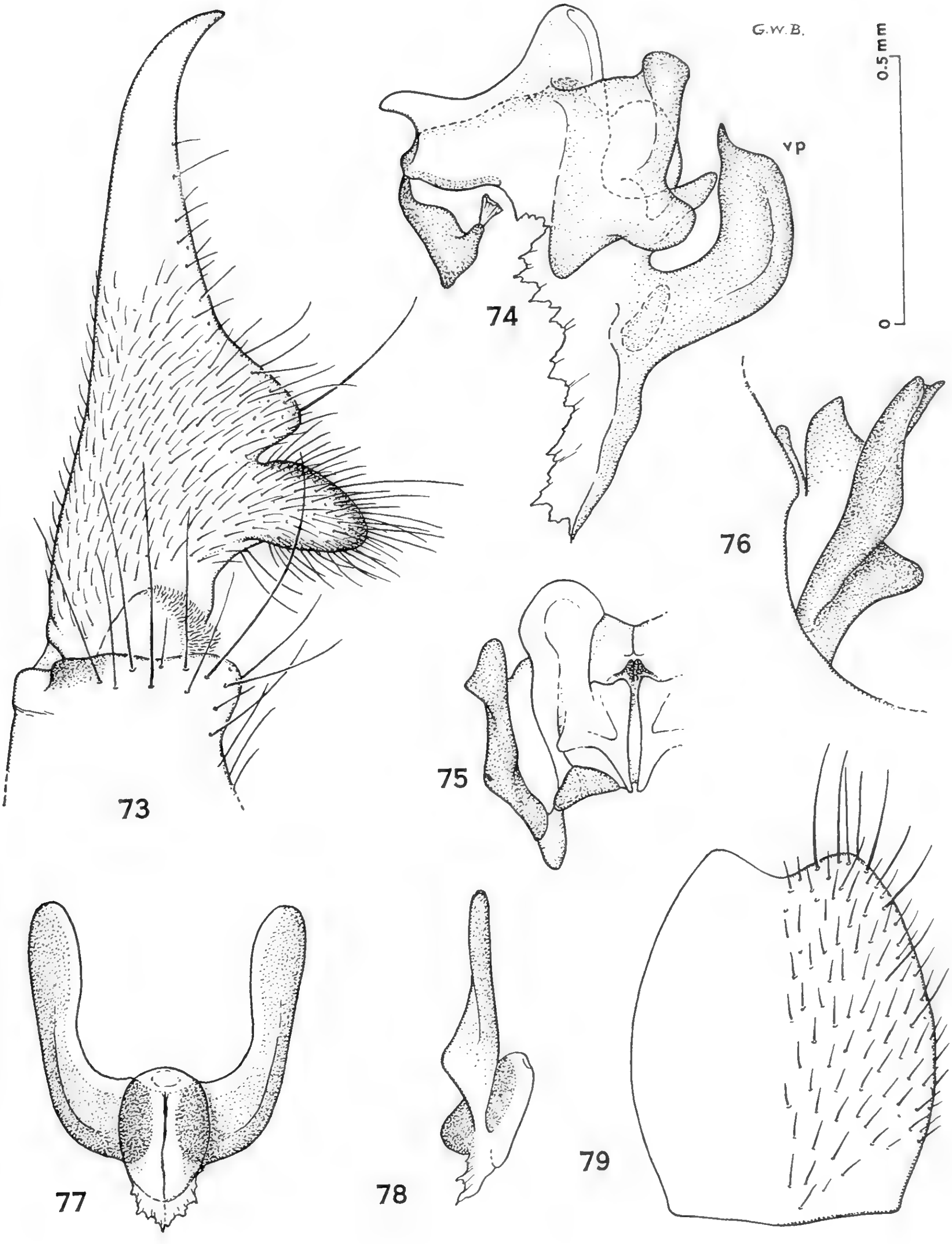
Description based on one callow male, pinned.

Head: Dorsum glossy blackish brown; frons below antennal sockets dark brown; rostrum yellowish brown, change in color between frons and rostrum abrupt; mouthparts brown, tips of palps dark brown. Antennal scape brown, pedicel dark brown, basal flagellomere dull brown, others dull dark brown (both antennae broken).

Thorax: Pronotum brownish black, bearing 4-5 bristles on each side along anterior margin. Mesonotum and metonotum brownish black, with paler areas near wing bases. Pleura and coxae dull brown, covered with short, whitish hair. Femora yellowish brown; tibiae dull brown; basitarsi dull brown, other tarsomeres dark brown.

Wings (Fig. 80): Almost colorless, slightly iridescent, with faint smoky brown markings. Apical band small and incomplete, with detached spots in cell 1st R_3 and cell 2nd R_5. Unforked pterostigmal band slender, faint and incomplete. Marginal spot absent. Basal band reduced to faint, large spot in cell R and smaller one in cell M.

Abdomen of male: Terga 1-4 dark brown; tergum 5 dark brown basally, brown apically. Sterna 2-5 brown. Segment 6 dark brown; segment 7 brown basally, pale yellowish brown apically; segment 8 pale yellowish brown; segment 9 yellowish brown except hypovalves dark brown. Posterior process of tergum 3 stout, extending over about two-thirds length of tergum 4. Hypovalves of sternum 9 darkened, very large, hairless on



FIGS. 73-79. *Neopanorpa angustiapicula,* new species, details of male and female genitalia. 73, left dististyle, ventral aspect; male paratype. 74, aedeagus, left lateral aspect; male paratype; vp—ventral paramere. 75, aedeagus, posteroventral aspect, left half with ventral paramere removed; paratype. 76, left ventral paramere and edge of lateral process, ventral aspect; paratype. 77, genital plate of female, ventral aspect; paratype. 78, same as 77, left lateral aspect. 79, subgenital plate of female, ventral aspect; paratype; hairs partially omitted.

mesal margins (Fig. 81). Ninth tergum (Fig. 84) broad, short, yellowish brown, with slightly rounded apical margin; ventral processes directed anteriorly (Fig. 85). Cerci pale basally, dark brown apically. Genital bulb broad and short; basistyles yellowish brown, dististyles yellowish brown, short and stout, their outer margins generally straight, curved at tips. Basal lobes of dististyles large, darkened, bearing many long hairs, flattened, each subdivided into two lobes, ventral one smaller, pointed, dorsal one larger, bluntly rounded (Figs. 83, 87). Above basal lobe on mesal surface of each dististyle a rounded ridge (Fig. 83) appearing as a blunt, angular projection in ventral aspect (Fig. 87). Aedeagus complicated, lightly sclerotized, yellowish brown, with more densely sclerotized ventral parameres and lateral processes. Ventral valves small, set unusually far dorsally on aedeagus (Figs. 87, 88); dorsal valves minute, concealed between dorsal parameres in lateral aspect and by ventral valves in ventral aspect. Ventral parameres somewhat spatulate, curved ventrad and caudad from ventral surface of aedeagus (Figs. 87, 88); dorsal parameres short, thick, bluntly rounded at apices (Figs. 86, 88). Lateral processes divided, with thick inner lamellae below and before ventral valves (latter subquadrate in outline in Fig. 88) and outer lamellae each bearing a knob-like process, with a deep pocket at each side, a little below ventral valves, separating lamellae (Figs. 87, 88).

Body length: Male, about 14.0 mm.

Length of fore wing: 11.5 mm.

Holotype: Male, southeastern Djambangan, Tengger Mts., East Java, 1800 m, July 1939, N. van Bemmel-Lieneman.

We consider species to be closely related to *angustiapicula* on the basis of the structure of genitalia, as discussed under *angustiapicula.* Both species are restricted to East Java. *Neopanorpa diloba* can be easily recognized by its faint, almost obliterated wing pattern, its long, wide hypovalves, and the characteristic flattened, divided basal lobes of the dististyles, from which the species is named.

Neopanorpa fractura Group

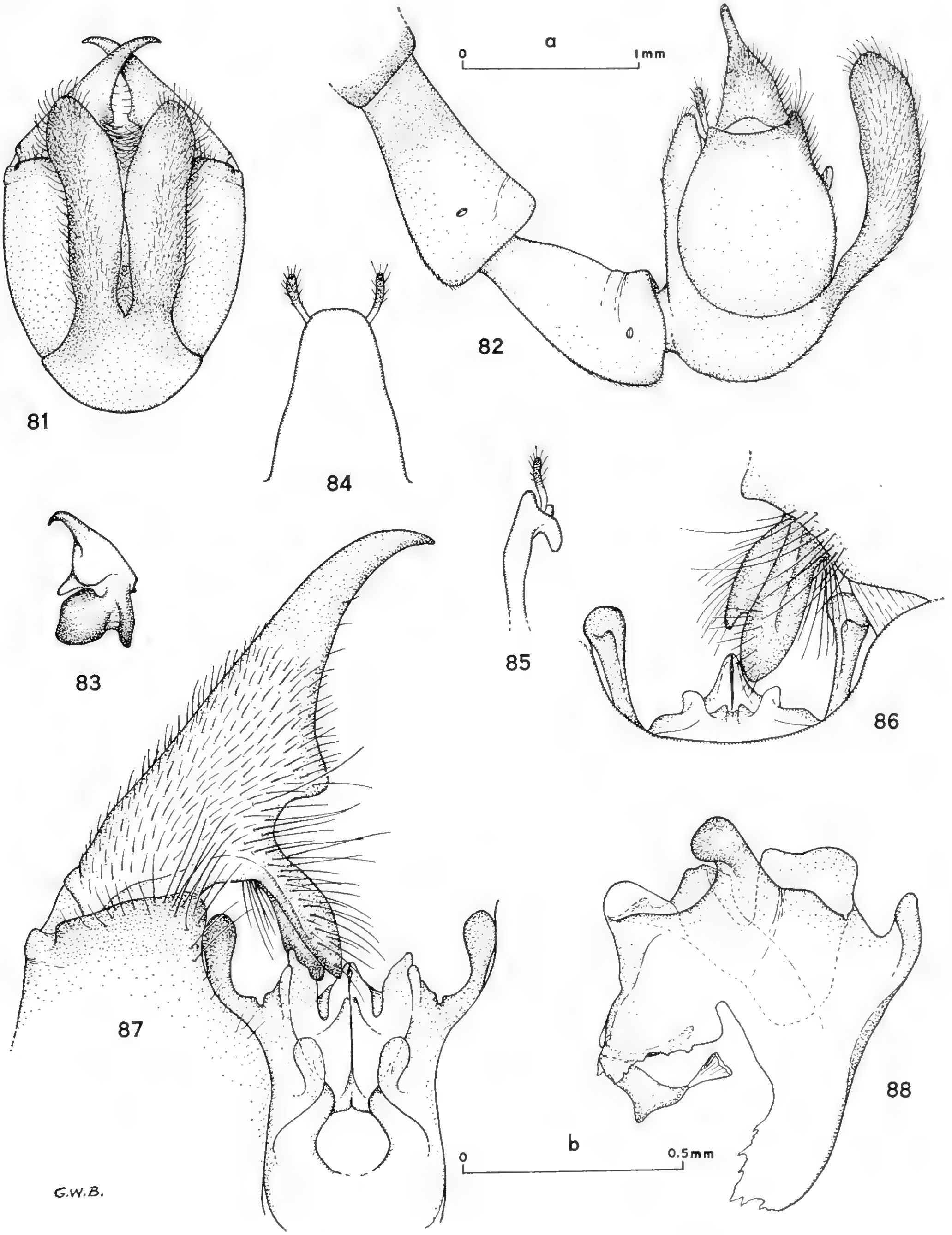
Neopanorpa fractura, new species

Description based on 15 males, 18 females, pinned.

Head: Dorsum glossy black; frons below antennal sockets dark brown; rostrum dark brown anteriorly, yellowish brown laterally; mouthparts brown except tips of palps dark brown. Antennal scape yellowish brown, pedicel brown, flagellum dull dark brown on basal segment, otherwise dull blackish brown, with 41 flagellomeres.

Thorax: Pronotum black, bearing about 4-5 bristles on each side at anterior margin. Mesonotum and metanotum blackish brown to black. Pleura and coxae yellowish brown to dingy dark brown (reddish brown in holotype). Femora and tibiae dingy yellowish brown; basitarsi dull brown, other tarsomeres dark brown.

Fig. 80. *Neopanorpa diloba,* new species, right fore wing of male holotype.



FIGS. 81-88. *Neopanorpa diloba,* new species, structural details of male holotype. 81, genital bulb, ventral aspect. 82, terminal abdominal segments, left lateral aspect. 83, right dististyle, posteromesal (dorsomesal) aspect, to show shape of basal lobe. 84, abdominal tergum 9, dorsal aspect. 85, same as 84, left lateral aspect. 86, basal lobe of left dististyle and aedeagus, dorsal aspect. 87, left dististyle, apex of basistyle, and aedeagus, ventral (posterior) aspect. 88, aedeagus, left lateral aspect. Scale a—FIGS. 81-85; scale b—FIGS. 86-88.

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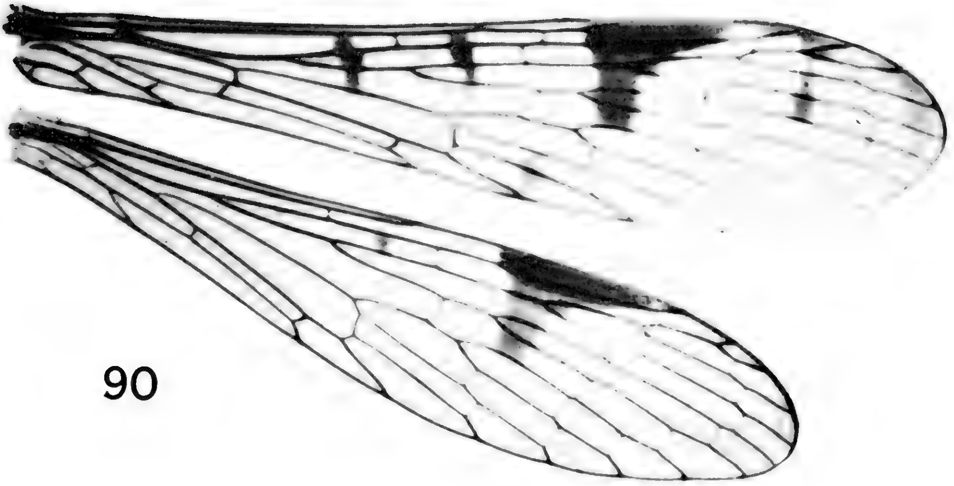

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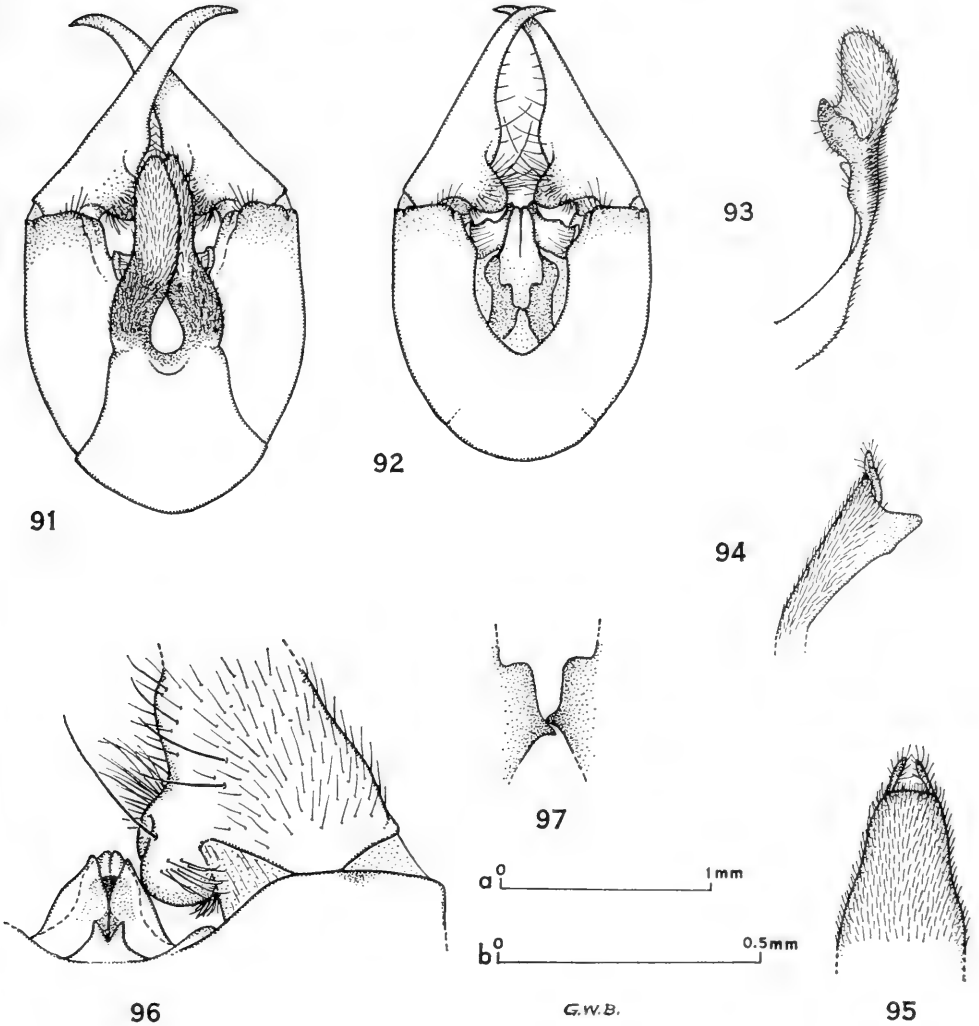
FIGS. 89-90. *Neopanorpa fractura*, new species, right wings of two male paratypes from north central Sumatra, showing variation in pigmentation.

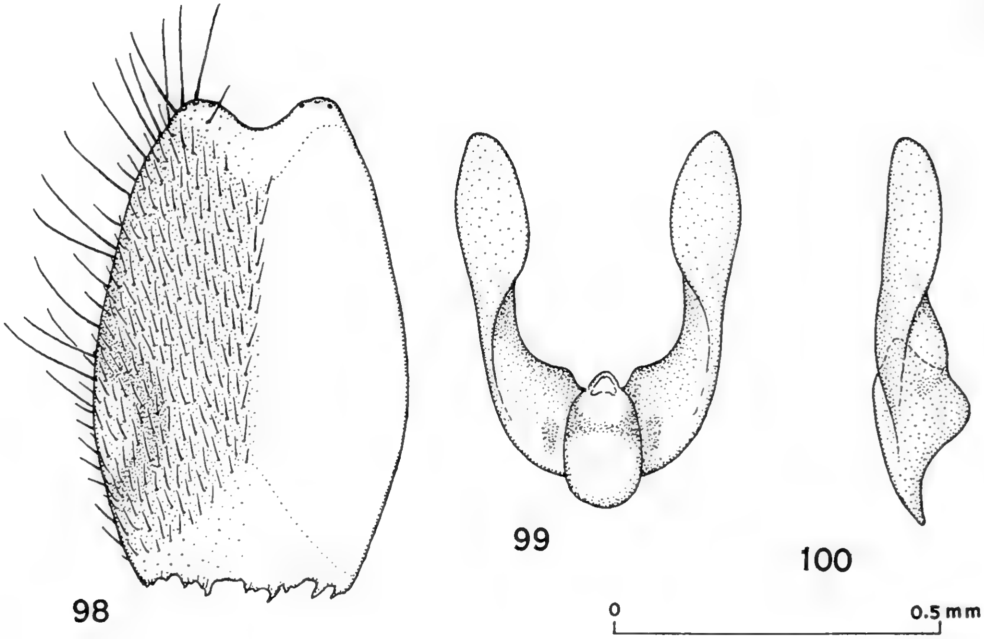
Wings (Figs. 89, 90): Clear, slightly iridescent, with markings smoky dark brown. In fore wing, apical band fragmented, reduced to brown tinge in distal portion of outermost row of radial cells and transverse spot, variable in extent, at level of distal fork of R_2. Pterostigmal band variable from complete and forked posteriorly (1 female), to entire but strongly constricted at mid-length and lacking distal branch (holotype and 10 paratypes), to interrupted at or near M_1 with proximal branch represented by one or two spots near wing margin (in most paratypes). Basal band usually represented by one or two spots, entire in holotype and 6 paratypes. Marginal spot conspicuous, basal spot absent. Hind wing: incomplete pterostigmal band present, weak apical band and marginal spot present in holotype but



FIGS. 91-97. *Neopanorpa fractura,* new species, structural details of male. 91, genital bulb, ventral aspect; holotype. 92, genital bulb, ventral aspect, with ninth sternum removed to show aedeagus; paratype. 93, hypovalve of ninth sternum, left lateral aspect. 94, ninth abdominal tergum, left lateral aspect. 95, same as 94, dorsal aspect. 96, base of left dististyle and aedeagus, dorsal aspect. 97, supposed rudimentary ventral parameres, ventral aspect. Scale a—FIGS. 91-95; scale b—FIGS. 96-97.

absent in most paratypes; basal spot present in some specimens.

Abdomen of male: Terga 1-5 usually black; sterna 2-5 yellowish brown. Segment 6 blackish brown. Segments 7-9 yellowish brown. Posterior process of tergum 3 a narrow triangle, widened basally, extending about half-way across tergum 4. Hypovalves glossy dark brown at base to dull brown at tip, bent mesad near mid-length, with inner margins broadly overlapping, outer margins strongly infolded dorsally, nearly touching inner margins; a stout, dorsal, lightly sclerotized projection near mid-length in lateral aspect (Fig. 93). Tergum 9 (Figs. 94, 95) broadly rounded to nearly truncate apically; ventral process with incurved edge. Basistyles yellowish brown; dististyles dark brown, their outer margins nearly straight except abruptly



Figs. 98-100. *Neopanorpa fractura,* new species, details of genitalia of female allotype. 98, subgenital plate, ventral aspect; hairs partially omitted. 99, genital plate, ventral aspect. 100, genital plate, right lateral aspect.

curved at tips. Inner basal lobes of dististyles directed anteriorly (downward), bearing long hairs anteroventrally, cleft mesally so that each basal lobe seems divided into two parts (Fig. 96), with a long seta projecting from near cleft, a few (4-8) smaller setae arising from mesodorsal surface of each basal lobe, and tuft of pale hairs beneath basal lobe (Figs. 92, 96). Ventral valves of aedeagus extend a little beyond dorsal valves; lateral processes simple, concave ventromesally; ventral parameres absent or possibly represented by moderately sclerotized bands on ventral surface of aedeagus, bearing small, mesally directed points (Figs. 92, 97). Dorsal parameres conspicuous, thin, translucent, broad and outwardly curved at base, mucronate at apex, each with a small flattened dorsal appendage projecting dorsad with outwardly deflected tip (Fig. 96).

Abdomen of female: Terga 1-6 black; sterna 2-5 pale yellowish brown, sternum 6 dark brown. Segments 7-10 brown. Cerci black. Subgenital plate (Fig. 98) yellowish brown, pale at apex and base, with indistinct, dark-bordered pale spot at margin near base, narrowed gradually from near mid-length, notched apically, bearing many long setae along lateral margins and each side of notch. Axial portion of genital plate ovoid; arms broad, twisted basally (Fig. 99).

Body length: Male, about 11-13 mm (holotype 13 mm); female, about 8-11 mm (allotype 9 mm). *Length of fore wing:* Male, 12-13 mm (holotype 13.2 mm); female, 12.0-13.2 mm (allotype 12 mm).

Holotype: Male, Brastagi, northern central Sumatra, 1400 m, Nov. 1950, M. A. Lieftinck. Allotype and 14 ♂, 17 ♀ paratypes, same data as for holotype. Holotype, allotype and most paratypes in the Rijksmuseum van Natuurlijke Historie, Leiden; 2 ♂, 2 ♀ paratypes in the Snow Entomological Museum, The University of Kansas.

This species with *sumatrana* and *crinita* form the *fractura* group because of the structure of the hypovalves (lightly sclerotized projection on dorsal surface), cleft basal lobes of the dististyles, and structure of the aedeagus of males and genital plates of females. It can easily be recognized by its incomplete apical band, strongly constricted or interrupted pterostigmal band, and the sclerotized projections of the hypovalves. The species is named from the divided appearance of the hypovalves (Fig. 93). It differs from *crinita* in not having long dorsal hairs on the hypovalves, in the shape of the hypovalves (Fig. 93) and the more rounded apex of the 9th tergum. It can be distinguished from *sumatrana* by the more complete wing markings and less prominent dorsal projections on the hypovalves in that species. Females can be distinguished from those of *sumatrana* by the wing pattern. Further differences are found in the subgenital plate and genital plate, which in *sumatrana* has distinct lateral lobes (compare Figs. 99, 124).

Neopanorpa crinita, new species

Description based on 6 males, 1 female, pinned.

Head: Dorsum shining black; frons below antennal sockets dark brown; rostrum dark brown anteriorly, yellowish brown laterally; mouthparts brown except tips of palps dark brown. Antennal scape yellowish brown, pedicel brown, flagellum dull dark brown at base, grading into dull blackish brown, with 40-41 flagellomeres (right flagellum broken in holotype).

Thorax: Pronotum black, bearing 3-5 bristles on each side along anterior margin. Mesonotum and metanotum blackish brown to black. Pleura dark brown to blackish brown near wing bases, yellowish brown to reddish brown near coxae, or discolored to completely dark brown (holotype and 1 male paratype) to black (allotype). Coxae yellowish brown (holotype) to dull brown, blackish brown in allotype. Femora yellowish brown (holotype and most paratypes) to dull dark brown (allotype); tibiae and tarsi brown.

Wings (Fig. 101): Almost colorless,

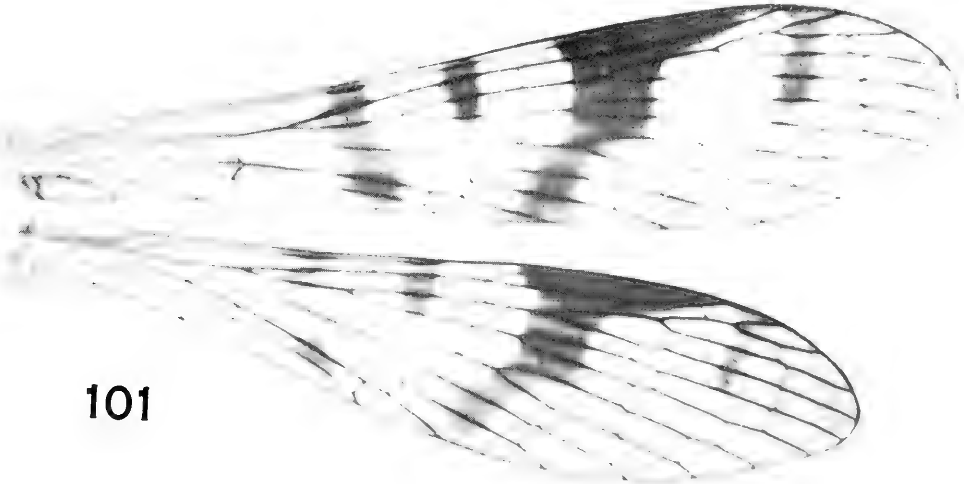


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FIG. 101. *Neopanorpa crinita,* new species, right wings of male paratype.

slightly iridescent, with dark smoky brown bands and spots. Apical band very weak, almost obliterated (holotype and 1 male paratype), or fragmented, reduced to brown tinge in distal portion of outermost row of radial cells and transverse spot, variable in extent, at level of distal fork of R_2 and terminating before vein R_5. Pterostigmal band variable, entire but lacking distal branch in holotype and 3 paratypes; distal branch reduced to a diffuse spot in 2 paratypes. Marginal spot present. Basal band usually entire, broken into two spots in 1 paratype. Basal spot absent or only faintly developed.

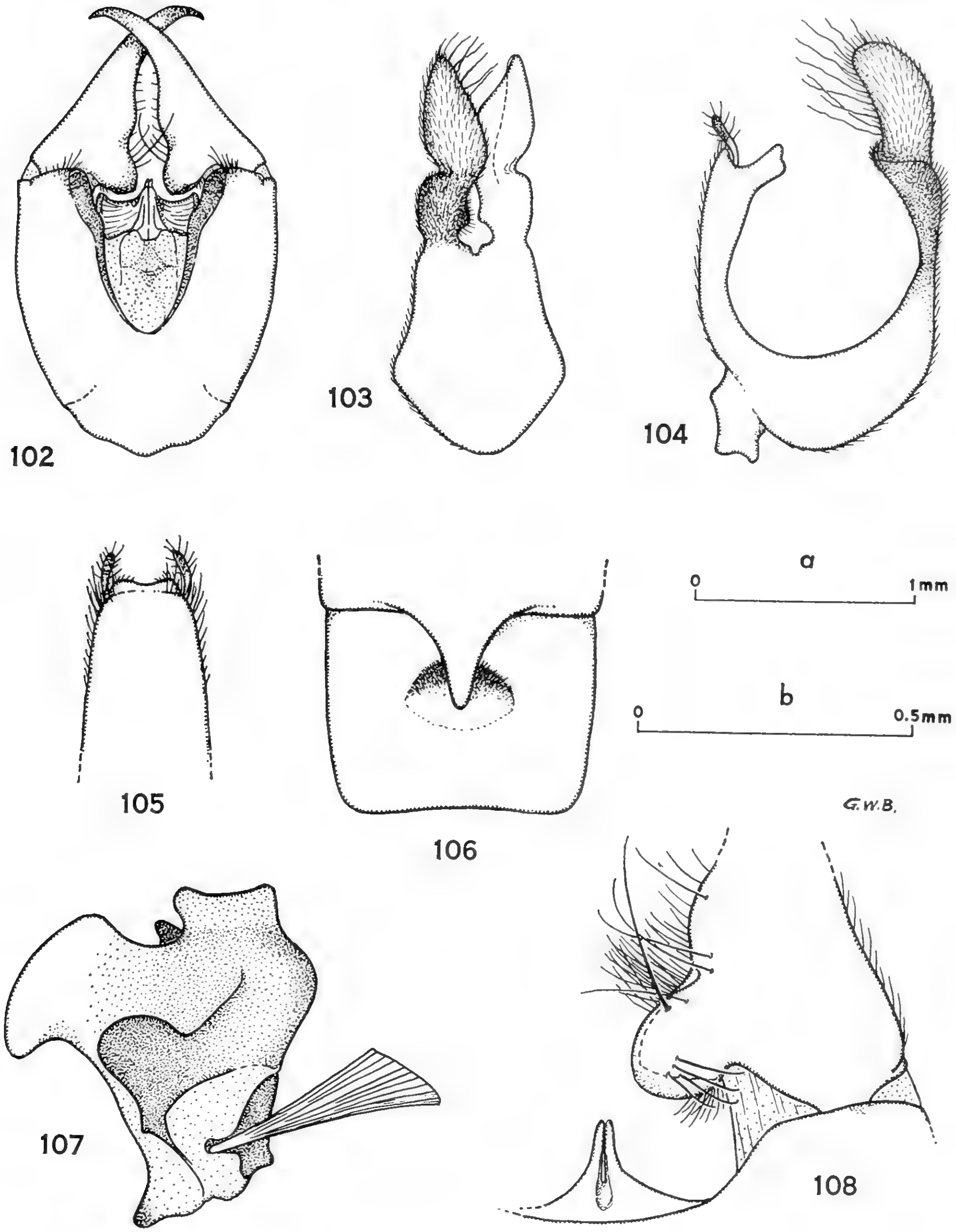
Abdomen of male: Terga 1-5 blackish brown to black (holotype); sterna 2-5 yellowish brown to sordid dark brown (holotype). Segment 6 blackish brown. Segments 7-9 brown, dark brown apically on segment 7. Posterior process of tergum 3 narrowly triangular, extending about half-way across tergum 4. Hypovalves dark brown at base to brown at tip, notched laterally and appearing bent near mid-length, with slight process on mesal margin near base (Fig. 103); inner margins overlapped mesally, outer margins strongly infolded dorsally, bearing long, crinkled hairs (except possibly broken off in 1 paratype), and a stout, dorsal, moderately sclerotized projection near mid-length in lateral aspect (Fig. 104). Tergum 9 slightly emarginate (Fig. 105) to nearly truncate apically, its ventral processes subrectangular. Basistyles yellowish brown to brown mesally; dististyles dark brown. Basal lobes of dististyles (Figs. 102, 108) directed anteriorly, bearing long hairs on ventral surface and tuft of shorter hairs anteroventrally, shallowly cleft mesally so that each basal lobe seems divided into two parts; a long seta projecting from near cleft, about 4 smaller spines arising from mesodorsal surface of each basal lobe. Ventral valves of aedeagus extending ventrad, somewhat hooked (Fig. 107); lateral processes simple, concave; ventral parameres absent; dorsal parameres thin, subquadrate blades, closely appressed in dorsal aspect (Figs. 107, 108).

Abdomen of female: Terga 1-6 black; sterna 2-6 sordid brown. Terga 7-9 blackish brown, corresponding sterna dark brown. Cerci blackish brown. Subgenital plate yellowish brown, pale and notched apically, with 5-6 setae on lobe at each side of notch, pale apical area otherwise hairless; low folds from anterobasal corners converging medially, area between folds pale, without hairs (Fig. 109). Axial portion of genital plate broadly subconical with darkly sclerotized, rounded lateral lobe at each side above base of distal arm; arms moderately sclerotized, twisted basally (Fig. 110).

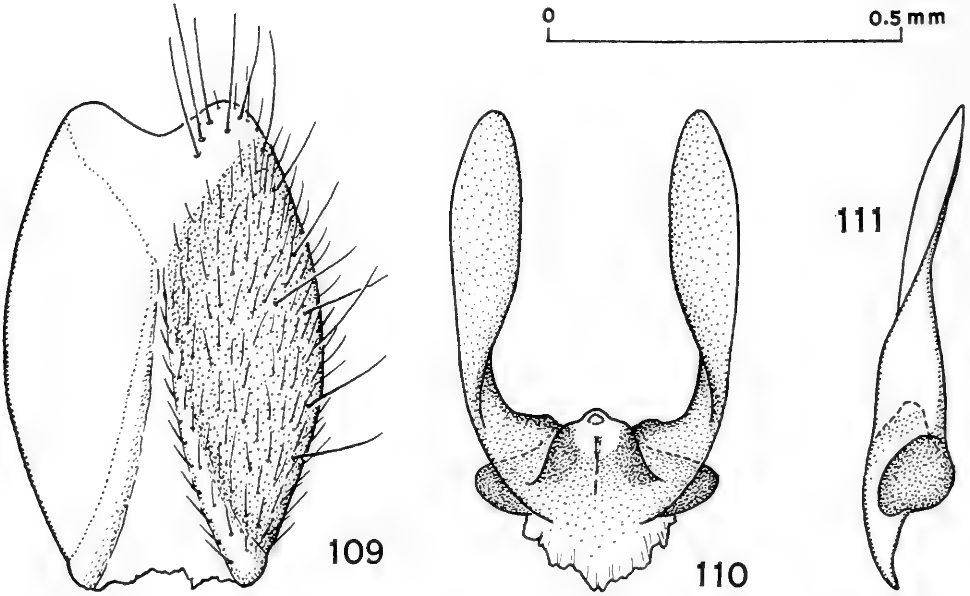
Body length: Male, about 12-14 mm (holotype 14 mm); female (allotype) about 9 mm. *Length of fore wing:* Male, 12-14 mm (holotype 13 mm); female (allotype), 12.3 mm.

Holotype: Male, Suban Ajam, Sumatra, July 1916, Jacobson. Allotype, same data as for holotype. One ♂ paratype, Giesting, Mt. Tanggamus, southwestern Lampongs, southern Sumatra, 800 m, 27 Dec. 1934, Lieftinck; 1 ♂, Wai Tebu, Mt. Tanggamus, southern Sumatra, 500 m, 24 June 1934, Toxopeus; 1 ♂, Mt. Tanggamus, 1000 m, 12 July 1934, Toxopeus; 1 ♂, Air Njuru, Dampu, Sumatra, 1400 m, Aug. 1916, Jacobson; 1 ♂, Muara Sako, Sumatra, Oct. 1915, Jacobson. Holotype, allotype and 3 ♂ paratypes in the Rijksmuseum van Natuurlijke Historie, Leiden; 2 ♂ paratypes in the Snow Entomological Museum, The University of Kansas.

N. crinita is very similar to *N. fractura*, but the two have quite different ranges. *N. crinita* may be distinguished from *fractura* and *sumatrana* by the long, crinkled hairs on the hypovalves, from which the species is named, and by the more abruptly bent shape of the hypovalves (cf. Figs. 91,



Figs. 102-108. *Neopanorpa crinita,* new species, structural details of male paratype. 102, genital bulb, ventral aspect, with ninth sternum removed to show aedeagus. 103, ninth abdominal sternum and hypovalves, ventral aspect, only partly shaded to show color pattern. 104, ninth abdominal tergum and sternum, left lateral aspect; most hairs omitted. 105, ninth abdominal tergum, dorsal aspect; most hairs omitted. 106, abdominal terga 3 and 4, dorsal aspect, showing notal organ. 107, aedeagus, right lateral aspect. 108, base of left dististype and dorsal parameres, dorsal aspect. Scale a—Figs. 102-106; scale b—Figs. 107-108.



Figs. 109-111. *Neopanorpa crinita,* new species, details of genitalia of female allotype. 109, subgenital plate, ventral aspect; hairs partially omitted. 110, genital plate, ventral aspect. 111, genital plate, right lateral aspect.

103) and less conspicuous sclerotized projection on the dorsal surface of each hypovalve (Figs. 93, 104). It can be further differentiated from *fractura* by its longer ventral valves, the thin, subrectangular dorsal parameres (more outwardly rounded in *fractura*) and the more complete pterostigmal band, especially the proximal branch. The thin, appressed dorsal parameres and the simpler wing pattern separate this species from *sumatrana.* In the female, the pale mesal zone and bordering folds of the subgenital plate and the darkened lateral lobes of the axial portion of the genital plate confirm the identification suggested by the wing patterns and together differentiate *crinita* from *fractura* and *sumatrana.*

Neopanorpa sumatrana, new species

Description based on 1 male, 4 females, pinned.

Head: Dorsum glossy black; frons below antennal sockets blackish brown; rostrum grayish brown basally, reddish brown apically, except yellowish brown along sides; mouthparts brown, dark brown at apex of palps. Antennal scape brown, pedicel dark brown, flagellum dull dark brown, with 41 segments (left flagellum broken on holotype).

Thorax: Pronotum black, bearing 4 bristles on each side along anterior margin. Mesonotum and metanotum black. Pleura mostly dull blackish brown, brown near coxae. Coxae and femora dull brown; tibiae and tarsi dull dark brown.

Wings (Fig. 112): Membrane colorless and slightly iridescent, bands and spots dark smoky brown. Apical band including small posterior pale spot in holotype and most paratypes. Pterostigmal band complete, forked posteriorly, joining apical band narrowly along costal margin, distal branch smaller than proximal branch. Marginal spot conspicuous. Basal band complete. Basal spot absent in holotype and most paratypes.

Abdomen of male: Terga 1-5 blackish brown, corresponding sterna yellowish brown. Segment 6 blackish brown, segments 7-9 reddish brown except hypovalves

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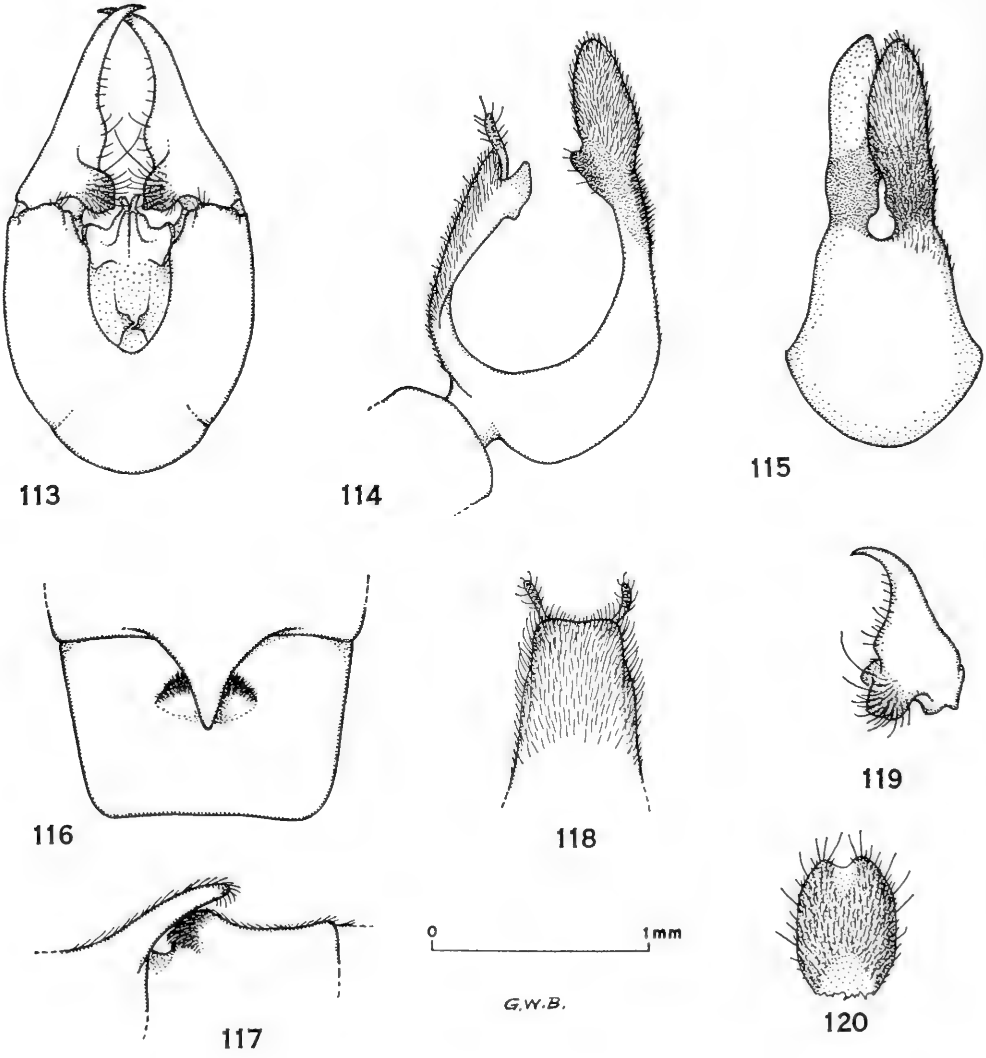
FIG. 112. *Neopanorpa sumatrana,* new species, right wings of female paratype.

of sternum 9 darker. Posterior process of tergum 3 triangular, extending about halfway across tergum 4 (Fig. 116). Hypovalves of sternum 9 dark brown at base to brown at tip, inner margins overlapped mesally, outer margins strongly infolded dorsally; near mid-length on dorsal surface, a stout, sclerotized projection (Fig. 114). Tergum 9 (Fig. 118) brown, truncate apically. Basistyles short, slightly longer than dististyles; dististyles long, their outer margins slightly concave before mid-length (Fig. 113). Basal lobes of dististyles (Fig. 123) directed downward (anteromesad), bearing long ventral hairs, cleft (Fig. 119) so as to form two parts; a long seta projecting from near cleft; about 7-10 smaller apically curved spines projecting from mesodorsal surface of each basal lobe (Figs. 119, 121); tuft of pale hairs in notch between basal lobe and base of dististyle. Ventral valves of aedeagus extend well beyond small dorsal valves; lateral processes simply concave, ventral parameres absent or possibly represented by small, moderately sclerotized points on anteroventral surface of aedeagus; dorsal parameres large, outwardly convex blades, appressed basally but with dorsal margins divergent (Fig. 121), more ventral margins curved outwardly around dorsal valves (Fig. 122).

Abdomen of female: Terga 1-6 black; sterna 2-5 yellowish brown, sternum 6 dark brown. Terga 7-9 blackish brown, corresponding sterna brown. Segment 10 and cerci black. Subgenital plate yellowish brown with whitish, notched apex, bearing many long setae along lateral margins and at each side of notch (Fig. 120). Axial portion of genital plate ovoid, with conspicuous, rounded lobe at each side; arms of distal portion broad, twisted basally, with outer margins pale (Fig. 124).

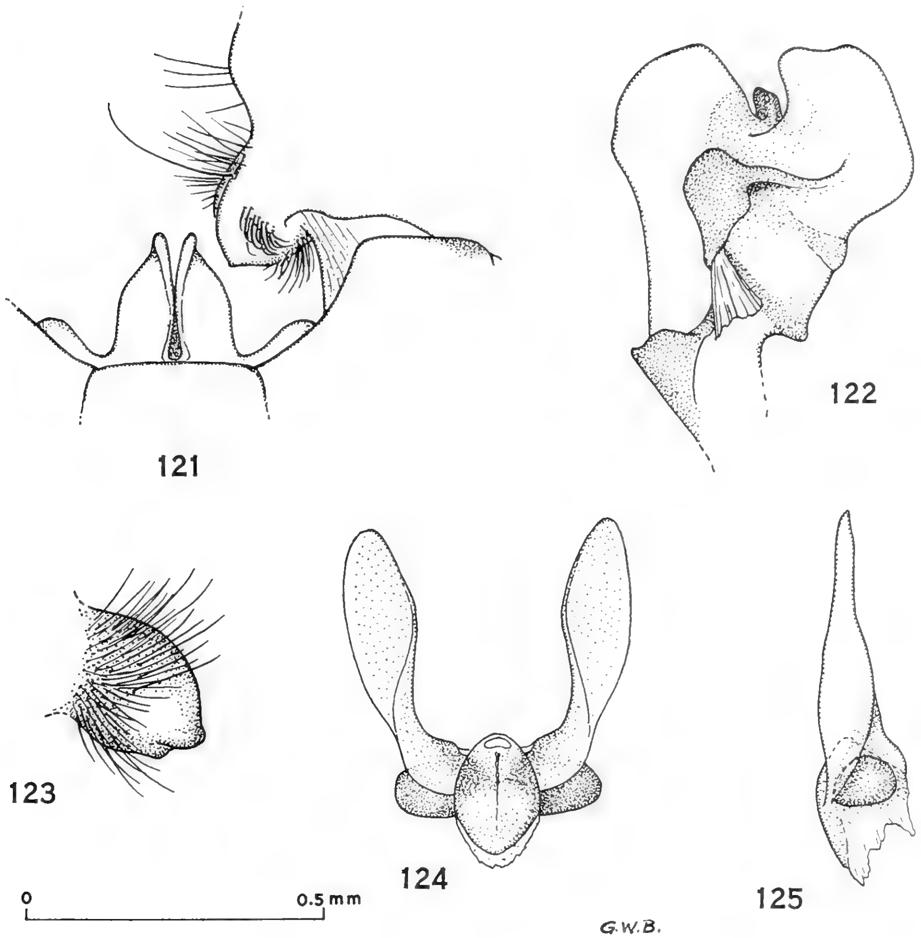
Body length: Male, about 10 mm (holotype); female, about 8-10 mm (allotype 9 mm). *Length of fore wing:* Male, 12.7 mm (holotype); female, 12.1-13.5 mm (allotype 13.5 mm).

Holotype: Male, Fort de Kock (Bukittinggi), Sumatra, 920 m, 1924, Jacobson. Allotype, Tandjunggadang, near west coast of Sumatra, 1200 m, Feb. 1926, Jacobson. Paratypes: 1 ♀, same data as for holotype; 2 ♀♀, same data as for allotype, except 1000 m. Holotype, allotype and 2 ♀ paratypes in the Rijksmuseum van Natuurlijke Historie, Leiden; 1 ♀ paratype in the Snow Entomological Museum, The University of Kansas.



Figs. 113-120. *Neopanorpa sumatrana,* new species, structural details of male holotype and female paratype. 113, genital bulb, ventral aspect, ninth sternum removed to show aedeagus. 114, ninth abdominal tergum and sternum, left lateral aspect. 115, ninth sternum and hypovalves, ventral aspect. 116, abdominal terga 3 and 4, dorsal aspect, showing notal organ. 117, same as 116, left lateral aspect. 118, ninth tergum, dorsal aspect. 119, right dististyle, posteroventral (slightly posteromesal) aspect, to show shape of basal lobe. 120, subgenital plate of female, ventral aspect.

We place this species in the *fractura* group because of the structure of the hypovalves, basal lobes of the dististyles, and aedeagus in the male and of the genital plate in the female. It may be distinguished from *fractura* by its complete, extensive wing markings, both in male and female, less protruding dorsal projection of the hypovalves, and the very characteristic, dorsal parameres, of which the dorsal part is much larger in *sumatrana* than that in *fractura*. The female is differentiated from that of *fractura* by the subgenital plate (narrowed more abruptly in *sumatrana*) and by the conspicuous lateral lobes of the genital plate.



Figs. 121-125. *Neopanorpa sumatrana,* new species, details of genitalia of male holotype and female paratype. 121, basal lobe of left dististyle and dorsal parameres, dorsal aspect. 122, aedeagus, right lateral aspect. 123, basal lobe of left dististyle, ventral aspect. 124, genital plate of female, ventral aspect. 125, same as 124, right lateral aspect.

Neopanorpa borneensis Group

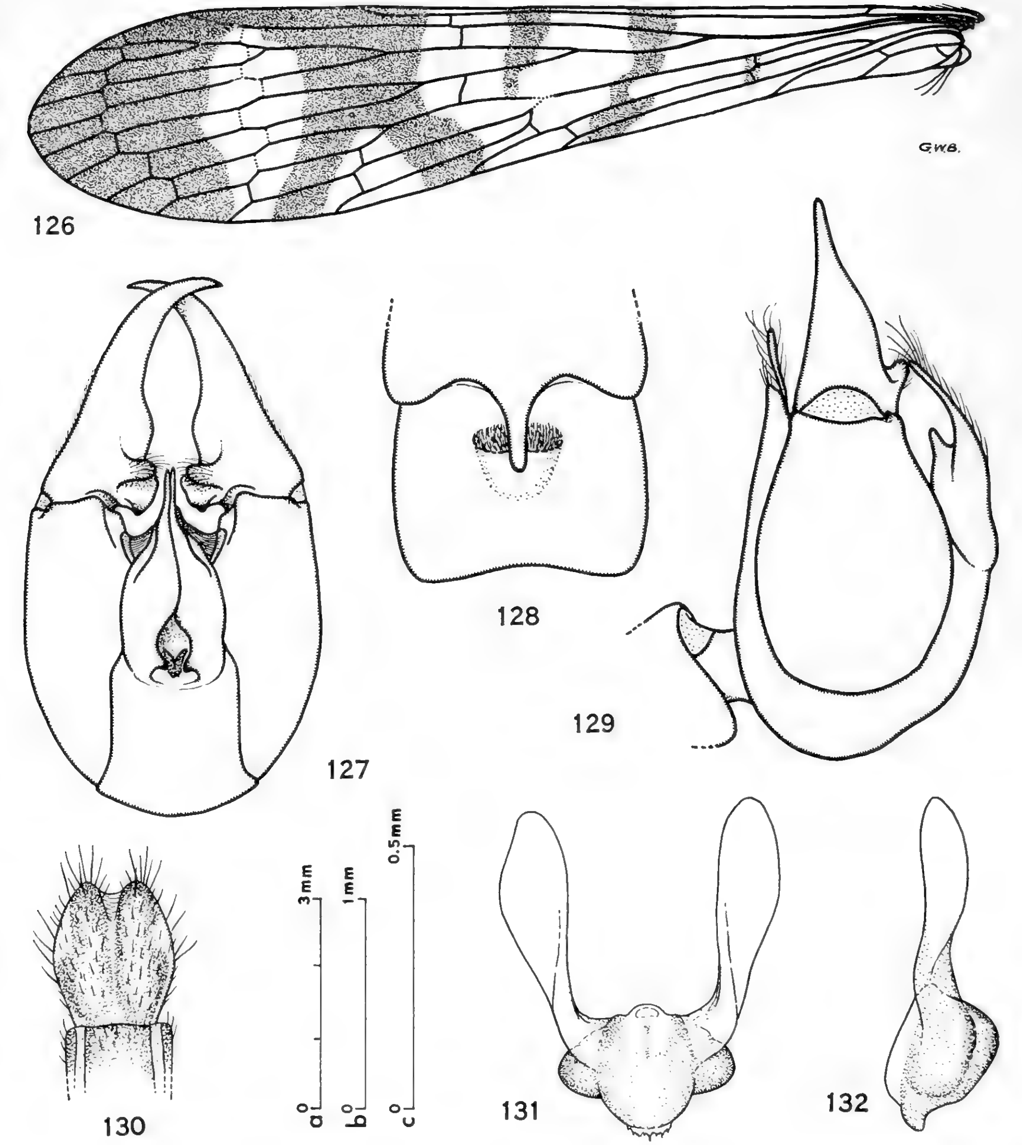
Neopanorpa borneensis Byers, 1966

Description mostly based upon original description (Byers, 1966), based on 2 males and 6 females, pinned.

Head: Dorsum glossy black; frons below antennal sockets dark brown; genae light yellowish brown; rostrum dark brown anteriorly, yellowish brown laterally, especially near base, except for thin line of brown along edge of eye; margin of labrum black. Antennal scape dark yellowish brown, pedicel brown; flagellum dark brown basally, grading into black, with 41 flagellomeres.

Thorax: Pronotum black, with 3 bristles at each side on anterior margin. Mesonotum and metanotum almost wholly black, each with small, poorly defined, yellowish brown areas on posterolateral shoulders of scutum near wing bases. Pleura and coxae dark yellowish brown. Femora yellowish brown; tibiae darker yellowish brown; tarsi brown, darkest apically.

Wings (Fig. 126): Almost colorless, marked with bands and spots of dark



Figs. 126-132. *Neopanorpa borneensis* Byers, structural details of male holotype and female allotype. 126, left fore wing of male. 127, genital bulb, ventral aspect. 128, abdominal terga 3 and 4, dorsal aspect, showing notal organ. 129, genital bulb, left lateral aspect. 130, subgenital plate of female, ventral aspect. 131, genital plate, ventral aspect. 132, same as 131, right lateral aspect. Scale a—Fig. 126; scale b—Figs. 127-130; scale c—Figs. 131-132.

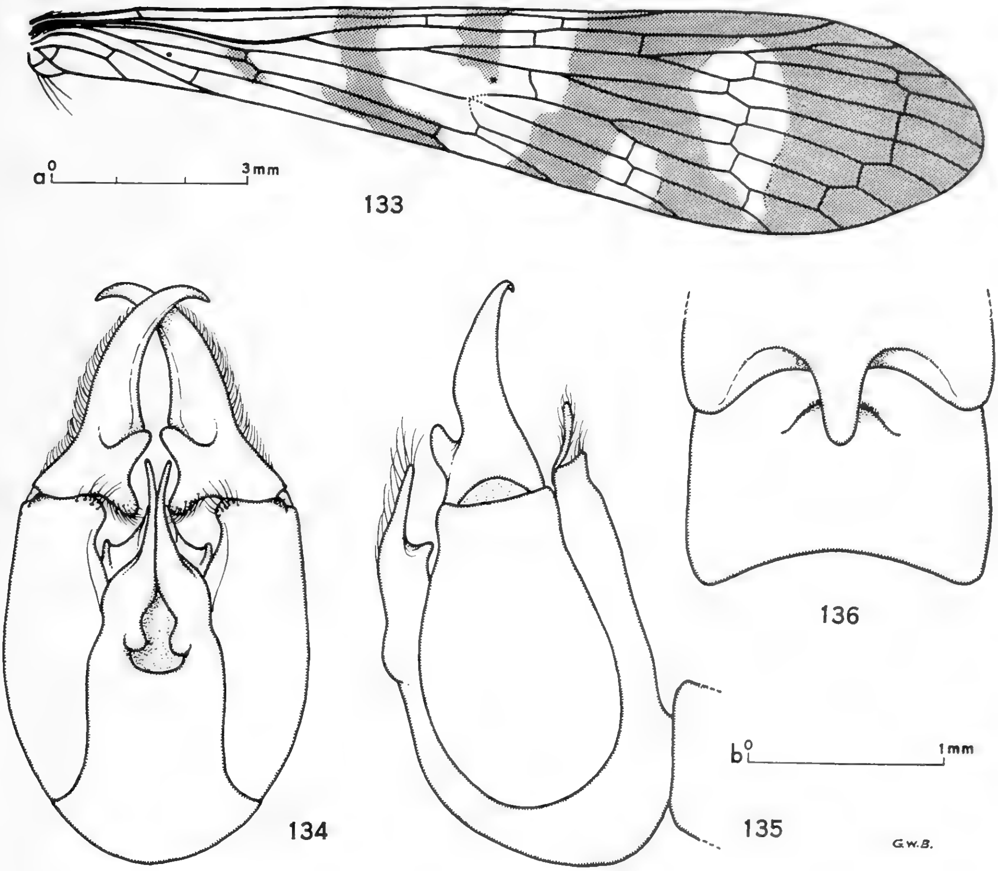
nean species has been discussed by Byers (1966).

Neopanorpa flavicauda Banks, 1931

Description modified from Banks (1931b) and Byers (1966).

Rostrum pale laterally. Antennal scape pale; left and half of right flagella lacking in lectotype. Legs yellowish brown.

Wings (Fig. 133): Clear, bands and spots almost black. Apical band complete. Pterostigmal band complete, broadly joined to apical band along costal margin, forked posteriorly, with distal branch as



FIGS. 133-136. *Neopanorpa flavicauda* Banks, structural details of male paralectotype. 133, right fore wing. 134, genital bulb, ventral (posterior) aspect. 135, genital bulb, right lateral aspect. 136, abdominal terga 3 and 4, dorsal aspect, showing notal organ. Scale a—FIG. 133; scale b—FIGS. 134-136.

broad as proximal branch; distal branch joined to apical band at margin in some specimens (not in lectotype). Marginal spot conspicuous. Basal band entire, slightly spurred proximad between veins Cu_1 and Cu_2. A small basal spot near mid-width of wing before basal band in most specimens.

Abdomen of male: Segments 7-9 pale yellowish brown. Segment 6 cylindrical and plainly longer than 5th; segments 7-8 shorter than 6th, 7th longer than 8th. Posterior process of tergum 3 linguiform in some males (Fig. 136), longer and more slender in lectotype than in male illustrated here. Dististyles thick, their outer margins markedly concave in basal half, abruptly curved at tips. Basal lobes of dististyles conspicuously divided into proximal and distal protuberances, distal one slightly the larger. Hypovalves of sternum 9 expanded basally, attenuate apically (Fig. 134), with a rounded basal lobe on mesal margin and a blunt dorsolateral projection near mid-length (Fig. 135). Aedeagus not examined.

Females have not been examined.

Lectotype: Male, Kenokok, Mt. Kinabalu, Sabah (British North Borneo), 1100 m, 26 April 1929, in the British Museum (Nat. Hist.), London. Paralectotypes: 4 ♂♂, 4 ♀♀, same data as for smoky brown. Apical band entire, somewhat faded posteriorly in both males, with included pale spot posteriorly in two females. Pterostigmal band entire, forked posteriorly, connected along costal margin to apical band. Cross-veins in area between apical and pterostigmal bands pale. Marginal spot extending from costa to M_{1+2} or farther. Basal band entire, strongly constricted near mid-length in male, not in female. Small basal spot present over cross-veins 1st m-cu and 1st cu.

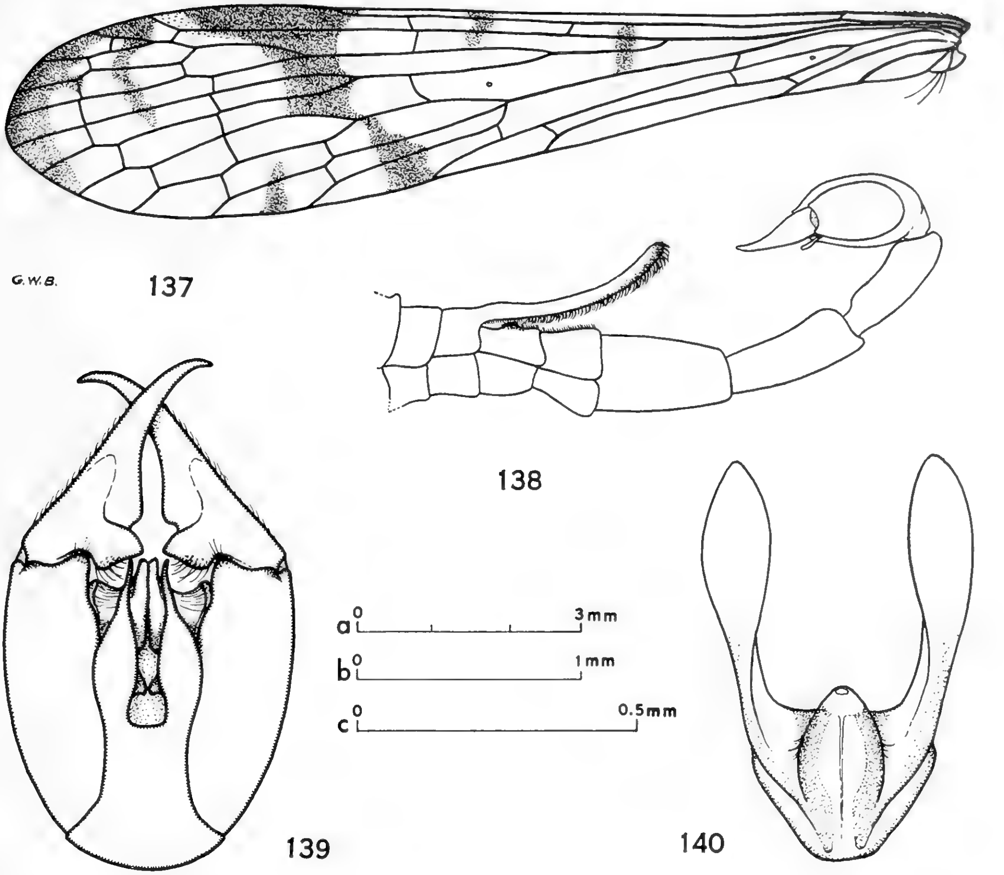
Abdomen of male: Terga 1-4 black, tergum 5 dark brown; corresponding sterna sordid yellowish brown mottled with brown. Segment 6 dark brown with yellowish brown apex; segments 7-8 yellowish brown; segment 9 dark yellowish brown, except tips of dististyles brown. Posterior process of tergum 3 slender, parallel-sided in apical half, extending about half-way across tergum 4 (Fig. 128). Prominence on tergum 4 rounded and smooth posteriorly, flattened and hairy anteriorly. Hypovalves dark yellow-brown, darkened apically, widened near mid-length, acuminate in apical half and bearing a few long hairs near apex, each with a stout, strongly sclerotized dorsolateral projection (Figs. 127, 129). Tergum 9 evenly tapered toward apex, with truncate apical margin. Dististyles stout, outer margins slightly concave near base, darkly sclerotized beyond mid-length. Basal lobes of dististyles comprising an elongate, hairy, ventral (posterior) projection and a more dorsal, thickened, less hairy portion sclerotized on lower, mesal margin (Fig. 127). Ventral valves of aedeagus sclerotized, rounded in lateral aspect, not projecting between hypovalves; bases of ventral parameres in form of narrow, acutely tipped blades projecting backward (ventrad) (shown as shaded V-shaped structure between bases of hypovalves, in Fig. 127).

Abdomen of female: All terga brownish black, sterna mottled, sordid brown; cerci black. Subgenital plate of sternum 8 broadly and shallowly notched at apex, with long setae on each apical lobe and on lateral margins of plate; pigmentation of plate in definite bilateral pattern with pale median streak (Fig. 130). Axial portion of genital plate broadly oval, flanked by wide, rounded, dorsoventrally thickened lateral lobes (Figs. 131, 132); arms of plate broadly spatulate, slightly twisted basally.

Body length: Male, about 12-13 mm (holotype 13 mm); female, about 10-14 mm (allotype 14 mm). *Length of fore wing:* Male, 13.6-14.4 mm (holotype 13.6 mm); female, 13.8-14.8 mm (allotype 14.6 mm).

Holotype: Male, Tenompok, 48 km E of Jesselton, Sabah (British North Borneo), 1460 m, 26-31 Jan. 1959, T. C. Maa. Allotype, female, Keningau, Sabah (British North Borneo), 12-17 Jan. 1959, T. C. Maa. Paratypes: 1 ♂, 5 ♀♀, Bundu Tukan, Sabah (British North Borneo), 18 Feb. 1959, T. C. Maa. Holotype, allotype and 4 paratypes in collection of the Bernice P. Bishop Museum, Honolulu, Hawaii; 1 ♂, 1 ♀ paratypes in Snow Entomological Museum, The University of Kansas. A male lacking abdominal segments beyond the 6th, from Kiam Base, north of Mt. Kinabalu, 4 Feb. 1959, was not made a paratype.

The three known Bornean species, *flavicauda, spicata* and *borneensis,* are easily differentiated from the Javanese and Sumatran species by the longer abdominal segments 7-8, the shapes of the accuminate-tipped hypovalves and aedeagus of the male, characters which also show the close relationship among them. The axial portion of the genital plate of Bornean species is usually rounded, as in species of the *fractura* group, and the lateral lobes of genital plate are much larger and more conspicuous, if present. The supposed relationship among these Bor-



FIGS. 137-140. *Neopanorpa spicata* Byers, structural details of male holotype and female allotype. 137, left fore wing, male. 138, abdomen of male, left lateral aspect, showing elongate posterior process of tergum 3 (notal organ). 139, genital bulb of male, ventral aspect. 140, genital plate of female, ventral aspect. Scale a—FIGS. 137-138; scale b—FIG. 139; scale c—FIG. 140.

lectotype, except 22, 23 and 26 April 1929, in the British Museum; 1 ♂, in the University Zoological Museum, Copenhagen; 2 ♂♂, 2 ♀♀ and 1 ♂ not labelled as a type but with the same data as the lectotype, in the Museum of Comparative Zoology, Harvard University.

For the probable relationships of this species, see under *N. borneensis.*

Neopanorpa spicata Byers, 1966

Description mostly repeated from original description (Byers, 1966), based on 11 males and 4 females.

Head: Dorsum glossy black; frons below antennal sockets dark brown; rostrum brown anteriorly, yellowish brown laterally; mouthparts yellowish brown. Antennal scape yellowish brown, pedicel brown; flagellum (both incomplete in holotype) black, with 40 to 42 flagellomeres.

Thorax: Pronotum black, with 4 or 5 bristles at each side on anterior margin. Mesonotum and metanotum mostly dark brownish black, each with poorly defined, pale yellowish brown areas on posterolateral shoulders of scutum near wing bases. Pleura and coxae sordid yellowish brown. Femora, tibiae and basitarsi sordid yellowish brown, apical tarsomeres brown.

Wings (Fig. 137): Mostly clear, slightly iridescent, with bands and spots smoky brown. Apical band in fore wings weakly indicated along margin in holotype, allotype and 7 paratypes, broader but deeply indented or including variously shaped clear areas in other paratypes. Pterostigmal band complete, constricted and almost broken near mid-length, forked posteriorly in some specimens. Marginal spot small, basal band short, not darkly colored (holotype) to complete but slender. A small basal spot in cell 1st Cu_1 in one paratype.

Abdomen of male: Terga 1-3 dark brown, terga 4-5 dark yellowish brown; sterna 2-5 dark yellowish brown. Segment 6 yellowish brown, segments 7-8 pale yellowish brown, segment 9 dark yellowish brown. Posterior process of tergum 3 long, stout, curved upward, densely set with black hairs especially on underside, extending to or slightly past mid-length of segment 6 (Fig. 138). Hypovalves of sternum 9 not darkened, separated throughout their length with small mesal lobe near base, widened near mid-length and tapered to acuminate tips (Fig. 139). Tergum 9 slightly narrowed toward truncate apex, with subapical ventral process on each side bent around segment 10. Diststyles long, slender, outer margins nearly straight except curved at tips. Basal lobes of diststyles strongly sclerotized mesally, shallowly excavated below. Ventral valves of aedeagus sclerotized, projecting posteriorly and ventrally (backward) between hypovalves; bases of ventral parameres in form of narrow, blunt-tipped blades projecting backward.

Abdomen of female: Terga 1-4 and about basal half of 5 brownish black; corresponding sterna pale yellowish brown; segments 6-10 dark yellowish brown; cerci black. Subgenital plate of sternum 8 apically notched with 2 thick, finger-like lobes above gonopore on dorsal surface. Axis of genital plate ovoid; genital plate without conspicuous lateral lobes (Fig. 140); arms of plate spatulate, somewhat twisted near base.

Body length: Male, about 11-13 mm (holotype 12 mm); female, about 9-11 mm (allotype 10 mm). *Length of fore wing:* Male, 12.2-13.2 mm (holotype 13.2 mm); female, 13.1-13.6 mm (allotype 13.6 mm).

Holotype: Male, Tenompok, 48 km E of Jesselton, Sabah (British North Borneo), 1460 m, 17-21 Oct. 1958, T. C. Maa. Allotype, female, same data as for holotype. Paratopotypes: 2 ♀♀, 17-21 Oct. 1958, L. W. Quate; 2 ♂♂, 20 Oct. 1958, L. W. Quate; 3 ♂♂, 1 ♀, 26-31 Jan. 1959, T. C. Maa. One additional ♂ paratype, Singkor, Sabah (British North Borneo), 19 Jan. 1959, Maa. The holotype is pinned together with a small ichneumonid wasp on which it was feeding at the time of capture. Holotype, allotype and 10 paratypes in the Bernice P. Bishop Museum, Honolulu, Hawaii; 2 ♂♂ and 1 ♀ paratypes in the Snow Entomological Museum, The University of Kansas.

The probable relationships are mentioned under *N. borneensis.* The elongate notal organ (posterior process of abdominal tergum 3), the longer abdominal segments 7-8 and the shapes of the hypovalves and aedeagus of the male allow *spicata* to be easily differentiated from other Bornean species of *Neopanorpa* and from the Javanese and Sumatran species.

UNGROUPED SPECIES

Neopanorpa lieftincki, new species

Description based on 3 males, 1 female, pinned.

Head: Dorsum glossy brownish black; frons below antennal sockets dark brown; rostrum dark brown anteriorly, yellowish brown laterally; mouthparts dark brown, tips of palps blackish brown. Antennal scape brown, pedicel dark brown, flagellum dull brown at base, grading into dull dark brown, with 42 (holotype) to 43 flagellomeres.

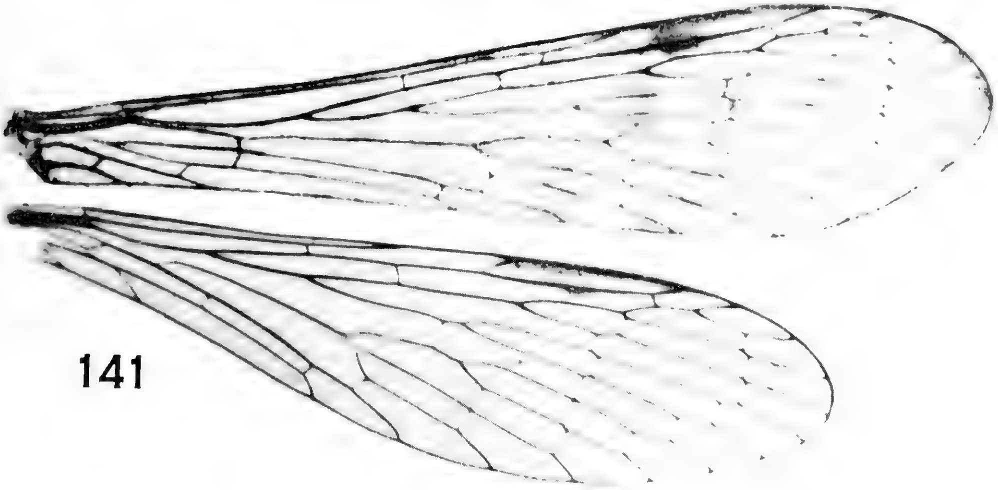


FIG. 141. *Neopanorpa lieftincki,* new species, right wings of female paratype.

Thorax: Pronotum brownish black, bearing 4 bristles on each side along anterior margin. Mesonotal and metanotal scuta mostly black, brown along posterolateral margins and dark brown near wing bases; scutella dark brown. Pleura and coxae dull yellowish brown, brown (two paratypes) or dark brown (female). Femora yellowish brown; tibiae and tarsi dark brown.

Wings (Fig. 141): Almost colorless and slightly iridescent, with faint smoky brown markings. Apical band reduced to small, faint spots, or almost absent. Pterostigmal band indistinct, slender, constricted or broken at mid-length, with distal branch present only as separate spot at posterior margin of wing. Marginal spot absent. Basal band represented by two faint spots. Hind wing clear except for faint, poorly defined pterostigma.

Abdomen of male: Terga 1-5 blackish brown to dark brown (one paratype); sterna 2-5 yellowish brown. Segment 6 blackish brown dorsally, dark brown ventrally. Segments 7-9 brown (7 reddish brown in one paratype), except hypovalves of sternum 9 dull yellowish brown and dististyles dark brown apically. Posterior process of tergum 3 short, triangular, extending about one-third across tergum 4 (process deformed in holotype, bearing a projection laterally on left, Fig. 147). Hypovalves of sternum 9 dull yellowish brown, expanded in apical 2/3, mesal margins broadly overlapped, outer margins strongly infolded dorsally, folded edges subparallel in ventral aspect (Fig. 142). Ninth tergum yellowish brown, slightly constricted near apex and bearing long hairs at both sides of very slight emargination (Fig. 146). Cerci pale basally, dark brown apically. Basistyles brown, with two large, membranous pouches (probably pheromone sacs) anteroventrally between them (Figs. 142, 145); dististyles brown at base, dark brown apically, outer margins slightly concave in basal half (Fig. 142). Basal lobes of dististyles semicircular in ventral aspect, with crescentic ventromesal concavity; a few large pale hairs on ventral and distal surfaces (Fig. 145); a long seta projecting from dorsal surface of lobe and about 4 apically curved, smaller spines projecting from anterodorsal surface (Fig. 144). Dorsal, basal margins of basal lobes clear, thin subacute blades. Aedeagus slightly sclerotized, reddish brown; ventral valves large, narrowing ventrally to broad, appressed blades, slightly divergent at apex, projecting well beyond much smaller, blackened dorsal valves (Fig. 148); lateral processes simple, concave posteromesally; dorsal parameres subrectangular with uneven dorsal margin (Fig. 148); ventral parameres absent.

Abdomen of female: Terga 1-6 black; sterna 2-5 sordid dark yellowish brown, sternum 6 dull brown. Segment 7 dark brown. Terga 8-10 brown, corresponding sterna light brown. Cerci dark brown. Subgenital plate mostly yellowish brown, brown laterally, with slightly notched apex and a whitish, hairless streak (about one-third length of plate) anterior to notch; bearing long setae along lateral margins and at each side of notch. Axial portion of genital plate ovoid, with stout, divergent anterior apodemes (Fig. 150); arms of plate broad, subtranslucent toward apex, twisted and yellowish brown basally.

Body length: Male, 14.3-19.1 mm (holotype 18.3 mm); female (allotype), 16.7 mm. *Length of fore wing:* Male, 13.2-14 mm (holotype 13.7 mm); female (allotype), 14 mm.

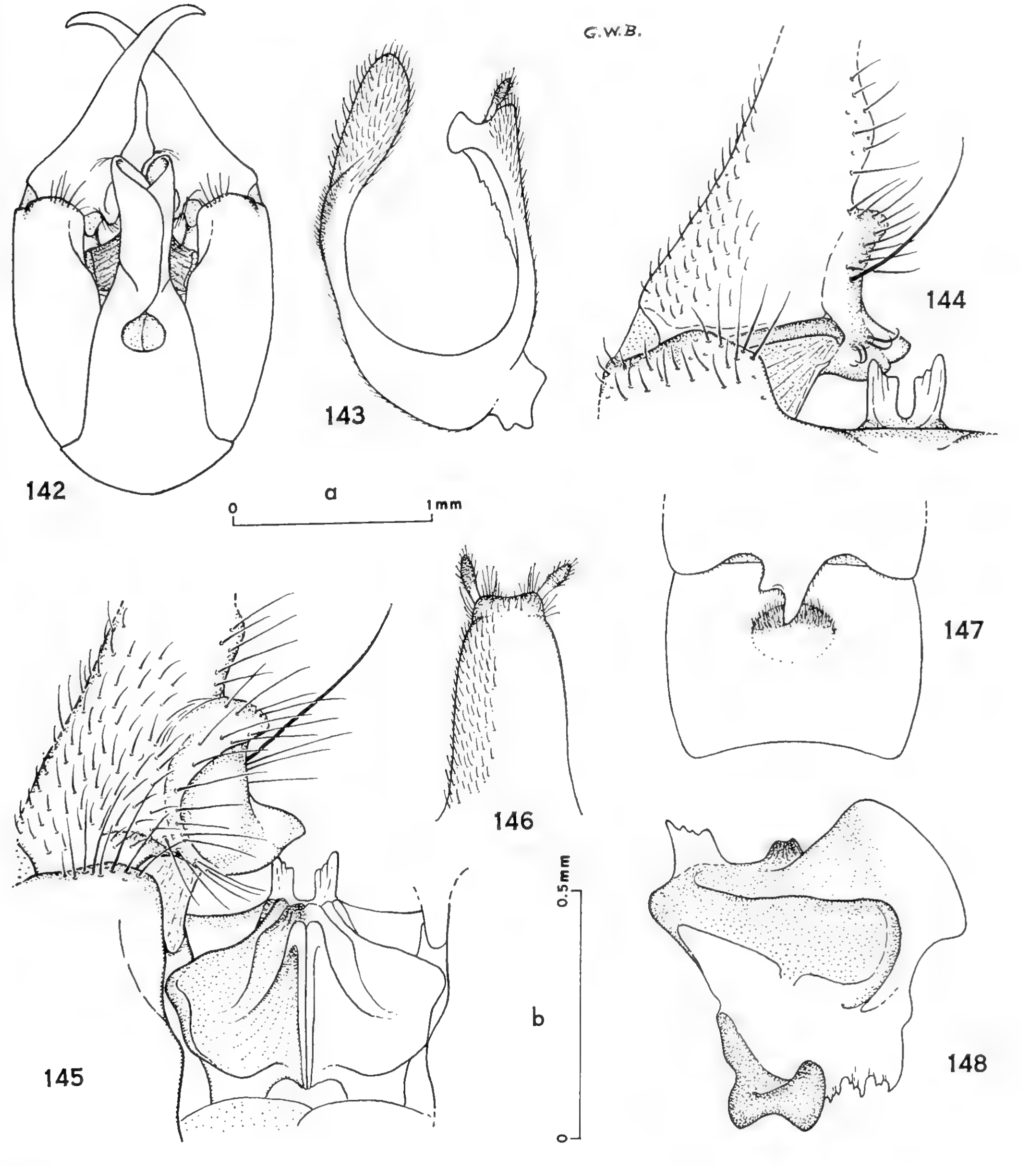
Holotype: Male, crater of Mt. Tanggamus, southwestern Lampongs, southern Sumatra (see map), 1900 m, 1 Jan. 1935, M. A. Lieftinck. Allotype, female and 2 male paratypes, same data as for holotype. Holotype, allotype and 1 ♂ paratype in the Rijksmuseum van Natuurlijke Historie, Leiden; 1 ♂ paratype in the Snow Entomological Museum, The University of Kansas.

Lieftinck (1936) says this species was immediately recognized as undescribed because of its vivid grass-green color during life. The four specimens he found were in the ancient crater of Mt. Tanggamus, about 33 m below the summit (2100 m). The crater holds a well-protected marsh with a luxuriant growth of *Rhododendron*. This species cannot be placed in any of the groups recognized above. It is close to the *muelleri* group on the basis of structure of aedeagus and the basal lobes of dististyles (except that it lacks the black dorsal spines). In the obscure, faint wing pattern, it looks identical with *diloba*. It differs from *diloba* by the shorter hypovalves and the way they are infolded. The genital bulb is also a little longer and more slender than those of *diloba* and *muelleri*, especially the dististyles. This species is named in honor of its discoverer, Dr. M. A. Lieftinck, in recognition of his great contributions to the knowledge of Indonesian Mecoptera.

COMPARISON BETWEEN *NEOPANORPA* AND *LEPTOPANORPA*

The genus *Leptopanorpa*, as mentioned earlier, occurs only in Indonesia, possibly in Java, only (there is a record of *L. charpentieri* from Sumatra, but it is doubtful), and contains 12 species. The records of *Leptopanorpa* from elsewhere than Java (*effusa*, Sikkim; *furcata*, Nepal; and *javanica*, in Hainan, Burma, etc.), pertain probably to *Neopanorpa* instead of to *Leptopanorpa* (Byers, 1965, 1971; Rust and Byers, 1976). Because of this confusion, *Neopanorpa* is compared with *Leptopanorpa* below.

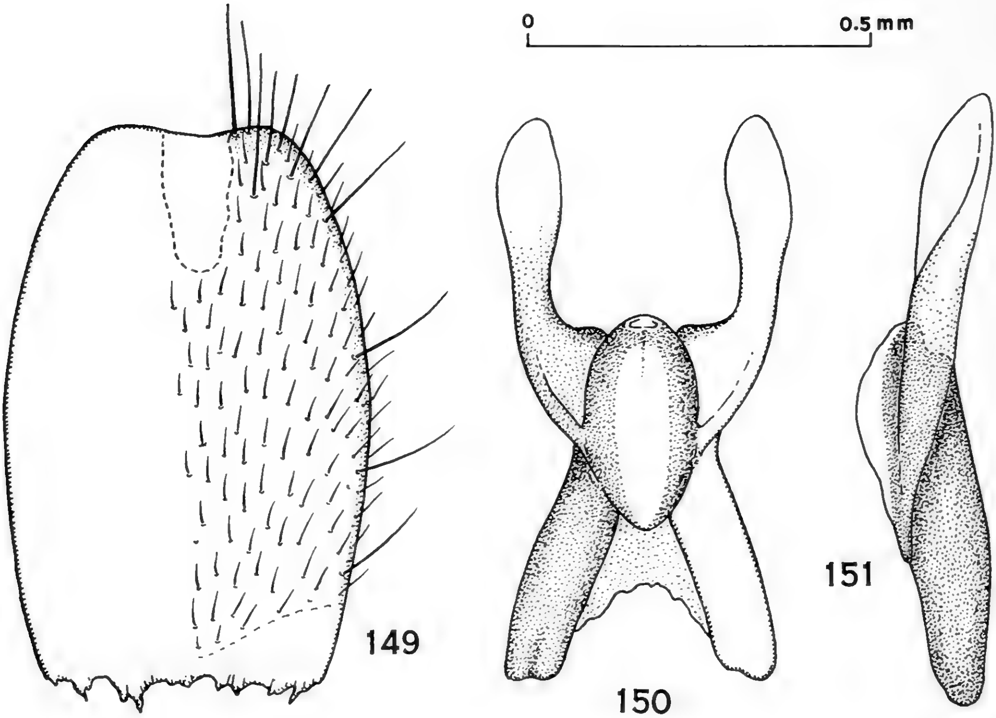
Neopanorpa and *Leptopanorpa* differ obviously in the body length of males. The body of males of *Neopanorpa* is about as long as the length of the wings or somewhat longer, but in *Leptopanorpa* it is usually much longer than the length of the wings (except *cingulata* and *javanica*). The different abdominal length is due mainly to the shape of abdominal segments 6-8. In *Neopanorpa*, these are robust and usually not elongate. In contrast, in *Leptopanorpa* they are ordinarily long and slen-



FIGS. 142-148. *Neopanorpa lieftincki,* new species, structural details of male. 142, genital bulb, ventral aspect; holotype. 143, ninth abdominal tergum and sternum, right lateral aspect; paratype. 144, base of right diststyle and dorsal parameres, dorsal aspect; paratype. 145, base of left diststyle and aedeagus, ventral aspect; paratype. 146, ninth abdominal tergum, dorsal aspect, most hairs omitted; paratype. 147, abdominal terga 3 and 4, dorsal aspect showing atypical (deformed) notal organ; holotype. 148, aedeagus, left lateral aspect; paratype. Scale a—FIGS. 142-143, 146-147; scale b—FIGS. 144-145, 148.

der (except in *cinglata, inconspicua, javanica* and *peterseni*). Wings of *Neopanorpa* are usually broad, whereas those of *Leptopanorpa* are slender and much narrowed basally, except in *javanica* (similar to *Neopanorpa*).

The shape of the genital bulb also differentiates these two genera. In *Neopanorpa,* it is broad, generally oval in ventral aspect, and without a stalk at the base of the 9th segment. In *Leptopanorpa,* it is slender, generally elliptical, and has



FIGS. 149-151. *Neopanorpa lieftincki,* new species, details of genitalia of female paratype. 149, subgenital plate, ventral aspect, hairs partially omitted. 150, genital plate, ventral aspect, only partly shaded. 151, genital plate, right lateral aspect.

either a fairly long, basal petiole (*ritsemae,* etc.) or a shorter one (*cingulata,* etc.).

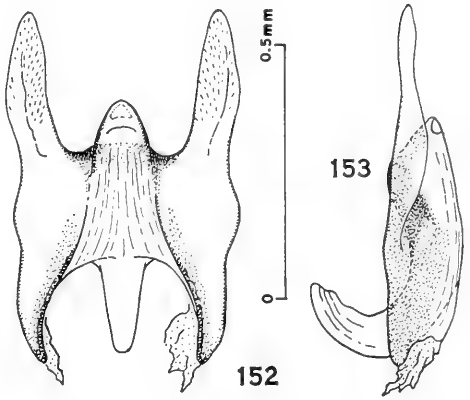
In the males of *Neopanorpa,* the hypovalves are usually broad, overlapping mesally or distally. Those of the Indian species *N. hirsuta* and *N. chillcotti* are more slender, as in some species of *Leptopanorpa.* However, in some species of *Leptopanorpa,* the hypovalves are broader than those of most *Neopanorpa,* yet never overlapping distally. The ninth abdominal tergum most easily differentiates these two genera. In most male *Neopanorpa,* tergum 9 has a broadly rounded distal margin, but in some species it is shallowly emarginate (e.g., *muelleri*); and in most it has subapical, lateroventral processes curving around segment 10 toward the interior of the genital bulb. In *Leptopanorpa* the median distal margin of tergum 9 either protrudes caudad slightly (as in *charpentieri*), or forms a distinct process (*ritsemae,* etc.). Terga of either genus have the lateroventral processes directed toward the interior of the bulb, as in most species of *Neopanorpa.*

The aedeagus of *Neopanorpa* is usually located more or less equidistantly from sternum 9 and tergum 9, whereas that of *Leptopanorpa* is more ventral in position, so that the dorsal parameres are approximately halfway between the ninth tergum and sternum. The ventral parameres of the aedeagus of *Neopanorpa* may be either fairly long on mainland Chinese species and a few Indonesian species (*diloba* and *angustiapicula*), short on most Indo-Chinese species, or absent, as from most Indonesian species, whereas those of *Leptopanorpa* are always large and complicated. The dorsal parameres of *Neopanorpa* are small, shorter than the ventral valves and almost invisible from dorsal view of the intact genital bulb, whereas those of *Leptopanorpa* are large, longer than the ventral valves and conspicuous in dorsal aspect. The ventral valves of *Neopanorpa* are the most conspicuous structures of the aedeagus in most species (except *diloba* and *angustiapicula*), whereas those of *Leptopanorpa* are much reduced and hardly visible. The lateral processes of *Neopanorpa* are broad and are evenly divided in *diloba* and *angustiapicula,* whereas those of *Leptopanorpa* are small.

One important difference is the shape of the basal lobes of the dististyles. They are rarely bilobed in *Neopanorpa* (except *diloba*) and most are concave anteroventrally (Indonesian and Indo-Chinese species), a few concave anteriorly (Indian species); but they are usually bilobed horizontally (in ventral aspect) in *Leptopanorpa,* except in *peterseni, cingulata, filicauda* and *inconspicua,* and are often concave dorsally.

The female of *Neopanorpa* is much like that of *Leptopanorpa* in general appearance, but the genitalia of the two genera are much different.

The subgenital plate in *Neopanorpa* is pale, apically, on most Indonesian species and some Indo-Chinese species. That of *Leptopanorpa* has a generally uniform color. The genital plates of *Neopanorpa* are much more flattened (except *umbonata*) than those of *Leptopanorpa* (except of *ritsemae, filicauda*). In *Neopanorpa,* the axial portion of the genital plate is sometimes forked anteriorly, whereas in *Leptopanorpa* it is either bluntly rounded or with broad basal plates, or protrudes ventrally, or bears a pair of small basal processes. The arms of the genital plate of *Neopanorpa* are usually broader than those of *Leptopanorpa* (except *robusta, cingulata* and *sarangana,* in which they are as broad as those of *Neopanorpa*). This difference is not easily noticed, unless specimens to compare are available.



FIGS. 152-153. *Leptopanorpa charpentieri,* female syntype. 152, genital plate, ventral aspect. 153, genital plate, left lateral aspect.

As discussed above, under the heading of Zoogeography, we have examined the syntypes (1 ♂, 1 ♀) of *Leptopanorpa charpentieri* (Burmeister) and have compared the genital structures of the female with those of all Indonesian species. The genital plate (Figs. 152, 153) is clearly that of a *Leptopanorpa* and, in our opinion, the same as that described for *L. nematogaster* (MacLachlan) by Lieftinck (1936: 302, plate 14).

KEY TO GENERA OF PANORPIDAE

1. Vein 1A in front wing joining wing margin far beyond level of origin of radial sector; two cross-veins between 1A and 2A; in hind wing, 1A united with Cu_2 for only a short distance near wing base .... *Panorpa*

   Vein 1A short, extending little more than half distance from wing base to origin of radial sector in front wing; one cross-vein between 1A and 2A; in hind wing, 1A fused with Cu_2 nearly its entire length except for short distal portion resembling diagonal cross-vein 2

2. Abdomen of male long and slender, segment 7 twice or more (usually 2.5-3.5 times) length of segment 5; segment 3, excluding appendage, as long as or longer than its width; segment 9 tapering to slender, often elongate petiole at base; abdominal tergum 9 with small to conspicuous median caudal projection; axial portion of genital plate of female dorsally expanded, appearing thick when viewed from side .... *Leptopanorpa*

Abdomen of male shorter, extending only slightly beyond wing tips, with segment 7 not twice length of segment 5 and usually 1-1.5 times as long; segment 3, excluding appendage, wider than long; segment 9 narrowing abruptly to short, inconspicuous petiole at base (except *N. effusa* and *N. furcata* of Himalayas); tergum 9 without median caudal projection; axial portion of genital plate of female without dorsal expansion .... *Neopanorpa*

GAZETTEER

Localities in the following gazetteer are arranged alphabetically. The number before each listed locality corresponds to a numbered locality on accompanying maps (Figs. 2-5). On the maps, localities are numbered from left (west) to right (east), except the maps of Java precede that of Sumatra. Data pertinent to each locality appear in the following sequence:

1. Name of locality as recorded on or translated from pin label.
2. Variant spellings of name, or synonymous names, in parentheses.
3. General region (W. J.—West Java; E. J.—East Java; C. J.—Central Java) in which locality is situated.
4. Geographic coordinates, if available, or reference to another locality that is well known.
5. Elevation where collection was made, if available.
6. Brief description of habitat, if available.

LOCALITIES

52. Airbangis, Sumatra; 0°12′ N, 99°23′ E; not below 1200 m; in the Padang Highland, not far from Fort de Kock.

55. Andalas, Tandj, Sumatra; 0°07′ S, 100° 41′ E; no elevation recorded; a village.

45. Bajukidul (Baju-Kidul), Mt. Raung, E. J.; 8°12′ S, 114°09′ E; 500-800 m; estate at foot of Mt. Raung, west of Banjuwangi; on the eastern coast of Java.

50. Bandarbaru (Bandar-Baru), northeastern Sumatra; 3°16′ N, 98°33′ E; 950 m; a village.

43. Baung, Banten, E. J.; 8°01′ S, 113°29′ E; at some altitude above Malang; a forest reserve.

23. Mt. Bengbreng, E. Djampang, W. J.; 7°13′ S, 107°20′ E; 400 m.

31. Mt. Bésér, W. J.; 7°11′ S, 109°39′ E; 1300 m.

1. Bibidjilan, Distr. Banten, south coast, W. J.; 200 m.

46. Blawan, Idjen Plateau, E. J.; 7°59′ S, 114°09′ E; 950 m.

26. Bodjongkalong, Djampangs, W. J.; 7° 00′ S, 107°42′ E; 300 m.

49. Brastagi, northeastern Sumatra; 1400 m; a mountain resort at foot of Mt. Sibajak, some hours by car south of capital, Medan.

54. Bukittinggi—see Fort de Kock.

9. Mt. Bunder, Salak, W. J.; about 6°42′ S, 106°44′ E; 800 m.

62. Mt. Dempu, Air Njuruk, Sumatra; 5° 07′ S, 104°55′ E; no elevation recorded.

13. Depok, W. J.; 6°24′ S, 106°50′ E; 50-100 m; a small nature reserve between Djakarta and Bogor.

44. Djambangan, Tengger Mts., E. J.; 7°58′ S, 113°37′ E; 1800 m.

11. Djampangtengah, Mt. Malang, W. J.; 7° 03′ S, 106°48′ E; no elevation recorded; a village.

41. Djunggo, Malang, E. J.; 7°48′ S, 112°31′ E; no elevation recorded.

54. Fort de Kock (Bukittingi), Sumatra; 0° 19′ S, 100°22′ E; 920 m; a city.

20. Mt. Gedeh, Tapos, W. J.; 6°47′ S, 106° 59′ E; 700-800 m and 1200-1700 m.

60. Giesting, Mt. Tanggamus, southwestern Lampongs, southern Sumatra; 5°25′ S, 104°42′ E; 450 m; an estate on slope of Mt. Tanggamus.

30. Mt. Guntur, Kamojang, W. J.; 7°08′ S, 107°50′ E; 1400 m.

— Jesselton (Kota Kinabalu), Sabah; 5°59′ N, 116°04′ E.

36. Kaliurang (Kali Urang), Djokjakarta (Djocja), C. J.; 7°36′ S, 110°25′ E; low country; a town near Djokjakarta.

29. Kamodjang, Preanger, Mt. Guntur, W. J.; 7°10′ S, 107°48′ E; 1400-1450 m; collection was made in crater, near Garut.

3. Mt. Karang, Bantam, W. J.; 6°03′ S, 106°09′ E; 800-1000 m.

47. Kendeng Mts., Idjen Plateau, E. J.; 8°00′ S, 114°15′ E; 2000 m (1200-1300 m, acc. to Lieftinck).

— Mt. Kinabalu (Kini Balu, Kina Balu, Kina Batu), Sabah (British North Borneo); 6°05′ N, 116°30′ E; collection at 3300 ft (1015 m).

24. Lembang, Preanger, W. J.; 6°49′ S, 107° 36′ E; 900 m; a summer resort above Bandung.

53. Lubuksikaping (Lubuk-Sikaping), western Sumatra; 0°08′ N, 100°10′ E; 450 m; a town.

39. Mt. Madiun, E. J.; 7°37′ S, 111°31′ E; 1200 m.

7. Mt. Malang, Djambangan, W. J.; 6°28′ S, 106°43′ E; 800 m.

27. Mt. Manglajang, Preanger, W. J.; 6°52′ S, 107°44′ E; 1400 m.

37. Marcodjambangan, Mt. Muria, northern Java; about 6°36′ S, 110°53′ E; 1000 m; one of the elevations of the Mt. Muria Complex.

15. Mt. Megamendung, W. J.; 6°38′ S, 106° 55′ E; 600 m; south-east of Bogor, in the hills near Mt. Gedeh.

56. Muarasako (Muara Sako), Sumatra; 2° 07′ S, 101°13′ E; no elevation recorded.

42. Nongkodjadjar (Nongkodjadar), Tengger Mts., E. J.; 7°54′ S, 112°49′ E; 1200 m; a summer resort.

33. Oengaran—see Mt. Ungaran.

48. Ongop-ongop, Idjen Plateau, E. J.; about 8°05′ S, 114°15′ E; 1850 m; a village.

19. Mt. Pangerango, W. J.; 6°46′ S, 106°57′ E; no elevation recorded.

14. Pantjar Mts., Mt. Gedeh, W. J.; 6°35′ S, 106°54′ E; 1500 m.

28. Pateungteung, W. J.; 7°09′ S, 107°46′ E; 1300 m; a town.

32. Patjet, Mt. Bésér, W. J.; 7°34′ S, 109°50′ E; 1300 m.

4. Preanger, W. J.; 7°12′ S, 106°47′ E; 1500 m; an upland area in W. J.

22. Radjamandala, W. J.; 6°50′ S, 107°20′ E; 335 m; a village.

16. Selabintana, Mt. Gedeh, W. J.; 6°52′ S, 106°57′ E; 1000 m; near Sukabumi.

34. Semarang, C. J.; 6°58′ S, 110°25′ E; no elevation recorded.

57. Serapai, Mt. Kurintji (Korinchi), Sumatra; about 1°42′ S, 101°16′ E; 1000-1400 m.

58. Subanajam (Suban Ajam), Sumatra; about 4°15′ S, 103°00′ E; 800-1000 m; in Bengkulen.

12. Sukabumi, W. J.; about 6°13′ S, 106°46′ E; no elevation recorded.

21. Sukanegara, Djampangs, W. J.; 7°06′ S, 107°07′ E; 700-1000 m; in a damp forest.

40. Sumberbrantas (Sumber Brantas), Mt. Ardjuno-Mt. Andjasmoro, E. J.; about 7°45′ S, 112°30′ E; 1500-2400 m.

51. Tandjunggading, west coast of Sumatra; 3°18′ N, 99°20′ E; 1000 m; a village.

59. Mt. Tanggamus (crater), southwestern Lampongs, southern Sumatra; 5°25′ S, 104°42′ E; 1900 m; *Neopanorpa lieftincki* n. sp. was taken here, in the forest below summit of Mt. Tanggamus.

25. Mt. Tangkubanprahu (Tangkuban Prahu), Preanger, W. J.; 6°44′ S, 107°36′ E; 1400 m.

35. Telomojo, Res. Kedu, C. J.; 7°22′ S, 110°24′ E; 1200 m.

— Tenompok, 48 km E of Jesselton, Sabah; approximately 6°00′ N, 116°30′ E; south foot of Mt. Kinabalu; elevation not recorded but probably near 2000 m.

18. Tjibodas, Mt. Gedeh, W. J.; 6°45′ S, 107°01′ E; 1550-1700 m.

2. Tjibunar Estate, Mt. Gedeh-Pangrango, W. J.; 6°50′ S, 106°04′ E; 1000 m; on west slope of Mt. Gedeh-Pangrango.

38. Tjilo, Muria Mts., C. J.; 6°40′ S, 110°54′ E; 800 m.

8. Tjiomas, Warungloa (Warung Loa), Mt. Salak, W. J.; 6°36′ S, 106°45′ E; 300-400 m; SE of Tjipeundeuj, Warungloa is a village at the foot of Mt. Salak, near Bogor.

5. Tjipeundeuj, Leuwiliang, W. J.; about 6°40′ S, 106°29′ E; 800-900 m; a village W of Bogor, in the hills near Mt. Gedeh.

17. Tjisarua, Mt. Pangerango-Gedeh, W. J.; 6°40′ S, 106°59′ E; 1000-1300 m.

10. Mt. Tjisuru, W. J.; about 7°24′ S, 106° 48′ E; 500-600 m; in the middle of the Djampangs District.

33. Mt. Ungaran, C. J.; 7°12′ S, 110°20′ E; 800-1200 m; where E. Jacobson collected many years.

61. Wai Lima, Lampongs, southern Sumatra; no elevation recorded; a coastal village in the Lampong District, extreme southern Sumatra.

60. Wai Tebu, Mt. Tanggamus, southern Sumatra; 300-500 m; a river near Giesting at foot of Mt. Tanggamus.

6. Wynkoops Bay, Pelabuhanratu, southwestern Java; 7°03′ S, 106°27′ E; no elevation recorded; in low country.

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