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An Ecological Study Of The Vegetation Of The Big Salt Marsh, Stafford County, Kansas

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ABSTRACT. This paper contains a qualitative and quantitative description of the vegetation of the Big Salt Marsh, Stafford County, Kansas. An analysis of the soil and water is included and correlations are shown between the edaphic conditions and plant distribution.

There is also a discussion of the salt tolerance of marsh species and their successional and climax relations.

Seed germination studies with *Bromus japonicus, Haplopappus phyllocephalus* subsp. *annuus* and *Suaeda depressa* indicate their salt tolerances.

INTRODUCTION

During the 1958, 1959, and 1960 growing seasons an ecological study was carried out on the Big Salt Marsh in the northeastern corner of Stafford County, Kansas. The study was made to determine the types of vegetation and the factors which affected plant distribution in this area.

The only investigation on the distribution of salt marsh vegetation in Kansas was by Schaffner (1898), who studied some northern Kansas salt marshes. Hitchcock (1898) made a cursory list of nine species he found on the Big Salt Marsh.

In these earlier works no quantitative methods were used in studying the vegetation and only a very small amount of data were presented on the salt tolerance of the species observed. The present work submits quantitative data and attempts to fill other gaps which are present in our knowledge of the vegetation and salinity tolerance of species in inland salt marshes.

No attempt has been made in this paper to review the entire literature on coastal halophytic vegetation and the physiology of halophytes in general. The reviews of Uphof (1941), Magistad (1945), Hayward and Wadleigh (1949), Hayward and Bernstein (1958) and Chapman (1960) provide a

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fairly complete bibliography and discussions of the literature on these subjects.

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LOCATION

According to Schoewe (1949) the Big Salt Marsh is located in the Great Bend Lowland of the Central Lowland physiographic province. The marsh, situated in the northeastern part of Stafford County, Kansas (T.21S., R.11W., and the northern row of sections of T.22S., R.11W.), covers parts of 12 sections (Fig. 1) and has an elevation of 1,737 feet above sea level. The total relief in this general area is less than 200 feet and on the marsh it is 40 feet. Sand-dune topography is characteristic of this general area except for relatively small sites such as the salt marsh.

ORIGIN OF SALT

Latta (1950) stated that waters in the Pleistocene, Meade Formation, in the vicinity of the Big Salt Marsh, were highly mineralized and contained high concentrations of chloride. He believed that the source of this water is in the Permian and Cretaceous rocks which are known to be highly mineralized. Hay (1891) estimated that the thickness of the salt masses ranged from one inch to one hundred feet. In a later study Bass (1926) estimated from oil well logs that the bed of rock salt was 150-200 feet thick and lay 1,000 feet below the surface. Kulstad (1959), using data from well samples, drillers logs and electric logs, calculated that the salt bearing rocks in this area were 300-350 feet thick and contained 60-80% salt.

A high bedrock ridge trending approximately perpendicular to the direction of ground water movement, according to Latta (1950), causes the highly mineralized waters at the base of the Meade Formation to be forced upward. These waters are discharged at the surface of the marsh where the salts are further concentrated by evaporation. A report of the ion content of the ground water by Latta (1950) at three locations in the vicinity of the Big Salt Marsh is cited in Table 1.

TABLE 1. Ground water relations at three locations in the Meade Formation in the vicinity of the Big Salt Marsh. Sample A was at T.21S., R11W., SW cor. sec. 24, 160-165 ft., sample B in T.21S., R.11W., NW cor. sec. 25, 207-212 ft. and sample C at T.21S., R.11W., NE sec. 27, 32 ft. All reports are recorded in P.P.M. Water analysis taken from Latta (1950).

Site	Dissolved solids	Fe	Ca	Mg	Na and K	HCO_3	SO_4	Cl	F	NO_3	SiO_2	CO_3
A	24,167	.96	433	315	8,377	372	1,803	13,050	.6	5.3	......	305
B	44,660	2.1	712	391	15,880	310	3,113	24,440	1.3	9.3	......	254
C	2,150	.11	131	10	664	382	116	895	1.0	142	......	313

CLIMATE

Weather Bureau reports at Hudson, Kansas, eight miles southwest of the Big Salt Marsh, give the annual precipitation in this area from 1931-1959 as an average of 23.99 inches, from a low of 14.17 inches in 1936 to a high of 39.61 inches in 1957. The average monthly precipitation for 1931-1959 was as follows: January, 0.62; February, 0.88; March, 1.31; April, 2.27; May, 4:11; June, 3.80; July, 3.19; August, 2.55; September, 2.14; October, 1.62; November, 0.78; December, 0.72. According to Park and Dennis (1947) the average growing season in this area lasts 172 days, April 28 through October 20, and from a calculation of the data above it was found that 72% of the total precipitation occurred during this period. Rainfall in this area is sporadic and the total for a given month may fall in a single rainstorm.

This marsh lies between the 98th and 99th meridians and within the 23 inch rainfall zone, which Weaver and Albertson (1956) report as being part of the Mixed Prairie Region of Kansas.

The average yearly temperature (°F), as recorded at the Hudson Weather Bureau from 1951-1958, was 56.5 with a range of 55.2 in 1958 to a high of 58.4 in 1953. The average monthly temperatures for 1951-1958 were as follows: January, 32.6; February, 37.6; March, 41.9; April, 55.0; May, 65.3; June, 78.5; July, 81.1; August, 80.6; September, 71.7; October, 59.3; November, 43.7; December, 35.2. The high air temperatures and low relative humidity during the summer months causes rapid evaporation of moisture from the soil and plants.

Data which Flora (1948) reported from the Wichita Weather Bureau indicates that the prevailing winds are from the south, except for the month of February. The wind velocity at Wichita for 1932-1935 averaged 12 miles per hour annually, and at Dodge City for the same period it was 12.9 miles per hour.

This area has a yearly average of 140-180 clear days and receives 70-80% of the total possible sunshine occurring from June through August. According to Borchert (1950), this grassland region, compared to forested areas, is typified by fewer days with precipitation, less cloud cover, and a lower relative humidity on the average during July and August. He also mentions that there is a great chance of a rainfall deficit during the summer and that low rainfall and snowfall are typical of winters.

HISTORY AND MANAGEMENT

According to Schoewe (1953), the Big Salt Marsh is one of the original 12 granted by congress to Kansas on its admission to statehood in 1861. Andreas (1883) has stated that no attempt at settlement was made in this portion of Stafford County prior to 1876. In 1876, however, a few people did move into the area, and, according to Sheridan (1956), a company was organized for the purpose of manufacturing salt on the marsh. Shortly after, it was found that this operation would be unremunerative and the undertaking was abandoned. Another factor which may have affected the vegetation in early times was grazing. A report in the Hutchinson News (1886) mentioned that there was an excellent area for stock pasturage along the salt marsh. Hay (1890) has also mentioned that salt marshes were used by native animals as a source of salt in early times.

Two original surveys in this county covered parts of the marsh area. The first, by Wilcox (1870), reported that the land was generally poor and more or less sandy and that there were no stones or timber in the area. Another survey by Thompson (1871) indicated that willows and cottonwoods were present. He stated also that waters of the salt marsh were quite salty and the drying up of the area caused the flats to be covered with a thin coating of salt.

At present, the most southern part of the study area, containing sandhills of an old beach ridge in sections 3, 4, 5, and 6, T.22S., R.11W., is heavily grazed throughout the growing season. Other areas which have been disturbed by grazing are the *Scirpus americanus-Eleocharis rostellata* areas along the western margin of the marsh. Some of these are heavily grazed throughout the growing season; however, the one quantitatively analyzed in this study has been only lightly grazed in April of some years. The sandhill prairie areas on the eastern margin of the marsh, south of the east-west road which bisects it, are being grazed at the present time. The prairie area analyzed has not been grazed in the recent past, but both it and the *S. americanus-E. rostellata* Community are mowed in late summer. The remainder of the communities, which make up the largest part of the area, are relatively undisturbed.

In the past some ridges were made on the marsh when shallow lakes were constructed, and these still persist. Another factor altering natural conditions is that several small ditches have been dug to increase the rate of drainage, and in recent years the drilling of oil wells on the marsh area has caused some disturbance, but none has produced oil. In the future, the marsh should be less disturbed than in previous periods, since it has been included in the Quivira Wildlife Refuge which is being administered by the Fish and Wildlife Service.

WATER RELATIONS

Water Table and Drainage

The marsh contains a complex of several shallow lakes, which are filled during wet periods when the water table is high. During the summer months there is a great deal of evaporation and a lowering of the water table, causing the surface of some of the lake beds to be covered by a white precipitate of salt.

The only outlet from the marsh is in the northeastern corner (Fig. 1) where a short tributary carries the marsh waters into Rattlesnake Creek. The waters on the marsh rarely reach depths greater than 2-3 feet because man-made ditches drain parts of the area.

METHODS AND RESULTS OF WATER ANALYSIS

Water samples were taken from lakes, small ponds, and ditches throughout the growing season. The saturation extract technique for determining total salts and titration with silver nitrate for chloride determination were used as described in Richards *et al.* (1954). The pH was determined with a Beckman model H_2 pH meter.

Water samples collected by the author in 1959 and 1960 indicated some seasonal fluctuation in salinity. The fluctuation in salt content which occurs in inland saline lakes was indicated by Flowers (1934) in his work on the Great Salt Lake, where he found a 1% increase in salt concentration with each one foot decrease in water level. The regularity of seasonal salt fluctuation in the waters of the Big Salt Marsh is much less than that reported by Purer (1942), Rawson and Moore (1944), and other authors. This can be explained by the fact that a regular fluctuation would occur only if there were definite dry and wet periods, and although there is a tendency for drying during July and August in this area, extremes in local weather conditions occur over short periods during the growing season. These fluctuations in weather, usually sporadic rains, cause fluctuation in salt content during any one month.

As mentioned by Penfound and Hathaway (1938), surface waters cannot be considered of primary significance in fixing the actual distribution of plants except as to their influence on ground water. This holds true for most plants since roots usually penetrate into the soil and do not trail along the surface; however, the condition of the surface water does directly affect the distribution of submerged or floating aquatics found in these areas.

It was found in this water analysis, as well as in the soil analysis which follows, that the chloride ion concentration fluctuated more or less directly with the total salinity. Table 2 shows that there was a general increase in the salt content during the month of July. This can be accounted for by a more or less uniform drying up of the marsh during this period, causing a concentration of salts and in some areas leading to a complete evaporation of surface water. In a study of the ground water relations in this general region Latta (1950) took a few surface water samples on the Big Salt Marsh. One sample of special interest was taken from site one (see Table 2) in July, 1944. It had a total salt content of 1.08% and a chloride content of 0.59%. This compares directly with the present author's record of July 1960 in which the total salts was 1.17% and the chlorides 0.65%, indicating that the higher July salinity may not be just an isolated incident but of general occurrence during each growing season. Exceptions to this trend of a higher July salinity are sites 5 and 11, which had only a negligible salt content, and site 9, which was brackish but followed no clear pattern. A second explanation for the data presented in Table 2 could be that there was an irregular fluctuation in salt content throughout the growing season and that drier periods produced the higher salinities.

The pH relations in the various ponds give no clue to the salinity relations nor do they indicate what vegetation might occur in a pond. The 11 ponds studied had a pH of 7.5-8.2, but in no way could it be correlated with salinity in any of these areas. Site 11, a fresh water seep, had a pH of 7.2-8.7, and an average of 8.0, while the area which reached the highest salinity, site 7, had a pH which averaged 7.5 and a range of 6.7-8.1.

The following is a list of the sites from which water samples were collected and tested for total salinity, chloride ion concentration, and pH throughout the growing season. The numbers given to the sites listed correspond with the numbers used in Table 2 and Fig. 2.

1. A small pool north of the east-west road bisecting the marsh in the SE¼ sec. 22, T.21S., R.11W.
2. The main drainage ditch connecting the south and north areas of the marsh which is located under a small bridge along the east-west road in the NE¼ sec. 27, T.21S., R.11W.
3. A small shallow pool north of the east-west road in the SE¼ sec. 21, T.21S., R.11W.
4. A roadside ditch on the north side of the east-west road in the SE¼ sec. 21, T.21S., R.11W.

5. A small pool just north of the east-west road located .4 miles east of the north-south road bordering the marsh on the west in the SE¼ sec. 20, T.21S., R.11W.
6. A large shallow lake in the northeast corner of the marsh in the SE¼ sec. 15, T.21S., R.11W.
7. The northeastern drainage outlet of the marsh in the NE¼ sec. 22, T.21S., R.11W.
8. A shallow lake, south of hunting cabin, in the S½ sec. 28, T.21S., R.11W.
9. A small pond along a man made hummock in the NW¼ sec. 33, T.21S., R.11W.
10. A large shallow lake in the southern part of the marsh in sec. 33, T.21S., R.11W.
11. A seepage area north of the east-west road which forms the southern boundary of the marsh in the SE¼ sec. 4, T.22S., R.11W.

TABLE 2. An analysis of the total salinity (T.S.), chloride ion concentration (Cl.) and pH of waters located on the Big Salt Marsh. Total salts and chloride are expressed as a percentage.

Site		May	June	July	Aug.	Sept.	Avg.
1.	T.S.	.48	.70	1.17	.52	.45	.66
	Cl.	.20	.33	.65	.24	.21	.32
	pH	8.3	7.1	8.5	7.7	7.3	7.7
2.	T.S.	.39	.75	1.15	.48	.27	.60
	Cl.	.16	.34	.61	.22	.12	.29
	pH	8.2	7.2	8.3	7.1	7.2	7.6
3.	T.S.	.39	.28	......	......	.25	.30
	Cl.	.17	.12	Dry	Dry	.10	.13
	pH	8.5	7.9	......	......	7.7	8.0
4.	T.S.	.21	.35	......	.30	.37	.30
	Cl.	.08	.15	Dry	.12	.21	.14
	pH	8.2	7.3	......	7.1	8.2	7.7
5.	T.S.	.05	.19	.16	.05	.18	.12
	Cl.	.01	.09	.06	.02	.07	.05
	pH	8.6	8.4	8.0	7.9	8.1	8.2
6	T.S.	.48	.39	.46	.22	.22	.35
	Cl.	.28	.18	.21	.10	.10	.17
	pH	7.7	7.3	8.7	8.3	8.0	8.0
7.	T.S.	.62	.55	2.96	.36	.29	.95
	Cl.	.30	.25	1.65	.15	.12	.49
	pH	8.1	6.7	7.6	8.0	7.2	7.5
8.	T.S.	.79	.54	1.26	.35	.28	.64
	Cl.	.42	.22	.50	.15	.16	.29
	pH	7.5	7.0	7.4	8.3	7.7	7.5
9.	T.S.	.52	.40	.42	.38	.45	.43
	Cl.	.25	.18	.28	.16	.25	.22
	pH	7.6	7.8	8.2	8.1	7.1	7.7
10.	T.S.	.76	.70	.80	.35	......	.65
	Cl.	.38	.30	.43	.15	......	.31
	pH	8.1	7.3	8.2	8.2	......	7.9
11.	T.S.	.02	.04	.03	.03	.05	.03
	Cl.	.01	.009	.009	.008	.01	.009
	pH	8.5	7.4	8.7	8.4	7.2	8.0

METHODS OF SOIL ANALYSIS

Total salinity was determined by the saturation extract method described in Richards *et al.* (1954). Chloride ion content and saturation percentage were also obtained by methods described in Richards *et al.* (1954). pH was determined by a Beckman model H_2 pH meter from a saturated soil paste. Mechanical analysis data were obtained following the method of Bouyoucos (1936), and for determining the organic content of soils the ignition method, described in Kurz and Wagner (1957), was used. Tables 3-6 contain the soil analyses data.

Soil samples were collected at two different depths. The first at 0-10 cm. and the second at 60-70 cm. The following is a list of sites from which soils were collected throughout the growing season and upon which tests were made for the various soil factors. The numbers given to the sites correspond with the site numbers used in Tables 3, 4, 5, and 6.

1. A Sandhill Mixed Prairie area 25 meters north of the east-west road bisecting the marsh and 25 meters east of a north-south road in the SE¼ sec. 22, T.21S., R.11W.
2. A *Sporobolus airoides* area 25 meters north of the east-west road and 50 meters west of the north-south road in the SE¼ sec. 22, T.21S., R.11W.
3. A Tall *Distichilis stricta* area 25 meters west of site 2 in the SE¼ sec. 22, T.21S., R.11W.
4. A Tall *Distichilis stricta* area 45 meters north of the east-west road and 25 meters east of the north-south man-made ridge in the SE¼ sec. 22, T.21S., R.11W.
5. Bare ground 50 meters north of the east-west road and 350 meters east of the north-south road in the SW¼ sec. 22, T.21S., R.11W.
6. A *Suaeda depressa* area 30 meters west of the north-south road and 100 meters north of the east-west road in the SE¼ sec. 21, T.21S., R.11W.
7. A *Suaeda depressa* area 300 meters west of site 6 in the SE¼ sec. 21, T.21S., R.11W.
8. A *Scirpus paludosus-Distichlis stricta* area 400 meters west of the north-south road and 139 meters north of the east-west road in the SE¼ sec. 21, T.21S., R.11W.
9. A *Distichlis stricta-Suaeda depressa* area 100 meters north of the east-west road and 150 meters west of the short false road in the SW¼ sec. 21, T.21S., R.11W.
10. A *Spartina pectinata-Distichlis stricta* area 100 meters north of the east-west road, directly north of the south road in the SW¼ sec. 21, T.21S, R.11W.
11. A *Distichlis stricta-Suaeda depressa* area 400 meters west of site 10 in the SW¼ sec. 21, T.21S., R.11W.
12. A *Spartina pectinata-Distichlis stricta* area 400 meters west of site 11 in the SW¼ sec. 21, T.21S., R.11W.
13. A *Distichlis stricta-Suaeda depressa* area 30 meters south of the east-west road bisecting the marsh and 200 meters west of the south road to a hunting cabin in the NW¼ sec. 28, T.21S., R.11W.
14. A *Scirpus americanus-Eleocharis rostellata* area 100 meters north of the east-west road and 300 meters east from the north-south road bordering the marsh on the west in the SE¼ sec. 20, T.21S., R.11W.
15. A *Distichlis stricta-Suaeda depressa* area 775 meters south of the east-west road and 200 meters west in the SW¼ sec. 28, T.21S., R.11W.

RESULTS OF SOIL ANALYSIS

SOIL TEXTURE

In an early survey of the soil in the marsh, Coffey, Rice, *et al.* (1912)

classified the surface soils as a silty clay and also mentioned that there were small spots of sand, sandy loam, and loam scattered throughout the area.

Park and Dennis (1947) stated that the soils of this area have been formed from outwash sands and silt which were mixed with loess deposits. They further mentioned that the soils were sandier on the tops of knolls and heavier and occasionally saline in the flats and depressions.

In this study the textural classes of the soils were arrived at by applying the actual percentages obtained in the mechanical analysis given in Table 3 to the triangular chart for soil textures in Lyon, Buckman, and Brady (1952).

In the present survey, the surface soils, 0-10 cm., of the prairie and *S. airoides* communities, sites 1 and 2, were classified as sand. The eastern part of the tall *D. stricta* Community was loamy sand, whereas the western part of this zone and all other soil sample sites except site 14 was classified as a sandy, clay loam. Site 14, dominated by a *S. americanus-E. rostellata* Community had a sandy loam.

Although the soils underlying the marsh were classified by Coffey *et al.* (1912) as a silty clay, in the present analysis at the 60 cm. level all sites except 11 and 14 were sand. Sites 11 and 14 were classified as a loamy sand.

ORGANIC MATTER

The organic content relations of the marsh were similar to other areas in that there was a general reduction in organic content from the surface soil downward. Table 3 shows that only in site 2 was there an exception, and the soils in this area had an extremely low organic content. The lowest organic content occurred in the sandy soils of the prairie and *S. airoides* areas. Site 14, located in the *S. americanus-E. rostellata* area, had the highest organic content, 23.4%, of any soil on the marsh.

SATURATION PERCENTAGE

The saturation percentage of the various soils was determined at all sites and is recorded in Table 3 as an average saturation percentage for the five months sampled. As would be expected, the sandiest soils, located in sites 1 and 2, had the lowest saturation percentages, 28% and 34%, of the surface soils. The sandy clay loam soils had a higher saturation percentage of 40-75% in the surface 10 cm., and the highest saturation percentage, 151%, was found in a sandy, clay loam soil of the *S. americanus-E. rostellata* Community. This soil had the highest organic content on the marsh, and, correspondingly, other sites with high organic content and clay content had high water-holding capacities. At the 60 cm. level the soils were generally sandy, and in all cases except sites 1 and 2 the saturation percentage was lower in these subsurface areas.

pH Relations

Table 4 shows that there is an irregular fluctuation in the pH of the surface as well as the subsoil in each of the community types during the growing season. In general the pH in the surface 10 cm. averaged lower or equal to the soil pH at the 60 cm. level. Daubenmire (1959) stated that surface soils have a tendency to be more acidic than sub-soils because of the greater quantities of acid-forming organic matter and the stronger leaching action in the upper levels. In only two cases, sites 5 and 13, did the surface pH average higher, and in both cases there was only 0.1 pH difference. The pH of the prairie area was 6.5, the *S. airoides* area 7.2, and in the remaining communi-

TABLE 3. An analysis of the saturation percentage, expressed as an average for the five months sampled, organic content, expressed as a percent of the organic matter in the September collection and the soil texture, expressed as a percent of the different size particles in the September collection. A equals 0-10 cm. and B equals 60-70 cm.

Site		Saturation Percentage	Organic Content	Soil Texture		
				Sand	Silt	Clay
1	A.	28	1.1	89.3	1.4	9.3
	B.	27	.4	91.3	1.4	7.3
2	A.	34	2.2	85.9	5.0	9.1
	B.	34	3.7	84.9	6.0	9.1
3	A.	43	2.5	78.9	6.5	14.5
	B.	40	.8	89.3	2.4	8.3
4	A.	75	6.2	58.7	10.0	31.3
	B.	39	1.6	89.7	.4	9.9
5	A.	40	5.3	69.9	5.4	24.7
	B.	30	1.0	87.7	.0	12.3
6	A.	40	3.6	72.7	7.0	20.3
	B.	34	2.6	83.9	3.6	12.5
7	A.	40	6.8	66.9	10.6	22.5
	B.	32	1.1	88.7	.0	11.3
8	A.	47	9.2	64.3	8.8	26.9
	B.	36	1.1	85.3	3.6	11.1
9	A.	41	9.3	65.9	10.0	24.1
	B.	31	1.7	89.9	.0	10.1
10	A.	56	17.9	49.9	20.0	30.1
	B.	32	4.6	91.9	.0	8.1
11	A.	44	11.2	68.3	8.6	23.1
	B.	31	4.4	78.9	6.0	15.1
12	A.	64	16.1	68.3	8.0	23.7
	B,	36	1.0	88.9	3.0	8.1
13	A.	44	6.6	51.9	13.4	34.7
	B.	32	2.2	84.5	7.4	8.1
14	A.	151	23.4	61.5	26.8	11.7
	B.	40	3.4	75.5	8.8	15.7
15	A.	62	17.5*	49.5*	22.4*	28.1*
	B.	33	1.1	91.5	.0	8.5

* The organic content and texture of soils from site 15 were obtained from the August collection.

ties averaged 7.7-8.4 in the surface soils. Keith (1958) mentioned in his cursory study of salinity relations in a Canadian salt marsh that pH may be an important factor in plant distribution after a certain salinity is reached. In this study as in those by Evans (1953) and Kurz and Wagner (1957) no correlation could be made between the various vegetation zones of the salt marsh proper and the pH values.

TOTAL SALINITY AND CHLORIDE ION CONTENT

As stated by Coffey *et al.* (1912), the factor which distinguishes the salt marsh soils from the other alluvial and aeolian soils of this area is the accumulation of salts, principally sodium chloride. The chief source of this sodium chloride is, as mentioned earlier, the rock salt deposits in the underlying Permian and Cretaceous rocks.

From the analysis of total salinity and chloride ion concentration given in Tables 5 and 6, it is clear that in general the total salinity and chloride ion concentration averages higher in the surface soils than in the subsoil sample. These findings also show that there is a variation in salinity and chlorinity between the various vegetation zones and also within each zone throughout the growing season. Here, as in the case of the ponds studied, the variation within a zone is not so great that one cannot separate the saline from nonsaline soils.

The main factors affecting the fluctuation of salinity in these soils appears to be rainfall and the evaporative capacity of the air. In accord with constant fluctuations in weather during the growing season there are corresponding fluctuations in the soil salinity. There is a tendency for the marsh area to dry up during July and August, and along with this there is a rise in salinity, but sudden showers during these months cause rapid salinity changes. Kurz and Wagner (1957), in their work on coastal marshes, reported that chlorinity fluctuates considerably within short periods of time, even at the same site, and they also mention that conditions of rain, drought, and seasonal temperatures are most important in modifying salinity relations. This same conclusion was reached by Stocker (1928) who stated, "These (salt) concentrations represent no constants; they show great fluctuations in the smallest space and especially also at different times." Novikoff (1958), in his work on the vegetation of the saline soils of Tunisia, also reported a temporal variation in soil salinity.

In comparing Tables 5 and 6 it should be noted, as one would expect, that the chloride ion concentration varies more or less directly with the total salinity. A similar correlation was made by Evans (1953) in his study of the halophytic vegetation of Lake Ellesmere, New Zealand. The salinity and chlorinity in the surface soil of the prairie was the lowest, with the salinity 0.003-0.02%, and averaging 0.01%. As one approaches the salt flats from the eastern prairie region there is a continuous increase in salinity, as illustrated

TABLE 4. An analysis of the pH of the soils sampled from the Big Marsh. A equals 0-10 cm. and B equals 60-70 cm.

Site		May	June	July	Aug.	Sept.	Avg.
1	A.	6.9	6.5	6.3	6.4	6.7	6.5
	B.	6.2	7.0	6.5	7.5	6.9	6.8
2	A.	7.9	7.2	6.8	6.5	7.6	7.2
	B.	8.2	8.3	8.9	7.5	8.5	8.2
3	A.	8.3	8.6	7.2	7.8	8.0	7.9
	B.	8.6	8.3	7.5	8.1	8.4	8.2
4	A.	8.6	8.3	8.0	8.2	8.2	8.2
	B.	8.0	8.2	8.0	8.8	8.1	8.2
5	A.	8.2	8.3	8.4	8.4	8.2	8.3
	B.	8.4	8.0	8.3	8.2	8.1	8.2
6	A.	8.8	8.1	8.2	8.3	8.0	8.2
	B.	8.4	8.4	8.1	8.1	8.1	8.2
7	A.	8.7	8.0	8.1	8.2	8.1	8.2
	B.	8.6	8.2	8.2	8.3	8.2	8.3
8	A.	8.3	8.6	8.4	8.4	8.4	8.4
	B.	9.2	8.9	9.0	8.8	8.7	8.9
9	A.	7.5	7.9	8.5	7.8	8.6	8.0
	B.	8.4	8.4	8.4	8.6	8.4	8.4
10	A.	8.0	8.0	8.2	8.5	8.1	8.1
	B,	8.4	8.8	8.3	8.4	8.7	8.5
11	A.	8.7	8.3	8.4	7.6	8.3	8.2
	B.	8.5	8.1	8.4	8.2	8.3	8.3
12	A.	8.6	8.8	8.6	8.3	8.1	8.4
	B.	8.6	8.6	8.4	8.6	8.2	8.4
13	A.	8.0	8.4	8.5	8.3	8.1	8.2
	B.	7.7	8.0	8.4	8.2	8.6	8.1
14	A.	7.7	7.9	7.6	7.9	7.8	7.7
	B.	7.4	8.6	8.5	8.4	8.0	8.1
15	A.	8.3	8.6	8.1	8.2	....	8.3
	B.	8.3	8.2	8.3	8.4	....	8.3

in sites 2, 3, and 4. This culminated in the area of highest salt content, the barren salt flats, where the surface soil salinity was 2.12-2.96%. Sites 6 and 7 had a cover of *S. depressa* and sites 9, 11, 13, and 15 a *D. stricta-S. depressa* Community. The soils at all of these sites were definitely saline, having seasonal averages of 1.04-2.15%. The soils of site 8, which contain an *S. paludosus-D. stricta* Community, were surrounded by highly saline soils. This area was most saline on its margins, where the May sample indicated a salinity of 1.10%, but was reduced toward its center as indicated by the 0.22-0.40% range for the remaining months. Sites 10 and 12 support a *S. pectinata-D. stricta* Community, and the surface soil salinity was 0.20-0.63% and 0.27-1.00% at each site respectively. The soils at site 14 maintain an *S. americanus-E. rostellata* Community and had a salinity in the surface 10 cm. of 0.23-

0.68%. This area of low salinity and chlorinity was on the western border of the study area.

The extreme change in salinity that can occur in an area due to local weather conditions is clearly noted at site 9. The September soil collection at this site was made the day after an extremely heavy rain, and the salinity and chlorinity in the surface soils were greatly reduced due to its diluting and leaching action. The 0.49% salt content at this site was almost 1% below the average salinity of 1.42% of the four preceding samples.

The importance of these salinity and chlorinity measurements is that they provide some information as to the extremes in variation that can occur in the various vegetation zones. It is usually not the average but the extremes

TABLE 5. An analysis of the total salinity of the soils sampled from the Big Marsh expressed as a percentage of the salts in the soil. A equals 0-10 cm. and B equals 60-70 cm.

Site		May	June	July	Aug.	Sept.	Avg.
1	A.	.02	.01	.003	.02	.005	.01
	B.	.009	.005	.003	.005	.002	.004
2	A.	.15	.04	.19	.10	.14	.12
	B.	.08	.04	.11	.01	.01	.05
3	A.	.34	.29	.63	.39	.31	.39
	B.	.18	.18	.25	.49	.31	.28
4	A.	.73	.75	.94	.79	.74	.79
	B.	.16	.35	.53	.65	.42	.42
5	A.	2.78	2.90	2.96	2.12	2.47	2.64
	B.	1.08	.98	.81	.73	.65	.85
6	A.	2.43	1.76	2.40	1.70	1.33	1.92
	B.	.98	.91	.80	1.29	1.15	1.02
7	A.	1.71	1.16	2.75	1.29	1.59	1.70
	B.	1.01	.74	.67	1.07	.33	.76
8	A.	1.10	.22	.27	.30	.40	.45
	B.	.32	.28	.29	.32	.45	.33
9	A.	1.43	1.27	1.55	1.45	.49	1.23
	B.	.57	.67	.35	.96	1.09	.72
10	A.	.20	.24	.39	.63	.62	.41
	B.	.07	.16	.40	.49	.36	.29
11	A.	.58	1.46	.67	1.52	1.01	1.04
	B.	.56	.76	.27	.70	.67	.59
12	A.	.59	.47	.27	1.00	.75	.61
	B.	.34	.12	.06	.25	.38	.23
13	A.	1.51	2.47	2.24	2.03	2.52	2.15
	B.	.72	.51	.56	.48	.41	.53
14	A.	.23	.18	.38	.53	.68	.40
	B.	.07	.03	.04	.05	.05	.04
15	A.	1.18	.82	1.34	2.45	......	1.44
	B.	.71	.67	.94	.45	......	.69

TABLE 6. An analysis of the chloride ion concentration of the soils sampled from the Big Marsh expressed as a percentage of the chloride in the soil. A equals 0-10 cm. and B equals 60-70 cm.

Site		May	June	July	Aug.	Sept.	Avg.
1	A.	.007	.002	.001	.007	.003	.004
	B.	.003	.0009	.0009	.001	.0007	.001
2	A.	.06	.02	.09	.04	.06	.05
	B.	.03	.01	.05	.003	.004	.01
3	A.	.18	.10	.31	.19	.18	.19
	B.	.10	.10	.15	.23	.19	.15
4	A.	.34	.42	.43	.30	.47	.39
	B.	.11	.24	.21	.37	.20	.22
5	A.	1.38	2.34	1.77	1.30	1.67	1.69
	B.	.65	.63	.44	.40	.39	.50
6	A.	1.20	1.12	1.52	.78	.96	1.11
	B.	.59	.58	.47	.74	.74	.62
7	A.	1.05	.88	1.72	.88	.75	1.05
	B.	.59	.44	.36	.54	.13	.41
8	A.	.68	.09	.15	.11	.19	.24
	B.	.17	.12	.15	.13	.25	.16
9	A.	.96	1.20	.93	.94	.16	.83
	B.	.37	.45	.16	.54	.69	.44
10	A.	.09	.14	.17	.36	.29	.21
	B.	.03	.08	.18	.28	.22	.15
11	A.	.25	.56	.38	.98	.60	.55
	B.	.24	.43	.12	.34	.39	.30
12	A.	.35	.23	.14	.46	.41	.31
	B.	.18	.07	.04	.11	.20	.12
13	A.	1.04	1.20	.80	1.16	1.10	1.06
	B.	.43	.27	.38	.27	.21	.31
14	A.	.09	.03	.12	.17	.23	.12
	B.	.04	.008	.01	.02	.02	.01
15	A.	.77	.46	.70	1.57	......	.87
	B.	.35	.40	.48	.24	......	.36

in salinity which are most limiting to plant distribution. The important question is not whether a plant can survive in an area such as site 9 after a heavy rainstorm, but whether it could survive throughout the growing season when at times the salinity surpassed 1%.

VEGETATION*

SEASONAL ASPECTS AND ZONAL DISTRIBUTION

Throughout the growing season notes were taken on the seasonal aspect and distribution of the vegetation. The following section is a résumé of this

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*An attempt was made to follow the nomenclature of Hitchcock (1950) for the classification of grasses and Fernald (1950) for the remainder of the vascular plants.

information, indicating phenology and zonal distribution (Table 8).

The central area of the marsh is a barren salt flat, and the various vegetation zones radiate out from it. Vegetational relations in this marsh differ from many coastal ones and the Kansas salt marshes described by Schaffner (1898) in that there is no definite sequence of community zonation which always occurs from the bare area outward. There are definite patterns of vegetation, but these are affected by variations in local topography, drainage, and salinity. To illustrate the lack of definite concentric zones one can find a prostrate *Suaeda* Community, an upright *Suaeda* Community, a *Sporobolus airoides* Community, a *Distichlis stricta-Suaeda depressa* or possibly a *Distichlis stricta* Community bordering or entering upon the barren salt flats.

TALL *Distichlis stricta* MEADOW COMMUNITY

The first major community of the salt marsh discussed here, the tall *D. stricta,* is located on the eastern border of the salt flats in the SE¼ sec. 22, T.21S., R.11W., south of this location on the eastern border and in wetter saline areas throughout the marsh. In this vegetation type there were 13 species of vascular plants, and only three of these, *Pluchea purpurascens, Rumex maritimus* var. *fueginus, Polygonum hydropiperoides,* appeared solely in this community.

The most characteristic and abundant plant in this zone was *D. stricta;* others flowering and fruiting in the spring, were *Poa arida, Hordeum jubatum,* and *Scirpus paludosus.* The flowering period of the last mentioned species continued through the summer months.

Distichlis stricta flowers throughout the summer months, and fruiting plants can be found from July through October. *Bassia hyssopifolia* and *Atriplex patula* var. *hastata* flower during the summer, while *Aster exilis, Aster ericoides,* and *Suaeda depressa* were found in anthesis in late summer and fall. These summer and fall species were of extremely rare occurrence in this community.

In this area one also finds extensions of prairie vegetation on hummocks of higher ground. The dense cover in this community is illustrated in Fig. 3.

Sporobolus airoides COMMUNITY

This community was located in the SE¼ sec. 22, T.21S., R.11W., between the Tall *D. stricta* community and the Sandhill Mixed Prairie community. It contained only 11 species of vascular plants, all of which were found in other communities on the marsh. This vegetation type also occurred on small, self-produced hummocks formed by the extensive root and rhizome systems of *S. airoides,* which was 1-3 feet in height. Harris (1920) and Hilgard (1914) have also mentioned such raised areas produced by this species.

The vegetation in this zone was dominated by *S. airoides,* which bloomed from June through August. In early spring *Poa arida* was the only plant in anthesis. *Elymus canadensis* was found blooming in late spring and early summer.

Flowering during the summer months were *Ambrosia psilostachya* var. *coronopifolia, Atriplex patula* var. *hastata, Conyza canadensis, Desmanthus illinoense, Euphorbia marginata,* and *Suaeda depressa. D. stricta* was found blooming also throughout the summer months but was much rarer than in the previously described community.

SANDHILL MIXED PRAIRIE COMMUNITY

The eastern border of the marsh, directly east of the *S. airoides* Community, in the SE¼ sec. 22, T.21S., R.11W., and southward along the eastern border was occupied by this community. It was found also on the higher, sandy hummocks in moister and more saline zones. Of the 110 species occurring in this mixed prairie community, 41 were not found elsewhere on the marsh.

In early spring, *Lithospermum incisum, Androsace occidentalis, Cerastium brachypodum, Lappula Redowskii, Veronica peregrina* var. *xalapensis* and *Viola kitaibeliana* var. *rafinesquii* were found in the flowering state.

From late spring through early summer, among others, the following species were in flower: *Achillea lanulosa, Agropyron smithii, Callirhoe involucrata, Elymus canadensis, Erigeron strigosis* var. *beyrichii, Festuca octoflora, Monarda citriodora, Panicum lanuginosum* var. *fasciculatum, Panicum scribnerianum,* and *Plantago purshii.* Also found in some abundance during this period were *Bromus japonicus* and *B. tectorum,* which are not common in undisturbed prairie.

The abundance of *B. japonicus* must be ascribed to the disturbance caused by present mowing during the summer and possibly to grazing in the past history of the area. Herbel and Anderson (1959) have reported annual brome grasses to be the major invaders due to disturbance by grazing in the Flint Hills of Kansas.

During the summer months *Artemesia ludoviciana, Cassia fasciculata, Coreopsis tinctoria, Cyperus filiculmis, Oenothera rhombipetala, Setaria geniculata, Solidago missouriensis,* and *Strophostyles leiosperma* were in the flowering state.

In the late summer and fall the tall grasses dominated the vegetation. These included *Andropogon gerardi, Andropogon scoparius, Panicum virgatum,* and *Sorghastrum nutans.* Other plants flowering at this time were *Ambrosia psilostachya* var. *coronopifolia, Bouteloua gracilis, Eragrostis trichodes, Froelichia campestris, Solidago altissima, Sporobolus asper,* and *Sporobolus cryptandrus.*

Moister areas in this zone contained species common to the *S. pectinata-D. stricta* and *S. americanus-E. rostellata* communities, described later. An early summer aspect of this community is shown in Fig. 5.

Suaeda depressa COMMUNITY

This community was composed of widely scattered individuals of *S. depressa* in both its depressed and erect (*S. erecta* (S. Wats) A. Nels.) forms (Figs. 7, 8). Along with the two forms of *Suaeda,* succulents such as *Sesuvium verrucossum* and, in one location, *Salicornia rubra* were found. This community type was scattered everywhere in and directly bordering the open salt flats in sections 21, 22, 27, 28, and 29, T.21S., R.11W.

Suaeda depressa was flowering and fruiting in late September and October. It was present, however, in this community from early May through October in its vegetative form. *Salicornia rubra* was in vegetative condition from July through October, and *Sesuvium verrucosum* was flowering and fruiting in late August and September.

As mentioned earlier, *S. depressa* has two distinct growth forms in this area, the depressed form, generally found in the more saline areas, and the upright form situated at slightly less saline locations. However, continuous fluctuations in salinity over short periods of time seemed to allow both forms to occur at the same location. Even the usually barren salt flat sometime had a very widely scattered cover of the depressed form. The occurrence of these two forms at the same location seems to leave no doubt whether or not the growth form has any significance in the distribution of this species or any real survival value. It also appears as if specimens which develop later in the season are all of the depressed form.

Distichlis stricta-Suaeda depressa COMMUNITY

This community covered the largest area of the marsh and was composed almost entirely of *D. stricta* and the upright growth form of *S. depressa* (Fig. 9). Large areas of sections 21, 22, 27, 28, and 29, T.21S., R.11W. were covered by this vegetation type.

Other species found here comprised only an extremely small part of the total vegetational cover, but they were occasionally of some local importance. Species of secondary importance included *Poa arida, Scirpus paludosus, Polygonum ramoisissimum, Sesuvium verrucossum, Sporobolus airoides, Tamarix gallica, Spartina pectinata,* and *Heliotropium curassavicum.*

Scirpus paludosus-Distichlis stricta COMMUNITY

This community type covered relatively small areas of the Big Salt Marsh and was primarily limited to the SE¼ section 21 and the SE¼ section 28, T.21S., R.11W. It contained a total of nine species, all of which were found in other areas, except for *Atriplex argentea.*

The dominants in this vegetation type (fig. 4) were *D. stricta* which bloomed through the summer months and *S. paludosus* which started blooming in late spring and continued through part of the summer. Other species in this area included *Polygonum ramosissumum, Suaeda depressa, Poa arida,* *Hordeum jubatum, Heliotropium curassavicum, Atriplex argentea,* and *Atriplex patula* var. *hastata.* Many of these species occurred also in the previously mentioned *D. stricta-S. depressa* Community, but in this, as in the latter community, with the exception of *S. depressa,* they played a very small role in the cover relations.

Polygonum ramosissimum, sometimes locally abundant in this and the previously discussed community, flowered throughout the summer months. *H. curassavicum,* which was extremely rare, flowered throughout the growing season.

Spartina pectinata-Distichlis stricta COMMUNITY

This community was located primarily in the SW¼ section 21, T.21S., R.11W. It was also found bordering the *Scirpus americanus-Eleocharis rostellata* Community and in the southwestern part of the marsh, and small colonies were found scattered throughout the *D. stricta-S. depressa* Community when the salinity was lowered.

Spartina pectinata, the tall dominant here (Fig. 12) was 70-130 cm. tall, and *D. stricta,* the short co-dominant, was 20-50 cm. tall. There were 24 taxa in this community, one of which, *Eustoma grandiflora* f. *fischeri,* seems to be limited to this area.

In the spring such species as *Amorpha fruticosa, Apocynum sibiricum, Hordeum jubatum, Juncus torreyi,* and *Juncus interior* were flowering. During the summer months the most prominent flowering plants were *D. stricta, Eustoma grandiflora, Asclepias incarnata, S. pectinata, Verbena hastata* and *Vernonia fasciculata.* In late summer and fall, species such as *Aster exilis, Iva annua,* and *Flaveria campestris* were in anthesis in this zone. *Spartina pectinata,* towered over the remaining species, and, as mentioned earlier, it should be considered the most characteristic species in the upper stratum of the community.

Scirpus americanus-Eleocharis rostellata COMMUNITY

This community contained 89 species, 41 of which were limited to this sedge-meadow type area located in sections 20, 29, 30 and 31, T.21S., R.11W. and bordering the marsh along its western edge.

The dominants in this area were *S. americanus,* the tall dominant, (70-160 cm.) and *E. rostellata,* the short dominant (30-70 cm.). These two species bloomed from late May through June. Besides the dominants, some of the characteristic flowering species during the spring (Fig. 13) were *Carex annectans, Carex lanuginosa, Carex praegracilis, Juncus interior, Juncus torreyi, Scirpus paludosus, Eleocharis tenuis, Scirpus lineatus,* and *Sphenopholis obtusata.*

During the summer months, *Agrostis alba, Asclepias incarnata, Cicuta maculata, Helianthus maximilliani, Lippia lanceolata* var. *recognita,* and

Verbena hastata were in bloom (Fig. 14). Flowering in late summer and fall were *Vernonia fasciculata, Aster ericoides, A. exilis, Lobelia siphilitica* and *Spiranthes cernua.*

FRESH-WATER-SEEP COMMUNITY

This area was south of the Grazed Sandhill Community and north of the east-west road forming the southern boundary of this study. It was situated a half mile west of an oil pump in the center of the region south of the sandhills in the SW¼ sec. 4, T.22S., R.11W.

The vegetation was in the center of the seepage area where a fresh water pond was located (Fig. 15), and was dominated by *Typha latifolia* and *Sagittaria latifolia.* The area contained 30 species, five of which were not found in any other area studied. Species limited to this area were *Berula pusilla, Mimulus glabratus* var. *fremontii, Myosurus minimus, Ranunculus sceleratus,* and *Spirodela polyrhiza.* Surrounding the pond on slightly higher ground were found the following species typical of the Sedge-Meadow Community described earlier: *Scirpus americanus, S. paludosis, Eleocharis macrostachya, E. rostellata, E. tenuis, Cicuta maculata, Flaveria campestris, Carex annectans,* and *C. praegracilis.*

TABLE 7. Distribution of Charophyceae.

Species	Ponds 1	3	8	9
Chara canescens	..	..	X	..
Chara evoluta	..	..	X	..
Chara globularis	X	X	X	X
Chara hornemani	X	..	X	..
Nitella opaca	..	..	X	..
Tolypella intricata	X	X	..	..

M. glabratus var. *fremontii, M. minimus,* and *R. sceleratus* were the earliest species in the pond area undergoing anthesis during early spring. *Typha latifolia* was blooming in the early summer months, *S. latifolia* from middle to late summer, and *Lycopus americanus* in mid-summer. *Flaveria campestris* flowered during late summer and fall and was one of the last species to flower in the area.

The water at this site was tested for pH, total salinity, and chloride ion concentration throughout the growing season. It had a very low salinity of 0.02-0.05%, a chloride ion concentration of 0.008-0.01%, and a pH of 7.2-8.7. Details of the exact monthly variations in these factors during the growing season are in Table 2.

Saline Pond Community

An aquatic community differing markedly from the Fresh-Water-Seep was located in the shallow saline lakes scattered throughout the marsh. Two species of flowering plants were found growing in these lakes. In June and July *Eleocharis acicularis* was flowering and *Potamogeton foliosus* was in anthesis from June through August.

The group of plants making up the greatest density (Fig. 16), in these brackish and saline lakes belongs to the class Charophyceae. Jewell (1927), in a study of the fauna of salt marshes in this county, mentioned that the shallow ponds were literally choked with *Chara*. The six species of Charophyceae found on the Big Salt Marsh include *Chara canescens, C. evoluta, C. globularis, C. hornemani, Nitella opaca,* and *Tolypella intricata.* These species are most abundant during the spring and early summer months. Later on in the summer when many of the shallow lakes dried up, these algae disappeared and only the thick walled zygotes, which fall to the bottom of the ponds, remained. The zygotes overwinter as such and germinate during the following spring. Table 7 provides data on the distribution of Charophyceae in four ponds.

The salinity in the ponds in which these plants grew was 0.48-1.17% in pond 1, 0.25-0.39% in pond 3, 0.28-1.26% in pond 8, and 0.38-0.52% in pond 9. The exact locations of these ponds are shown in Fig. 2, and more detailed data as to the properties of their waters are given in Table 2.

Rawson and Moore (1944) studied brackish waters in Canada and reported that *Chara* spp. were prevalent at 0.01-0.78% salinity. On the Little Salt Marsh in Kansas which Jewell (1927) studied, the salinity was 0.40-0.81%. Moore and Jewell clearly indicated that members of the Charophyceae are tolerant of a wide range of salinity, and certain species such as those mentioned in this study can withstand great fluctuations.

Grazed Sandhill Community

According to Latta (1950), this grazed sandhill area occurs on an old beach ridge which in past ages formed the border of an ancient lake much larger than the present one. The ridge is 10-15 ft. high, 200-900 ft. wide and located in the grazed portion of the marsh, in sections 3, 4, 5, and 6, T.21S., R.11W., which form the southern border of the salt flats, and also the eastern border of the marsh.

A total of 74 species of vascular plants were found in this area, 35 of which are limited to this locality. Some species blooming in the spring (Fig. 17) were *Callirhoe involucrata, Cryptantha crassisepala, Festuca octoflora, Mirabilis albida, Pyrrhopappus grandiflorus, Hordeum pusillum, Monarda citriodora,* and *Oenothera laciniata* var. *grandiflora.*

During the early summer *Argemone polyanthemos* was the most conspicuous flowering plant (Fig. 18) and provided a definite seasonal aspect. Other plants present at this time and characteristic of a later aspect were *Eriogonum anuum* and *Conyza canadensis.*

The following species bloomed through the summer and early fall: *Haplopappus ciliatus, Haplopappus divaricatus, Amaranthus tamariscinus, Ambrosia psilostachya* var. *Coronopifolia, Cenchrus longispinus, Eragrostis cilianensis, Salsola kali* var. *tenuifolia, Cycloloma atriplicifolium,* and *Paspalum ciliatifolium.*

Hummock Communities

Hummock vegetation occurred in many of the community types discussed earlier, but since in most cases the majority of species found growing on hummocks in the various communities were similar, all will be discussed in this section. The hummocks contained a combined total of 56 species, six of these only on raised areas. One point to be made about the hummocks is that some were natural and others man-made, but this had little effect on the vegetation which finally occupied them.

After studying the various plant communities on the marsh, it was immediately apparent that besides the horizontal distribution described earlier, there was also a vertical one. This vertical distribution was not very exact for any of a multitude of 56 species were found on the hummocks. One obvious fact is that if the hummock were present in a non-saline or slightly saline area, only sandhill species occupied it. If it was in a more saline area, the species closest to the margin were those more tolerant of high salinities.

Two low hummocks of 1-3 feet occupying areas close to or on the open salt flats, will be mentioned first. One was dominated by *Sporobolus airoides* which occasionally occurred on the open salt flats. Fig. 20 illustrates this hummock type and a full discussion of the soil relations at this site are in the quantitative description of this community. A second type, also of interest, occurred in an area where *D. stricta-S. depressa* was the main vegetation type, but species such as *S. pectinata, H. jubatum, P. arida,* and *S. paludosus* were present also but scattered. This hummock type, found in only two places on the marsh, was completely dominated by *Baccharis salicina* (Fig. 19). Soil analysis here indicated a salinity of 0.50% in the surface 10 cm. at the top of the hummock and 0.20% at 60 cm.; the chloride content of these two samples were 0.23% and 0.11% respectively. This, as well as the analysis of the *S. airoides* hummock described later, indicates that in such low hummocks the salinity factor is still an important element in plant distribution. *Tamarix gallica* was found occasionally also occupying low, sandy hummocks.

On the higher sandy hummocks, where the salinity range was the same as that of the Beach Ridge and Prairie communities, there was a slightly higher salinity at the lowest margins. A community of *S. airoides* was the commonest vegetation surrounding the base of these, and only when a hummock was in a completely non-saline area was this species usually absent. Upward on the hummocks were found species tolerant of only a slight amount of salinity, such as *Aster ericoides, A. exilis, Atriplex patula* var. *hastata, Haplopappus phyllocephalus* subsp. *annuus, Bassia hyssopifolia, Muhlenbergia asperifolia, Polygonum ramosissimum, S. pectinata, Setaria geniculata,* and *Sporobolus texanus.*

The remainder of species on the top of the raised areas are for the most part intolerant of high salinities and include such non-halophytic taxa as *Achillea lanulosa, Amaranthus tamariscinus, Artemesia ludoviciana, Asclepias verticillata, Bromus japonicus, Callirhoe involucrata, Celtis occidentalis, Cenchrus longispinus, Euphorbia dentata, Gaura parviflora, Helianthus annuus, Lepidium virginicum, Panicum scribnerianum, Panicum capillare, Panicum virgatum,* and *Sorghastrum nutans.* A more complete listing of species on the hummocks and their phenological relations are in Table 8.

The species on the tops of hummocks had no regular distribution, and any of them might be found on any hummock studied. A species such as *Euphorbia dentata* might have little or no significance on most hummocks, but then for some unexplained reason it comprised the greatest part of the vegetation on others. This was true for many of the species discussed, and it would be extremely difficult to state exactly which species should be considered the dominants of this community type.

The following is a list of the species limited to the hummock sites, but these should not be considered community indicators because in each case they occurred on only a few hummocks: *Baccharis salicina, Celtis occidentalis, Scutellaria latifolia, Solanum nigrum, Sporobolus flexuosus,* and *Sporobolus texanus.*

LIFE FORM

The life-form spectra provided in Table 9 for the various marsh communities is based on the percentage of species representing each life-form. As mentioned by Chapman (1960) and Cain and Castro (1959) this method provides an indication of the life-form groups present but not the quantitative relations of species within the various communities. Since the next section of this paper is devoted to a quantitative study of the marsh communities, no mention of these relations is necessary here. In all communities mentioned in Table 9 for which species names are given in the community title, the species cited are the most abundant and their life-forms dominate.

As Raunkiaer (1934) found in his study of Fano, the therophyte life-form appears to be dominant in the pioneer stage of the marsh, but in areas of lower salinity, hemicryptophytes, geophytes, and other life-forms are of

TABLE 8. Season and zonal distribution of the vegetation of the Big Salt Marsh. A—Prairie, B—Tall *D. stricta Meadow*, C—*D. stricta-S. depressa*, D—*S. pectinata-D. stricta*, E—*S. americanus-E. rostellata*, F—Grazed Sandhill, G—*S. airoides*, H—*Hummock*, I—Fresh Water Seep, J—Saline Pond, K—*S. depressa*, L—*S. paludosus-D. stricta*. Life Form: Th—Therophyte, G—Geophyte, H—Hemicryptophyte, Hh—Hydro-helophyte, P—Phanerophyte, L—Liana. Phenology: A—Flowering or Sporulating, F—Fruiting, X—Presence.

		PLANT DISTRIBUTION																	
		SEASONAL						ZONAL											
SPECIES	Life Form	M	JN	JY	Ag	S	O	A	B	C	D	E	F	G	H	I	J	K	L
Achillea lanulosa	H	A	A	F	..	..	..	X	..	..	..	..	..	..	X	..	..	..	..
Agropyron smithii	H	A	A	F	..	..	..	X	..	..	..	X	..	..	X	..	..	..	..
Agrostis alba	H	..	A	A	F	..	..	..	..	..	..	X	..	..	..	..	..	..	..
Agrostis hiemalis	H	A	F	..	..	..	..	X	..	..	..	..	..	..	..	..	..	..	..
Alisma triviale	He	..	..	A	A	F	..	..	..	..	..	X	..	..	..	..	..	..	..
Allium mutabile	G	A	F	..	..	..	..	X	..	..	..	..	..	..	..	..	..	..	..
Amaranthus tamariscinus	Th	..	..	A	A	A	F	X	..	..	..	..	X	..	X	..	..	..	..
Ambrosia psilostachya var. *coronopifolia*	G	..	..	A	A	A	F	X	..	..	X	..	X	X	X	..	..	..	..
Ambrosia trifida	Th	..	..	..	A	F	..	X	..	..	..	..	..	..	..	..	..	..	..
Amorpha fruticosa	Ph	A	AF	F	..	..	..	..	..	..	X	X	..	..	..	..	..	..	..
Andropogon gerardi	H	..	..	..	A	A	AF	X	..	..	..	..	X	..	..	..	..	..	..
Andropogon hallii	H	..	..	..	..	..	AF	X	..	..	..	..	..	..	..	..	..	..	..
Andropogon scoparius	H	..	..	..	..	A	AF	X	..	..	..	..	X	..	..	..	..	..	..
Androsace occidentalis	Th	AF	..	..	..	..	..	X	..	..	..	..	..	..	..	..	..	..	..
Apocynum sibiricum	H	A	A	A	F	..	..	X	..	..	X	X	..	..	..	..	..	..	..
Argemone polyanthemos	Th	..	A	A	A	AF	AF	..	..	..	..	..	X	..	..	..	..	..	..
Aristida oligantha	Th	..	AF	AF	F	..	..	..	..	..	..	..	X	..	..	..	..	..	..
Artemesia ludoviciana	H	..	A	A	A	A	..	X	..	..	..	..	..	..	X	..	..	..	..
Asclepias incarnata	He	..	A	A	A	F	..	..	..	..	X	X	..	..	..	..	..	..	..
Asclepias speciosa	H	A	A	A	AF	F	..	X	..	..	..	..	X	..	X	..	..	..	..
Asclepias tuberosa	H	..	A	..	..	..	..	X	..	..	..	..	..	..	..	..	..	..	..
Asclepias verticillata	A	..	A	A	A	A	..	X	..	..	..	..	..	..	X	..	..	..	..
Asclepiodora viridis	H	A	..	..	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..
Aster ericoides	H	..	..	..	A	A	AF	X	X	..	..	X	..	X	X	..	..	..	..
Aster exilis	Th	..	..	..	A	A	AF	X	X	..	..	X	..	..	X	..	..	..	..
Atriplex argentea	Th	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	X
Atriplex patula var. *hastata*	Th	..	..	A	AF	AF	F	X	X	..	..	..	..	X	X	..	..	..	X
Baccharis salicina	Ph	..	..	A	F	..	..	..	..	..	..	..	..	..	X	..	..	..	..
Bassia hyssopifolia	Th	..	..	A	AF	F	..	..	X	..	..	..	..	..	X	..	..	..	..
Berula pusilla	He	..	A	AF	F	..	..	..	..	..	..	..	..	..	..	X	..	..	..
Bouteloua curtipendula	H	..	..	AF	F	..	..	..	..	..	..	..	X	..	..	..	..	..	..
Bouteloua gracilis	H	..	..	..	AF	AF	AF	X	..	..	..	..	X	..	..	..	..	..	..
Bromus japonicus	Th	A	AF	F	..	..	..	X	..	..	..	..	..	..	X	..	..	..	..
Bromus tectorum	Th	AF	F	..	..	..	..	X	..	..	..	..	X	..	..	..	..	..	..
Calamovilfa gigantea	H	..	..	..	A	AF	..	X	..	..	..	..	..	..	..	..	..	..	..
Callirhoe alcaeoides	H	A	A	..	..	..	..	X	..	..	..	..	..	..	..	..	..	..	..
Callirhoe involucrata	H	A	A	AF	F	..	..	X	..	..	..	..	X	..	X	..	..	..	..
Callitriche heterophylla	Hh	F	..	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	..

SPECIES	Life Form	PLANT DISTRIBUTION SEASONAL						ZONAL											
		M	JN	JY	Ag	S	O	A	B	C	D	E	F	G	H	I	J	K	L
Capsella bursa-pastoris	Th	AF	..	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	..
Carex annectans var. *xanthocarpa*	H	A	F	..	..	..	..	..	..	..	..	X	..	..	..	X	..	..	..
Carex brevior	H	A	F	..	..	..	..	X	..	.	..	X	..	..	..	..	..	..	..
Carex buxbaumii	H	AF	..	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	..
Carex lanuginosa	H	AF	F	..	..	..	..	X	..	..	..	X	..	..	..	..	..	..	..
Carex meadii	H	F	..	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	..
Carex praegracilis	H	AF	F	..	..	..	..	..	..	..	..	X	..	..	..	X	..	..	..
Carex stipata	H	F	..	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	..
Cassia fasciculata	Th	..	..	A	A	AF	..	X	..	..	..	..	..	..	..	..	..	..	..
Celtis occidentalis	Ph	X	X	X	X	X	X	..	..	..	..	..	..	..	X	..	..	..	..
Cenchrus longispinus	Th	..	..	A	AF	AF	F	X	..	..	..	..	X	..	X	..	..	..	..
Cerastium brachypodum	Th	AF	..	..	..	..	..	X	..	..	..	..	..	..	..	..	..	..	..
Chenopodium leptophyllum	Th	..	AF	..	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..
Chloris verticillata	H	..	AF	AF	AF	AF	..	..	..	..	..	..	X	..	..	..	..	..	..
Cicuta maculata	Th	..	..	A	AF	F	..	..	..	..	..	X	..	..	..	X	..	..	..
Cirsium undulatum	H	..	A	AF	F	..	..	X	..	..	..	X	X	..	X	..	..	..	..
Cirsium undulatum f. *album*	H	..	..	A	F	..	..	..	..	..	..	..	X	..	..	..	..	..	..
Cleome serrulata	Th	..	..	A	A	AF	..	..	..	..	..	..	X	..	X	..	..	..	..
Cleomella angustifolia	Th	..	A	A	A	AF	..	..	..	..	..	..	X	..	..	..	..	..	..
Commelina erecta var. *angustifolia*	H	..	A	A	A	F	..	X	..	..	..	..	X	..	..	..	..	..	..
Conyza canadensis	Th	..	..	..	A	AF	F	X	..	..	..	..	X	X	X	..	.	..	..
Coreopsis tinctoria	Th	..	..	A	AF	..	..	X	..	..	..	..	..	..	..	..	..	..	..
Cornus drummondii	Ph	X	X	X	X	X	..	..	..	..	..	X	..	..	..	..	..	..	..
Croton capitatus	Th	..	..	..	A	F	..	..	..	..	..	..	X	..	..	..	..	..	..
Croton glandulosus var. *septentrionales*	Th	..	..	..	A	..	..	X	..	..	..	..	X	..	..	..	..	..	..
Cryptantha crassisepala	Th	..	..	AF	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..
Cucurbita foetidissima	H	..	A	A	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..
Cuscuta glomerata	Th	..	..	..	A	F	..	..	..	..	..	X	X	..	..	..	..	..	..
Cycloloma atriplicifolia	Th	..	..	..	..	..	F	..	..	..	..	..	X	..	..	..	..	..	..
Cyperus acuminatus	Th	..	..	A	AF	..	..	X	..	..	..	..	..	..	..	..	..	..	..
Cyperus filiculmis	G	..	..	A	AF	..	..	X	..	..	..	..	..	..	..	..	..	..	..
Cyperus strigosus	H	..	..	AF	AF	AF	..	..	..	..	..	X	X	..	..	X	..	..	..
Delphinium verescens	H	A	A	..	..	..	..	X	..	..	..	..	..	..	..	..	..	..	..
Descurainia pinnata	Th	AF	..	..	..	..	..	X	..	..	..	..	..	..	X	..	..	..	..
Desmanthus illinoense	H	..	..	A	AF	F	..	X	..	..	..	..	..	X	X	..	..	..	..
Digitaria sanguinalis	Th	..	..	AF	AF	AF	AF	X	..	..	..	..	..	..	..	..	..	..	..
Distichlis stricta	G	A	A	AF	AF	AF	..	X	X	X	X	X	..	X	..	..	..	..	X
Echinochloa crusgalli var. *mites*	Th	..	..	AF	AF	AF	..	X	..	..	..	..	..	..	X	..	..	..	..
Eleocharis acicularis	H	..	A	AF	F	..	..	..	..	..	..	..	..	..	..	..	X	..	..
Eleocharis macrostachya	H	A	A	F	..	..	..	..	..	..	..	X	..	..	..	X	..	..	..
Eleocharis rostellata	H	A	A	F	..	..	..	..	..	..	X	X	..	..	..	X	..	..	..
Eleocharis tenuis	H	A	AF	F	..	..	..	X	..	..	..	X	..	..	..	X	..	..	..

		PLANT DISTRIBUTION																	
		SEASONAL						ZONAL											
SPECIES	Life Form	M	JN	JY	Ag	S	O	A	B	C	D	E	F	G	H	I	J	K	L
Elymus canadensis	H	A	AF	AF	..	..	..	X	..	..	..	..	X	X	X	..	..	..	..
Elymus virginicus	H	A	AF	F	..	..	..	X	..	..	..	..	..	..	X	..	..	..	..
Equisetum laevigatum subsp. *funstonii*		..	A	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	..
Eragrostis cilianensis	Th	..	..	..	..	AF	AF	..	..	..	..	..	X	..	..	..	..	..	..
Eragrostis oxylepis	H	..	..	..	..	AF	..	..	..	..	..	..	X	..	..	..	..	..	..
Eragostis spectabilis	H	..	..	..	..	AF	..	..	..	..	..	..	X	..	..	..	..	..	..
Eragrostis trichodes	H	..	..	..	..	AF	AF	X	..	..	..	..	..	..	..	..	..	..	..
Erigeron philadelphicus	Th	A	..	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	..
Erigeron strigosus var. *beyrichii*	Th	A	A	A	F	..	..	X	..	..	..	X	..	..	..	..	..	..	..
Eriogonum annuum	Th	..	..	A	AF	AF	..	X	..	..	..	..	X	..	..	..	..	..	..
Eupatorium perfoliatum	H	..	..	..	A	A	..	..	..	..	..	X	..	..	X	..	..	..	..
Euphorbia dentata	Th	..	..	..	A	A	..	..	..	..	..	..	X	..	X	..	..	..	..
Euphorbia glyptosperma	Th	..	A	AF	F	..	..	X	..	..	..	..	X	..	X	..	..	..	..
Euphorbia marginata	Th	..	..	A	A	AF	AF	X	..	..	..	X	..	X	..	..	..	..	..
Euphorbia missurica var. *intermedia*	Th	..	..	AF	..	..	..	X	..	..	..	..	..	..	..	..	..	..	..
Euphorbia obtusata	Th	..	..	AF	..	..	..	X	..	..	..	..	..	..	..	..	..	..	..
Eustoma grandiflora	H	..	A	A	AF	AF	AF	..	..	..	X	X	..	..	..	..	..	..	..
Eustoma grandiflora f. *fischeri*	H	..	..	..	A	..	..	..	..	..	X	..	..	..	..	..	..	..	..
Festuca octoflora	Th	A	F	..	..	..	..	X	..	..	..	..	X	..	..	..	..	..	..
Fimbrystilis castanea	H	..	..	AF	F	..	..	..	..	..	..	X	..	..	..	..	..	..	..
Flaveria campestris	Th	..	..	..	..	A	A	..	..	..	X	X	..	..	..	X	..	..	..
Froehlichia campestris	Th	..	..	A	A	A	AF	X	..	..	..	..	..	..	..	..	..	..	..
Galium aparine	Th	A	F	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	..
Gaura parviflora	Th	..	A	A	AF	AF	..	X	..	..	..	..	..	..	X	..	..	..	..
Gerardia tenuifolia var. *macrophylla*	Th	..	..	..	..	AF	..	..	..	..	..	..	X	..	..	..	..	..	..
Glycyrrhiza lepidota	H	A	F	..	..	..	..	X	..	..	..	X	..	..	X	X	..	..	..
Gnaphalium obtusifolium	Th	..	..	..	..	F	..	..	..	..	..	..	X	..	..	..	..	..	..
Haplopappus ciliatus	Th	..	..	A	A	AF	AF	X	..	..	..	..	X	X	..	..	..	..	..
Haplopappus divaricatus	Th	..	..	A	A	AF	AF	X	..	..	..	..	X	X	..	..	..	..	..
Haplopappus phyllocephalus subsp. *annuus*	Th	..	..	..	..	AF	AF	..	..	..	..	..	..	..	X	..	..	..	..
Hedeoma hispida	Th	..	A	A	A	..	..	..	..	..	..	..	X	..	..	..	..	..	..
Helianthus annuus	Th	..	..	A	A	AF	..	X	..	..	..	..	..	..	X	..	..	..	..
Helianthus maximilliani	H	..	..	..	A	A	AF	..	..	..	..	X	..	..	X	..	..	..	..
Helianthus petiolaris	Th	A	A	A	A	AF	AF	..	..	..	..	..	X	..	X	..	..	..	..
Heliotropium curassavicum	Th	A	A	A	A	A	..	..	..	X	..	..	..	..	..	..	..	..	X
Heterotheca latifolia var. *mcgregoris*	Th	..	..	..	..	A	..	..	..	..	..	..	X	..	..	..	..	..	..
Hordeum jubatum	H	A	AF	F	..	..	..	X	X	..	X	X	..	..	X	X	..	..	X
Hordeum pusillum	Th	A	F	..	..	..	..	X	..	..	..	X	..	..	X	..	..	..	..
Iva annua	Th	..	..	..	A	A	F	X	..	..	X	..	..	..	..	..	..	..	..
Juncus interior	He	A	AF	AF	F	..	..	X	..	..	X	X	..	..	..	X	..	..	..

		PLANT DISTRIBUTION																	
		SEASONAL						ZONAL											
SPECIES	Life Form	M	JN	JY	Ag	S	O	A	B	C	D	E	F	G	H	I	J	K	L
Juncus Torreyi	He	..	A	AF	..	..	..	..	..	..	X	X	..	..	..	..	..	..	..
Lactuca ludoviciana f. *campestris*	Th	..	..	A	AF	AF	..	X	..	..	..	..	..	..	X	..	..	..	..
Lactuca scariola	Th	..	..	..	AF	..	..	..	..	..	..	..	X	..	..	..	..	..	..
Lappula redowskii	Th	AF	..	..	..	..	..	X	..	..	..	..	..	..	..	..	..	..	..
Leersia oryzoides	H	..	..	..	..	F	..	..	..	..	..	X	..	..	..	..	..	..	..
Lepidium virginicum	Th	AF	AF	..	..	..	..	X	..	..	..	..	X	..	X	..	..	..	..
Leptoloma cognatum	H	..	..	AF	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..
Liatris glabrata	G	..	..	A	..	..	..	X	..	..	..	..	..	..	..	..	..	..	..
Liatris lancifolia	G	..	..	A	..	..	..	..	..	..	..	X	..	..	..	..	..	..	..
Linaria canadensis var. *texana*	Th	A	F	..	..	..	..	X	..	..	..	..	..	..	..	..	..	..	..
Lippia lanceolata var. *recognita*	H	..	A	A	A	A	A	..	..	..	..	X	..	..	..	X	..	..	..
Lithospermum incisum	H	AF	..	..	..	..	..	X	..	..	..	..	..	..	..	..	..	..	..
Lobelia siphilitica var. *ludoviciana*	H	..	..	..	..	A	..	..	..	..	X	X	..	..	..	..	..	..	..
Lobelia splendens	H	..	..	..	..	A	..	..	..	..	..	X	..	..	..	..	..	..	..
Lotus americanus	Th	..	A	A	A	..	..	X	..	..	..	..	..	..	..	..	..	..	..
Lycopus americanus	H	..	..	A	AF	F	..	..	..	..	..	X	..	..	..	X	..	..	..
Lythrum californicum	H	..	A	AF	..	..	..	X	..	..	..	..	..	X	..	..	..	..	..
Marsilea vestita	....	..	..	..	X	..	..	X	..	..	..	..	..	..	..	..	..	..	..
Melilotus alba	Th	..	A	A	..	..	..	X	..	..	..	..	..	..	X	..	..	..	..
Mimulus glabratus var. *fremontii*	He	A	..	..	..	..	..	..	..	..	..	..	..	..	..	X	..	..	..
Mirabilis albida	H	..	AF	F	..	..	..	X	..	..	..	..	X	..	..	..	..	..	..
Mollugo verticillata	Th	..	..	A	A	..	..	X	..	..	..	..	..	..	..	..	..	..	..
Monarda citriodora	Th	..	A	F	..	..	..	X	..	..	..	..	X	..	..	..	..	..	..
Muhlenbergia asperifolia	H	..	..	..	AF	AF	AF	..	..	..	..	..	..	..	X	X	..	..	..
Myosurus minimus	Th	AF	..	..	..	..	..	..	..	..	..	..	..	..	..	X	..	..	..
Oenothera laciniata	Th	A	A	A	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..
Oenothera laciniata var. *grandiflora*	Th	A	A	A	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..
Oenothera rhombipetala	Th	..	..	A	A	A	..	X	..	..	..	X	..	..	..	..	..	..	..
Oxalis stricta	H	A	..	..	..	..	..	X	..	..	..	..	..	..	..	..	..	..	..
Panicum agrostoides	H	..	..	..	..	AF	..	..	..	..	X	..	..	..	..	..	..	..	..
Panicum capillare	Th	..	..	A	A	AF	AF	X	..	..	..	..	..	..	X	..	..	..	..
Panicum lanuginosum var. *fasciculatum*	H	AF	F	..	..	..	..	X	..	..	..	..	..	..	..	..	..	..	..
Panicum lanuginosum var. *lindheimeri*	H	F	..	..	..	..	..	X	..	..	..	X	..	..	..	..	..	..	..
Panicum scribnerianum	H	AF	F	..	..	..	..	X	..	..	..	X	..	..	X	..	..	..	..
Panicum virgatum	G	..	..	A	AF	F	..	X	..	..	..	X	..	..	X	..	..	..	..
Parthenocissus quinquefolia	L	..	X	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	..
Paspalum ciliatifolium	H	..	AF	AF	AF	AF	AF	X	..	..	..	..	X	..	..	..	..	..	..
Petalostemum purpureum	H	..	..	A	..	..	..	X	..	..	..	..	..	..	..	..	..	..	..
Phleum pratense	H	..	AF	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	..

		PLANT DISTRIBUTION																	
		SEASONAL						ZONAL											
SPECIES	Life Form	M	JN	JY	Ag	S	O	A	B	C	D	E	F	G	H	I	J	K	L
Physalis virginiana	H	A	AF	..	..	..	..	X	..	..	..	..	..	..	..	..	..	..	..
var. *hispida*																			
Plantago purshii	Th	A	AF	F	..	..	..	X	..	..	..	..	X	..	..	..	..	..	..
Pluchea purpurascens	Th	..	..	A	..	..	..	..	X	..	..	..	..	..	..	..	..	..	..
Poa arida	H	AF	F	..	..	..	..	..	X	X	X	X	..	X	..	X	..	..	X
Poa pratensis	G	A	..	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	..
Polygonum convolvulus	Th	..	A	AF	..	..	..	..	..	..	..	X	X	..	..	..	..		
Polygonum hydropiperoides	He	..	..	AF	..	..	..	..	..	X	..	..	..	..	..	..	..	..	..
Polygonum lapathifolium	Th	..	..	..	..	A	..	..	..	X	..	X	..	..	..	..	..	..	..
Polygonum pensylvanicum	Th	..	..	AF	..	..	..	X	..	..	..	..	..	..	..	..	..	..	..
var. *laevigatum*																			
Polygonum ramosissimum	Th	..	..	AF	AF	AF	..	..	..	X	..	..	..	..	X	..	..	..	X
Populus sargentii	Ph	A	..	..	..	..	..	..	..	..	..	X	X	..	..	..	..	..	..
Portulaca oleracea	Th	..	..	..	A	F	..	..	..	..	..	..	X	..	..	..	..	..	..
Portulaca parvula	Th	..	..	..	A	F	..	..	..	..	..	..	X	..	..	..	..	..	..
Potamogeton foliosus	Hy	..	A	A	A	F	..	..	..	..	..	..	..	..	..	..	X	..	..
Prunus angustifolia	Ph	..	..	X	..	..	..	X	..	..	..	..	..	..	..	..	..	..	..
Psoralea digitatum	H	..	..	A	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..
Pyrrhopappus grandiflorus	H	A	F	..	..	..	..	X	..	..	..	..	X	..	..	..	..	..	..
Ranunculus sceleratus	Th	A	..	..	..	..	..	..	..	..	..	..	..	..	..	X	..	..	..
Ratibida columnifera	H	..	A	F	..	..	..	X	..	..	..	..	..	..	..	..	..	..	..
Rhus radicans	L	A	AF	F	..	..	..	..	..	..	..	X	..	..	..	..	..	..	..
Rosa arkansana	Ph	A	..	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	..
var. *suffulta*																			
Rumex alluvius	H	..	..	F	..	..	..	..	..	..	..	X	..	..	..	..	..	..	
Rumex crispus	H	A	AF	AF	..	..	..	..	..	..	..	X	..	..	..	X	..	..	
Rumex maritimus	Th	..	..	..	F	..	..	X	..	..	..	..	..	..	..	..	..	..	..
var. *fueginus*																			
Sagittaria cuneata	He	..	..	A	F	..	..	..	..	..	..	X	..	..	..	..	..	..	
Sagittaria latifolia	He	..	..	A	AF	AF	..	..	..	..	..	X	..	..	..	X	..	..	..
Salicornia rubra	Th	..	..	X	X	X	..	..	..	..	..	..	..	..	..	..	..	X	..
Salix amygdaloides	Ph	A	..	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	
Salix interior	Ph	A	..	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	..
Salix nigra	Ph	A	..	..	..	..	..	..	..	..	..	X	..	..		..	..	..	..
Salsola kali	Th	..	..	..	..	..	AF	..	..	..	..	..	X	..	..	..	..	..	..
var. *tenuifolia*																			
Salvia azurea	H	..	..	..	..	A	..	X	..	..	..	..	..	..	..	..	..	..	..
var. *grandiflora*																			
Sambucus canadensis	Ph	..	..	..	..	F	..	..	..	..	..	X	..	..	..	..	..	..	..
Scirpus americanus	He	A	AF	AF	F	..	..	..	..	..	X	X	..	..	..	X	..	..	..
Scirpus atrovirens	He	..	AF	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	..
Scirpus lineatus	He	..	A	A	..	..	..	..	..	..	..	X	..	..	..	..	..	..	..
Scirpus paludosus	He	A	AF	AF	F	..	..	..	X	X	X	X	..	..	..	X	..	..	X
Scirpus validus	He	A	A	F	..	..	..	..	..	..	..	X	..	..	..	X	..	..	
Scutellaria latifolia	H	..	..	..	A	..	..	..	..	..	..	..	..	..	X	..	..	..	..
Sesuvium verrucosum	Th	..	..	A	A	A	..	..	..	X	..	..	..	..	..	..	..	X	

		PLANT DISTRIBUTION																	
		SEASONAL						ZONAL											
SPECIES	Life Form	M	JN	JY	Ag	S	O	A	B	C	D	E	F	G	H	I	J	K	L
Setaria geniculata	G	..	..	A	AF	AF	AF	X	..	..	..	X	X	..	X	..	..	..	..
Setaria glauca	Th	..	..	..	AF	F	..	..	..	..	..	X	..	..	..	..	..	..	..
Silene antirrhina	Th	..	F	..	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..
Sisyrinchium angustifolium	H	A	A	..	..	..	..	..	..	..	..	X	..	..	..	X	..	..	..
Solanum nigrum	Th	..	..	AF	..	..	..	..	..	..	..	..	..	..	X	..	..	..	..
Solanum rostratum	Th	..	..	A	A	A	F	..	..	..	..	..	X	..	..	..	..	..	..
Solidago altissima	H	..	..	..	..	A	AF	X	..	..	..	..	..	..	X	..	..	..	..
Solidago missouriensis	H	..	..	A	AF	AF	..	X	..	..	..	..	..	..	..	..	..	..	..
Sorghastrum nutans	H	..	..	..	A	AF	AF	X	..	..	..	..	..	..	X	..	..	..	..
Spartina pectinata	H	..	..	A	AF	AF	..	X	..	X	X	..	..	..	X	X	..	..	..
Specularia perfoliata	Th	..	A	..	..	..	..	X	..	..	..	X	..	..	..	..	..	..	..
Spermolepis inermis	Th	AF	..	..	..	..	..	X	..	..	..	..	..	..	..	..	..	..	..
Sphenopholis obtusata	H	..	AF	..	..	..	..	..	..	..	X	..	..	..	..	..	..	..	..
Spiranthes cernua	H	..	..	..	..	A	A	..	..	..	..	X	..	..	..	..	..	..	..
Spirodela polyrhiza	Hy	..	..	X	..	..	..	..	..	..	..	..	..	..	..	X	..	..	..
Sporobolus airoides	H	..	A	AF	AF	F	..	X	..	X	..	..	..	X	..	..	..	..	..
Sporobolus asper	H	..	..	..	..	AF	AF	X	..	..	..	X	X	..	X	..	..	..	..
Sporobolus cryptandrus	H	..	..	..	..	..	AF	X	..	..	..	..	..	..	X	..	..	..	..
Sporobolus flexuosus	H	..	F	..	..	..	..	..	..	..	..	..	..	..	X	..	..	..	..
Sporobolus pyramidatus	H	..	..	..	AF	..	..	..	..	..	..	..	X	..	..	..	..	..	..
Sporobolus texanus	H	..	..	..	AF	AF	AF	..	..	..	..	..	..	..	X	..	..	..	..
Strophostyles leiosperma	Th	..	..	A	A	AF	..	X	..	..	..	..	X	..	..	..	..	..	..
Suaeda depressa	Th	..	..	A	A	A	AF	..	X	X	X	X	..	X	..	..	..	X	X
Tamarix gallica	Ph	A	A	A	F	..	..	..	..	X	..	..	..	..	X	..	..	..	..
Taraxacum officinale	H	A	..	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	..
Teucrium canadense	H	..	..	A	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..
Thelesperma megapotamicum	H	..	A	..	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..
Tradescantia occidentalis	H	..	A	AF	F	..	..	X	..	..	..	..	..	..	..	..	..	..	..
Tragopogon major	Th	AF	..	..	..	..	..	X	..	..	..	..	..	..	..	..	..	..	..
Tribulus terrestris	Th	..	..	..	..	AF	..	..	..	..	..	..	X	..	..	..	..	..	..
Tripsacum dactyloides	H	..	A	..	..	..	..	X	..	..	..	..	.	..	..	..	..	..	..
Typha angustifolia	He	..	A	AF	..	..	..	..	..	..	X	X	..	..	..	..	..	..	..
Typha latifolia	He	..	A	AF	..	..	..	..	..	..	X	X	..	..	..	X	..	..	..
Urtica dioica	H	..	..	..	..	AF	..	..	..	..	..	X	..	..	..	..	..	..	..
Verbena bracteata	Th	..	..	A	A	F	..	..	..	..	..	..	X	..	..	..	..	..	..
Verbena hastata	H	..	..	A	A	AF	..	..	..	..	X	X	..	..	..	X	..	..	..
Verbena stricta	H	..	A	A	A	AF	..	X	..	..	..	..	X	..	..	..	..	..	..
Vernonia fasciculata	H	..	..	A	A	A	AF	..	..	..	X	X	..	..	..	..	..	..	..
Veronica peregrina var. *xalapensis*	Th	AF	..	..	..	..	..	X	..	..	..	..	..	..	..	..	..	..	..
Vicia angustifolia	Th	..	..	A	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..
Viola kitaibeliana var. *rafinesquii*	Th	AF	..	..	..	..	..	X	..	..	..	..	..	..	..	..	..	..	..
Viola papilionacea	H	AF	..	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	..
Vitis riparia	L	AF	F	..	..	..	..	..	..	..	..	X	..	..	..	..	..	..	..
Xanthium pensylvanicum	Th	..	..	..	..	AF	F	..	..	..	..	X	..	..	..	X	..	..	..

importance. The *Suaeda depressa* Community is the pioneer on the open salt flats and, as noted in Table 9, was made up entirely of therophytes. In the *Spartina pectinata-Distichlis stricta* area, the hemicryptophytes and the hydro-helophytes comprised the largest number of species, 46 and 29% for each group respectively. In all of the remaining communities in which *Distichlis stricta,* a geophyte, was one of the dominants, the largest number of species belong to the hemicryptophyte and therophyte life-forms. The Saline Pond Community contained only two vascular plants, *Eleocharis acicularis,* a hemicryptophyte, and *Potamogeton foliosus,* a hydrophyte. *Sporobolus airoides,* also tolerant of high salinities, is a hemicryptophyte which dominated a community containing a 46% hemicryptophyte and 36% therophyte complement.

In the dry non-saline areas such as the Sandhill Mixed Prairie, Hummock, and Grazed Sandhill communities (Table 9) the hemicryptophytes and therophytes dominated. The high proportion of therophytes, 59% in the Grazed Sandhill Community, was due probably to the disturbance caused by grazing, which opens new areas for these annuals to invade. In the *Scirpus americanus-Eleocharis rostellata* Community the two dominants belong to the hemicryptophyte and helophyte life-form groups and the largest number of species, 53%, are hemicryptophytes. The Fresh Water Seep, quite similar to the *S. americanus-E. rostellata* Community, was dominated also by hemicryptophytes.

A summary of the life-form relations on the entire marsh indicated that the largest number of species belong to the hemicryptophyte and therophyte life-forms.

QUANTITATIVE ANALYSIS

The characteristic communities on the marsh were more intensively studied by use of a modification of the line intercept method of Canfield (1941) in which only the plants hitting the line were counted, and the basal area was measured as a percentage of the line covered. These transects provided quantitative information as to relative density, basal area, and frequency of the species. Transects were set up in all major vegetation zones and in transition zones between them. After several experimental attempts, a three meter line transect size was chosen for use in this study. In order to check the accuracy of this method, the transect length was always doubled to see if any new species would be added. In none of the transects was any new species added by doubling or tripling the length.

The transects were distributed more or less uniformly over the study area. This method, employing a regular distribution of transects, was chosen because an attempt was being made to describe the entire area, and it was felt that a random distribution of samples might give a bias to one part of the study area over another.

TABLE 9. Life form spectra of the marsh communities studied.

Community	No. of Species	Panerophytes %	Hemicryptophytes %	Geophytes %	Hydro-Helophytes %	Therophytes %	Lianas %
Tall *D. stricta*	13	..	23	8	15	54	..
S. airoides	11	..	46	18	..	36	..
Sandhill Mixed Prairie	110	1	47	7	1	44	..
S. depressa	3	..	..	..	..	100	..
D. stricta-S. depressa	10	10	30	10	10	40	..
S. paludosus-D. stricta	9	..	22	11	11	56	..
S. pectinata-D. stricta	24	4	46	8	29	13	..
S. americanus-E. rostellata	88	9	48	6	17	17	3
Fresh Water Seep	30	..	53	..	30	17	..
Saline Pond	2	..	50	..	50	..	..
Graded Sandhill	74	1	37	3	..	59	..
Hummock	56	5	45	5	6	45	..
Total Marsh Flora	241	5	41	4	8	41	1

To check the quantitative analysis, the abundance estimate analysis of Braun-Blaunquet (1932) was also used, but this only corroborated the transect analyses. In most cases species with a rare or very rare ranking were those that did not occur on the transects, whereas all other estimate classes were represented.

Suaeda depressa COMMUNITY

This community borders and invades the bare salt flats in many areas of the marsh. The principle species, *S. depressa,* was found in both its depressed and erect forms (Fig. 7, 8). The ten transect analysis made in July are summarized in Table 10. In other parts of the community, succulents such as *Sesuvium verrucosum* and, in one isolated area, *Salicornia rubra* were encountered.

This area had the lowest basal area, 0.06%, of any community on the marsh, and the plants were very widely scattered, being 1-40 meters apart. In 70% of the transects no vegetation could be found on the three meter transect line; however, in these areas the vegetation was widely scattered and 15-40 meters separated individual plants.

TABLE 10. Analysis of *Suaeda depressa* community. Ten transect summary.

Species	Density No.	Basal Area %	Frequency %	Height cm.
Suaeda depressa	8	.06	30	1-30

The transects which were made in this community at soil sample sites 6 and 7 are delineated in tables 11 and 12.

TABLE 11. Transect analysis at soil sample site 6.

Species	Density No.	Basal Area %	Growth Form
Suaeda depressa	2	.16	depressed

At site 6 the soils in the surface 10 cm. had a pH of 8.0-8.8, an average saturation percentage of 40%, a low organic content of 3.6%, and a soil texture classified as a sandy, clay loam, whereas the soil texture at the 60 cm. level was sand. The total salinity at the site averaged 1.92%, and the chlorinity averaged 1.11% in the surface 10 cm.

TABLE 12. Transect analysis at soil sample site 7.

Species	Density No.	Basal Area %	Growth Form
Suaeda depressa	4	.40	erect

At site 7 the pH was 8.0-8.7, the saturation percentage 40%, the organic content 6.8%, and the soil texture a sandy, clay loam in the surface 10 cm. and sand at the 60 cm. level. The total salinity in this area averaged 1.70% and chlorinity 1.05%. Tables 3-6 provide a fuller account of the soil relations.

The relation between the prostrate and erect form of *Suaeda* is still obscure. Through a large part of the growing season it appears, as evidenced by the soil samples, that the prostrate form occurs in the more saline areas; however, an observation in September 1960 modified this assumption. At this time recently germinated forms of *Suaeda* had begun development on the open salt flats and in the open areas of its former distribution, but all forms were found to be prostrate whether they developed in an area where previously there were upright forms or on the formerly barren salt flats.

TALL *Distichlis stricta* MEADOW COMMUNITY

Bordering the eastern margin of the salt flats were three major zones of vegetation. The first, a Tall *D. stricta* zone was separated from the flats by a man-made ridge in the northeastern part of the marsh, but it bordered the flats or the *S. depressa* Community in the southeastern and southern parts of the marsh. The ridge, 3-5 ft. high, supported many weedy species including *Tamarix gallica, Bromus japonicus, Cenchrus longispinus, Melilotus alba, Gaura parviflora, Chenopodium leptophyllum, Lactuca ludoviciana* and a host of others, whereas, the Tall *D. stricta* Community contained none of the above species and had a much smaller number of species.

Actually this community contained only 13 species of vascular plants, five of which were present in the spring and early summer, including *D. stricta, Scirpus paludosus, Poa arida, Hordeum jubatum,* and *Suaeda depressa,* whereas the remainder included eight species of extremely rare occurrence which appeared in late summer. Even though this community had only 13 species, it had the highest basal cover, 12.25%, of any community on the Big Salt Marsh.

A ten transect analysis of the vegetational relations made in June in this community is in Table 13. In this zone (Tables 13 and 15), *D. stricta* was very evenly distributed and occurred at all transect sites. It comprised 94.46% of the total vegetation and had a basal area of 11.35% or 92.65% of the total. *S. paludosus,* found in scattered colonies, had a basal area of 0.89% or 7.27% of the total, a frequency of 30%, and a relative density of 5.38%.

TABLE 13. An analysis of the Tall *Distichlis stricta* Meadow Community. Ten transect summary. Total density, 2529.

Species	Relative Density %	Basal Area %	B. A. % Total %	Frequency %
Distichlis stricta	94.46	11.35	92.65	100.00
Scirpus paludosus	5.38	.89	7.27	30.00
Poa arida	.16	.01	.08	10.00
		12.25		

In a single transect, *S. paludosus* was the codominant and had a relative density of 48% and a basal area of 5.80%, 75.30% of the total. This transect is described in Table 14 and the basal area relations are cited in Table 15.

TABLE 14. Transect analysis of area with *S. paludosus-D. stricta* codominance. Total density, 79.

Species	Relative Density %	Basal Area %	B. A. % Total %	Height cm.
Distichlis stricta	52.00	1.90	24.70	20-60
Scirpus paludosus	48.00	5.80	75.30	75-90
		7.70		

Poa arida comprised less than one percent of the total vegetation in this zone and with *H. jubatum* was very widely scattered to rare.

The comparison of the basal area of species at the various transect sites (Table 15) indicates clearly that *D. stricta* was the dominant, having the highest basal area at 90% of the sites sampled. Only at site 3 was another species important in the cover relations. Table 15 indicates *S. paludosus* was dominant and traces of it were found also in transects 6 and 9. The remaining species provided very little additional cover.

The soils in the surface 10 cm. in the eastern section of the community at site 3 had a pH of 7.2-8.6, an average saturation percentage of 43%, an organic content of 2.5%, and a soil texture classified as loamy sand and as sand at the 60 cm. level. The total salinity was 0.29-0.63% and the chlorinity 0.10-0.31% in the surface 10 cm. The vegetational relations at site 3 is indicated in Table 16.

At site 4, in the western part of this community, the soils at the 10 cm. level had a pH of 8.0-8.6, a saturation percentage of 75%, an organic content of 6.2%, and a soil texture classified as a sandy, clay loam and at the 60 cm. level as a sand. The total salinity was 0.73-0.94% and the chlorinity 0.34-0.47%. Table 17 delineates the vegetation relations at site 4. Tables 3-6 provide more complete data on the soil relations in the area.

Soils in the area were covered with 2-6 inches of water during wetter periods of the growing season, and the combination of salinity and inundation tended to prevent the invasion of species from the prairie, hummocks, and the adjoining western ridge. Dry land plants of these regions are eliminated by the standing water, and the salinity eliminates non-halophytic aquatic plants.

TABLE 15. A comparison of the basal area of species at ten transect sites within the Tall *D. stricta* Meadow community. B. A. is expressed as a percentage of the actual cover.

	Transects									
Species	1	2	3	4	5	6	7	8	9	10
Distichlis stricta	11.90	9.10	1.90	7.20	13.80	15.00	18.00	20.20	9.70	6.74
Scirpus paludosus	......	......	5.80	......	......	1.90	......	......	1.20	......
Poa arida	......	......	......	.10	......	......	......	......	......	......
Total	11.90	9.10	7.70	7.30	13.80	16.90	18.00	20.20	10.90	6.74

The fairly high basal area, 12.25%, in the area provided a dense cover of living and dead plant material (Fig. 3) which did not allow invaders to enter, making it a more or less closed community.

Sporobolus airoides COMMUNITY

The main body of this community was on the eastern portion of the marsh between the Tall *D. stricta* Community on the west and the Sandhill Mixed Prairie Community on the east. It also occurred on small, self-produced hummocks on the open salt flats (Fig. 20). There was a sharp 1-2 ft. rise between this and the *D. stricta* Community and a very sharp change in the character of the vegetation.

TABLE 16. Transect analysis at soil sample site 3.

Species	Density No.	Basal Area %	Height cm.
Distichlis stricta	188	11.9	35-50

Sporobolus airoides was the dominant species in the area, making up 90.50% of the density and covered 96.04% of the total basal area. It had a very wide distribution and a frequency of 100%. The remainder of the species in this community comprised only 3.96% of the total vegetation cover and only 9.50% of the relative density. *D. stricta* also occurred in this zone, but it had a relative density of only 5.85%, a relative basal area of only 1.98%, and was found in only 40% of the transect sites. This was an abrupt change from the Tall *D. stricta* Community described earlier where it made up 94.46% of the relative density, 92.65% of the total basal area, and had a frequency of 100%.

TABLE 17. Transect analysis at soil sample site 4.

Species	Density No.	Basal Area %	Height Cm.
Distichlis stricta	251	13.8	40-60

Another species in the area was *Ambrosia psilostachya* var. *coronopifolia* which had a frequency of 40%, covered 0.99% of the total vegetated area, and had a relative density of 2.08%. Other species were *Aster ericoides* which had a frequency of 30% and *Elymus canadensis* with a frequency of 10%. A complete analysis of the transects made during July and September is in Table 18.

The basal area relations at all transect sites within this community is delineated in Table 20. The data clearly show the complete dominance of

TABLE 18. Analysis of the *Sporobolus airoides* community. Ten transect summary. Density, 266.

Species	Relative Density %	Basal Area %	B. A. % Total %	Frequency %
Sporobolus airoides	90.50	4.86	96.04	100.00
Distichlis stricta	5.85	.10	1.98	40.00
Ambrosia psilostachya var. *coronopifolia*	2.08	.05	.99	40.00
Aster ericoides	1.16	.04	.79	30.00
Elymus canadensis	.41	.01	.20	10.00
		5.06		

S. airoides at all transect sites. This species made up an average of 96.04% of the total basal area whereas the remaining taxa covered only a negligible portion of the area and had a total combined cover of only 3.96% of the total.

The vegetation relations at soil sample site 2 are given in Table 19. The surface 10 cm. of soil had a pH of 6.5-7.9, a saturation percentage of 34%, a loss on ignition of 2.2%, and a soil texture classified as sand. The salinity was 0.04-0.19% and the chlorinity 0.02-0.09% in the surface 10 cm. More complete data on seasonal soil relations in this area are in Tables 3-6.

At the site of Fig. 20, an example of this community invading the open salt flats, the salinity was 1.60% and the chlorinity 1.16% in the surface 10 cm. of soil. The soil salinity and chlorinity analyses were made in July. The salinity and chlorinity content at this site were much higher than in the site described earlier where *S. airoides* occupied larger areas. Other species on the hummock were *Poa arida* and *Suaeda depressa*.

TABLE 19. Transect analysis at soil sample site 2. Density, 30.

Species	Relative Density %	Basal Area %	B. A. % Total %	Height cm.
Sporobolus airoides	90.04	5.34	95.36	80-90
Ambrosia psilostachya var. *coronopifolia*	6.64	.13	2.32	18-20
Elymus canadensis	3.32	.13	2.32	75-80
		5.60		

The lack of a great deal of lateral translocation of salts from the Tall *D. stricta* Community to the *S. airoides* and Prairie communities is evident, for, as noted in Table 5, the former had an average salinity of 0.39%, the next of 0.12%, and the latter of 0.01%.

SANDHILL MIXED PRAIRIE COMMUNITY

This area formed the eastern border of the marsh and was covered with a Sandhill Mixed Prairie vegetation. The average basal area from eight transects made in June was 5.97% and varied from 3.04-9.13% (Table 22). *Panicum scribnerianum*, a short grass, made up 19.78% of the total density, had a frequency of 100%, and a basal area of 0.89% or 14.88% of the total.

Elymus canadensis, Agropyron smithii, and *Sporobolus airoides* were found in 25% of the transects made. *A. smithii* had a relative density of 7.28%, *S. airoides*, 6.24%, and *E. canadensis*, 0.48%. These species had a combined cover which accounted for 22.75% of the total vegetated area.

Tall grasses that play an important role in this community had the following relative densities: *Sorghastrum nutans*, 8.47%; *Panicum virgatum*, 7.28%; *Andropogon gerardi*, 8.53%. In the same order these species comprised 8.70%, 11.88%, and 16.73% of the total basal area.

TABLE 20. A comparison of the basal area of species at ten transect sites within the *S. airoides* community. B. A. is expressed as a percentage of the actual cover.

Species	Transects 1	2	3	4	5	6	7	8	9	10
Soporobolus airoides	5.34	4.35	4.74	4.95	5.40	3.86	5.94	4.01	4.95	5.14
Ambrosia psilostachya var. *coronopifolia*	.13	......	......	.13	......	.11	......	......	.13	......
Distichlis stricta	......	.11	......	......	.41	.19	......	.35	......	......
Aster ericoides	......	......	......	.13	......	......	.19	......	.11	......
Elymus canadensis ..	.13	......	......	......	......	......	......	......	......	......
Total	5.60	4.46	4.74	5.21	5.81	4.16	6.13	4.36	5.19	5.14

Bromus japonicus, an annual which invades mowed and grazed prairies in this area of Kansas, made up 27.97% of the total density, had a frequency of 87.50%, and a basal area of 0.86% or 14.38% of the total.

The taxa mentioned above along with other widely scattered grasses, including *Eragrostis trichodes* and *Andropogen scoparius,* had a combined relative density of 89.40% and a cumulative basal area of 5.39% or 90.15% of the total. The remainder of the vegetation was composed of other widely scattered grasses and forbs. Table 21 provides an indication of the quantitative relations of the vegetation in this area obtained from eight transects.

A comparison of the basal area at all transect sites is in Table 22. It can be seen that the species making up the highest amount of cover varied at different transect sites, and no species played a dominant role in more than two. *Panicum scribnerianum* had a frequency of 100%, and a basal area of 0.26-1.85%, but in no transect did it make up the largest portion of the vegetation. This species, however, must be considered one of the chief indicators of the lower strata of this community type because of its wide distribution throughout the area. Weaver (1954), in his discussion of upland species, stated that "because of its wide distribution and rather common occurrence, it is one of the most important secondary species."

The vegetational relations at soil sample site 1 are delineated in Table 23. At this site the surfac 10 cm. of soil had a pH of 6.3-6.9, a saturation percentage of 28%, the lowest marsh organic content of 1.1%, and a soil texture classified as sand and also as sand at the 60 cm. level. The salinity in the surface soil was 0.003-0.02% and the chlorinity 0.001-0.007%. More complete data concerning the soil relations are in Tables 3-6.

As mentioned earlier, the translocation of salts into this community from adjoining more saline ones seemed to be slight or almost nonexistent. One reason for this is that the sandy prairie soils allow rapid infiltation of rainwater, so that even if there were any lateral translocation the salts would be leached out.

TABLE 21. Analysis of the Sandhill Mixed Prairie community. Eight transect summary. Density, 638.

Species	Relative Density %	Basal Area %	B. A. % Total %	Frequency %
Bromus japonicus	27.97	.86	14.38	87.50
Panicum scribnerianum	19.78	.89	14.88	100.00
Andropogon gerardi	8.53	1.00	16.73	12.50
Sorghastrum nutans	8.47	.52	8.70	25.00
Agropyron smithii	7.28	.67	11.21	25.00
Panicum virgatum	7.28	.71	11.88	25.00
Sporobolus airoides	6.24	.67	11.21	25.00
Artemesia ludoviciana	4.33	.35	5.85	37.50
Plantago purshii	3.63	.09	1.50	75.00
Agrostis hiemalis	3.37	.05	.83	12.50
Ambrosia psilostachya var. *coronopifolia*	.79	.05	.83	12.50
Elymus canadensis	.48	.02	.33	25.00
Monarda citriodora	.41	.008	.13	25.00
Achillea lanulosa	.35	.05	.83	25.00
Tradescantia occidentalis	.29	.02	.33	12.50
Lepidium virginicum	.29	.004	.06	12.50
Oxalis stricta	.25	.01	.16	25.00
Erigeron strigosus var. *beyrichii*	.14	.007	.11	12.50
Junctus interior	.12	.003	.05	12.50
		5.972		

Scirpus paludosus-Distichlis stricta COMMUNITY

In the north-central portion, and scattered irregularly in other more or less open areas of the marsh were colonies of *S. paludosus* with a *D. stricta* codominant. A complete summary of the ten transect analysis made in this community during June is in Table 24. This summary shows the average basal area in this community was 2.17%.

Distichlis stricta had a relative density of 63.6%, a frequency of 100%, and a relative basal area of 43.04%. The tall dominant in this area, *S. paludosus*, had a relative density of 31.80%, a frequency of 100%, and a basal area of 54.99% of the total vegetational cover. These two species accounted for 95.40% of the total density and covered 98.03% of the total vegetated area.

Another species was *Polygonum ramosissimum* with a relative density of 3.8%, a frequency of 60%, and covered 1.84% of the total vegetated area. An erect form of *Suaeda depressa* had a relative density of 0.8%, a frequency of 10%, and a basal area of 0.13% of the total. Other rarer species were *Poa arida*, *Hordeum jubatum*, *Heliotropium curassavicum*, *Atriplex argentea* and *A. patula* var. *hastata*.

TABLE 22. A comparison of the basal area of species at eight transect sites within the Sandhill Mixed Prairie Community. B.A. is expressed as a percentage of the actual cover.

Species	Transects 1	2	3	4	5	6	7	8
Andropogon gerardi	......	......	......	8.03	......	......	......	......
Panicum scribnerianum	.73	1.20	.80	.26	.53	1.85	1.43	.33
Bromus japonicus	.10	.26	......	.33	1.31	1.75	.36	2.80
Agropyron smithii	.75	......	......	......	......	4.63	......	......
Sporobolus airoides	......	......	......	......	3.56	......	......	1.86
Sorghastrum nutans	.93	3.23	......	......	......	......	......	......
Panicum virgatum	......	......	2.52	......	......	......	3.20	......
Artemesia ludoviciana	......	......	.25	......	......	.46	2.13	......
Plantago purshii	.13	.10	.03	.30	......	.15	.03	......
Agrostis hiemalis	......	......	.41	......	......	......	......	......
Ambrosia psilostachya var. *coronopifolia*	......	......	......	......	......	......	......	.46
Achillea lanulosa	......	......	......	.10	.33	......	......	......
Elymus canadensis	.13	.06	......	......	......	......	......	......
Tradescantia occidentalis	.23	......	......	......	......	......	......	......
Oxalis stricta	......	......	......	......	......	......	.03	......
Monarda citriodora	......	.03	.03	.05	......	......	......	......
Erigeron strigosus var. *Beyrichii*	......	......	......	.06	......	......	......	......
Lepidum virginicum	.03	......	......	......	......	......	......	......
Juncus interior	......	......	......	......	.03	......	......	......
Total	3.04	4.88	4.04	9.13	5.76	8.84	7.18	5.45

The basal relations listed in Table 25 show the clear dominance of *S. paludosus* and *D. stricta* at each transect site over the remaining species. The basal area at the various sites was 1.41-3.06%, that of *D. stricta* was 0.35-1.20%, and the basal area of *S. paludosus* was 0.70-1.93%. *P. ramosissimum* had a

TABLE 23. Transect analysis at soil sample site 1. Density, 43.

Species	Relative Density %	Basal Area %	B. A. % Total %
Agropyron smithii	27.92	.75	24.75
Sorghastrum nutans	23.29	.93	30.00
Panicum scribnerianum	25.60	.73	24.09
Plantago purshii	9.38	.13	4.29
Bromus japonicus	6.91	.10	3.30
Tradescantia occidentalis	2.33	.23	7.59
Elymus canadensis	2.33	.13	4.29
Lepidium virginicum	2.33	.03	.99
		3.03	

TABLE 24. Analysis of *Scirpus paludosus-Distichlis stricta* community. Ten transect summary. Density, 341.

Species	Relative Density %	Basal Area %	B. A. % Total %	Frequency %
Distichlis stricta	63.60	.94	43.04	100.00
Scirpus paludosus	31.80	1.19	54.99	100.00
Polygonum ramosissimum	3.80	.04	1.84	60.00
Suaeda depressa	.80	.003	.13	10.00
		2.173		

TABLE 25. A comparison of the basal area of species at ten transect sites within the *S. paludosus-D. stricta* community. B.A. is expressed as a percentage of the actual cover.

	Transects									
Species	1	2	3	4	5	6	7	8	9	10
Scirpus paludosus	1.93	1.06	.76	1.04	.70	1.07	1.60	.96	1.10	1.61
Distichlis stricta	1.13	.35	1.01	.58	1.20	1.12	1.20	1.40	.48	.96
Polygonum ramosissimum	------	------	------	.10	.06	.06	------	.10	------	.10
Suaeda depressa	------	------	------	------	.03	------	------	------	------	------
Total	3.06	1.41	1.77	1.72	1.99	2.25	2.80	2.46	1.58	2.67

fairly broad distribution in this area, but its basal area was low, 0.06-0.10% at the various sites.

The vegetational relations at soil sample site 8 are described in Table 26. The surface 10 cm. of soil had a pH of 8.3-8.6, a saturation percentage of 47%, an organic content of 9.2%, and a soil texture classified as sandy, clay loam and as sand at the 60 cm. level. The salinity in the surface soil was 0.27-1.10% and the chlorinity 0.09-0.68%. More complete data concerning the soil relations are in Tables 3-6.

Distichlis stricta-Suaeda depressa COMMUNITY

To the west of the salt flats and in large areas of the southern section of the marsh the vegetation was composed mainly of dwarfed forms of *D. stricta* and *S. depressa*. Figure 9 illustrates the dwarfed form and low basal area in this community. This community was broken up into five separate zones,

TABLE 26. Transect analysis of soil sample site 8. Density, 46.

Species	Relative Density %	Basal Area %	B. A. % Total %	Height cm.
Distichlis stricta	54.36	1.13	36.93	12-30
Scirpus paludosus	45.64	1.93	63.07	25-45
		3.06		

and Tables 27-31 provide the information found in these analyses. Table 32 contains a 70 transect summary of the vegetational relations.

Distichlis was the most abundant species, having a relative density of 86.56%, a frequency of 96.82%, and a basal area of 1.07% or 86.53% of the total. *Suaeda depressa,* the codominant, had a relative density of 13.13%, a frequency of 62.37%, and a basal area of 0.13% or 11.50% of the total. The remaining species in the area, including *Scirpus paludosus, Spartina pectinata, Sesuvium verrucossum, Poa arida, Polygonum ramosissimum,* and others mentioned earlier comprised less than 1% of the total density, had a basal area of less than 2% of the total, and a very limited distribution.

Even though this community contained many of the same species as the Tall *D. stricta* Community, it could never be confused with it. The main reason for the distinction between the two is that this one had a greatly reduced basal area and the species had a dwarfed growth form which also clearly distinguished it from all others.

Soil samples were taken in four parts of the community. Table 33 pro-

TABLE 27. Analysis of *D. stricta-S. depressa* community. An 11 transect summary. Zone A. Density, 295.

Species	Relative Density %	Basal Area %	B. A. % Total %	Frequency %
Distichlis stricta	78.95	.79	87.00	90.00
Suaeda depressa	21.05	.12	13.00	63.00
		.91		

TABLE 28. Analysis of *D. stricta-S. depressa* community. A 12 transect summary. Zone B. Density, 320.

Species	Relative Density %	Basal Area %	B. A. % Total %	Frequency %
Distichlis stricta	85.22	.99	85.10	100.00
Suaeda depressa	14.60	.16	13.80	83.30
Spartina pectinata	.18	.01	1.10	8.30
		1.16		

TABLE 29. Analysis of *D. stricta-S. depressa* community. A 9 transect summary. Zone C. Density, 342.

Species	Relative Density %	Basal Area %	B. A. % Total %	Frequency %
Distichlis stricta	96.04	1.59	97.30	100.00
Suaeda depressa	3.96	.04	2.70	66.00
		1.63		

TABLE 30. Analysis of *D. stricta-S. depressa* community. A 16 transect summary. Zone D. Density, 497.

Species	Relative Density %	Basal Area %	B. A. % Total %	Frequency %
Distichlis stricta	78.53	1.18	84.85	93.00
Suaeda depressa	20.84	.16	12.02	75.00
Scirpus paludosus	.63	.04	3.13	12.50
		1.38		

TABLE 31. Analysis of *D. stricta-S. depressa* community. A 22 transect summary. Zone B. Density, 638.

Species	Relative Density %	Basal Area %	B. A. % Total %	Frequency %
Distichlis stricta	93.04	.99	83.90	100.00
Suaeda depressa	6.52	.15	12.71	40.00
Scirpus paludosus	.44	.04	3.39	9.09
		1.18		

TABLE 32. A summary of transect data obtained from five separate transect analyses of this community. A 70 transect summary. Density, 2092.

Species	Relative Density %	Basal Area %	B. A. % Total %	Frequency %
Distichlis stricta	86.56	1.07	86.53	96.82
Suaeda depressa	13.13	.13	11.50	62.37
Scirpus paludosus	.28	.02	1.78	5.71
Spartina pectinata	.03	.001	.19	1.42
		1.221		

TABLE 33. Transect analysis at soil sample site 9. Density, 18.

Species	Relative Density %	Basal Area %	B. A. % Total %	Height cm.
Distichlis stricta	77.76	.70	70.00	15-20
Suaeda depressa	22.22	.30	30.00	25-28
		1.00		

vides the vegetational relations at sample site 9, in the eastern part of Zone A of the *D. stricta-S. depressa* Community.

The soils at site 9 had a pH of 7.5-8.6, an average saturation percentage of 41%, an organic content of 9.3%, and a soil texture in the surface 10 cm. of sandy, clay loam and sand at the 60 cm. level. The total salinity was 0.49-1.55% and the chlorinity 0.16-1.20% in the surface 10 cm.

Soils in the western part of Zone D were studied at soil sample site 11, and the vegetational relations are described in Table 34. The soils had a pH of 7.6-8.7, an average saturation percentage of 44%, an organic content of 11.2%, and a soil texture in the surface 10 cm. which was a sandy clay loam and a loamy sand at the 60 cm. level. The total salinity was 0.58-1.52% and the chlorinity 0.14-0.46% in the surface 10 cm.

TABLE 34. Transect analysis at soil sample site 11. Density, 53.

Species	Relative Density %	Basal Area %	B. A. % Total %	Height cm.
Distichlis stricta	86.72	1.84	88.89	17-21
Suaeda depressa	13.24	.23	11.11	15-20
		2.07		

Soils of zone B were sampled at site 15 and the vegetational analysis in this area is recorded in Table 35. The pH of the soils was 8.1-8.6, the saturation percentage 62%, the organic content 17.5%, and the soil texture in the surface 10 cm. a sandy clay loam and sand at the 60 cm. level. The total salinity was 0.82-2.45% and the chlorinity 0.46-1.57% in the surface 10 cm.

TABLE 35. Transect analysis at soil sample site 15. Density, 26.

Species	Relative Density %	Basal Area %	B. A. % Total %	Height cm.
Distichlis stricta	26	0.99	100.00	18-22

The fourth soil analysis was made in zone E at site 13. The vegetational analysis is recorded in Table 36. The pH of the soils was 8.0-8.5, the saturation percentage 44%, the organic content 6.6%, and the soil texture in the surface 10 cm. a sandy, clay loam and sand at the 60 cm. level. The total salinity aws 1.51-2.52% and the chlorinity 0.80-1.20% in the surface 10 cm.

A summary of the soil conditions in the area indicated that pH was 7.5-8.7, the saturation percentage 41-62%, the organic content 6.6-17.5%, and the soil texture in the surface 10 cm. a sandy, clay loam and sand to sandy loam

TABLE 36. Transect analysis at soil sample site 13. Density, 32.

Species	Relative Density %	Basal Area %	B. A. % Total %	Height cm.
Distichlis stricta	90.63	1.06	91.38	18-25
Suaeda depressa	9.37	.10	.62	10-15
		1.16		

TABLE 37. Results of a transect on the southwest border of zone E of the *D. stricta-S. depressa* community. Density, 92.

Species	Relative Density %	Basal Area %	B. A. % Total %
Distichlis stricta	44.56	1.64	25.74
Scirpus americanus	36.96	3.40	53.37
Eleocharis rostellata	10.87	.40	6.29
Spartina pectinata	7.61	.93	14.60
		6.37	

at the 60 cm. level. The salinity, which appeared to be the controlling factor in determining the vegetation in this community, was 0.49-2.52% and the chlorinity 0.14-1.57%. Further data concerning soil relations are in Tables 3-6.

The comparison of basal area (Table 38) for 12 transects in zone B of the *D. stricta-S. depressa* area indicate their overall dominance. The rhizomatous growth habit (Fig. 10), gives *D. stricta* a great advantage in spreading into the more saline areas. *S. pectinata* was at only one location indicating that this transect was in a slightly moister situation than was typical for this community.

A single transect, run southwest of zone E (Table 37), appeared to have the typical vegetation of the *S. pectinata-D. stricta* Community merging with that of *S. americanus-E. rostellata*. To the southeast of zone E a five transect summary (Table 39) related a vegetation type similar to the Tall *D. stricta* Community. It was typical for this and the previously mentioned community to enter or border the *D. stricta-S. depressa* area when there was a lowering of salinity and some added source of fresh water. Besides the species listed in Tables 37 and 39, *Bassia hyssopifolia*, *Eustoma grandiflora*, *Scirpus validus* and *Typha latifolia* were widely scattered in the general area.

Spartina pectinata-Distichlis stricta COMMUNITY

Species making up this community formed a dense sword of vegetation. In one location on the marsh, as mentioned earlier, this community was ex-

TABLE 38. A comparison of the basal area of species at transect sites in Zone B of the *D. stricta-S. depressa* community. B.A. is expressed as a percentage of the actual cover.

	Transects											
Species	1	2	3	4	5	6	7	8	9	10	11	12
Distichlis stricta	1.60	1.17	.88	1.06	1.08	.86	.55	1.10	.96	.53	1.13	.90
Suaeda depressa	.25	.10	......	.06	.13	.21	.10	.50	.06	.30	.28	......
Spartina pectinata	.16	......	......	......	......	......	......	......	......	......	......	......
Total	2.01	1.27	.88	1.12	1.21	1.07	.65	1.60	1.02	.83	1.41	.99

TABLE 39. Results of a five transect study on this southeast border of zone E of the *D. stricta-S. depressa* Community. Density, 752.

Species	Relative Density %	Basal Area %	B. A. % Total %	Frequency %
Distichlis stricta	95.60	5.98	94.32	100.00
Poa arida	4.10	.27	4.26	30.00
Scirpus paludosus	.30	.09	1.42	10.00
		6.34		

tensive, and in other areas small patches of the *S. pectinata-D. stricta* vegetation type were found. The transect analysis made in this community during July is summarized in Table 40, and Fig. 12 illustrates the vegetation.

The short dominant, *D. stricta,* was 20-50 cm. tall, had a relative density of 50.77%, a basal area of 27.46% of the total, and a frequency of 100%. The tall (70-130 cm.) dominant, *S. pectinata,* was the most characteristic species of the area. It had a relative density of 18.34%, a basal area of 45.80% of the total and a frequency of 100%.

On its western margin this community bordered one dominated by *Scirpus americanus* and *Eleocharis rostellata.* These two species infiltrated the *S. pectinata-D. stricta* Community, had relative densities of 6.36% and 18.92% respectively and a combined basal area of 1.28% or 21.94% of the total. *Poa arida* was scattered through the community, and had a frequency of 50%, a relative density of 3.80%, and a basal area of 0.13% or 2.24% of the total. Other species, including *Juncus torreyi, J. interior, Scirpus paludosus* and *Apocynum sibiricum,* had frequencies (Table 40) of 10-20%, relative densities of less than 1%, and a combined basal area of 0.15% or 2.56% of the total area covered.

TABLE 40. Analysis of *Spartina pectinata-Distichlis stricta* community. Ten transect summary. Density, 771.

Species	Relative Density %	Basal Area %	B. A. % Total %	Frequency %
Distichlis stricta	50.77	1.66	27.46	100.00
Eleocharis rostellata	18.92	.61	10.45	30.00
Spartina pectinata	18.34	2.67	45.80	100.00
Scirpus americanus	6.36	.67	11.49	50.00
Poa arida	3.80	.13	2.24	50.00
Juncus torreyi	.56	.03	.51	20.00
Juncus interior	.49	.03	.51	10.00
Scirpus paludosus	.45	.07	1.20	20.00
Apocynum sibiricum	.31	.02	.34	20.00
		5.89		

Two species not occurring on the transects, *Hordeum jubatum* and *Eustoma grandiflora,* were rare to widely scattered through this area.

Table 42 provides a comparison of the basal area of species at the various transect sites. *S. pectinata* had the highest cover at 60% and the combination of *S. pectinata* and *D. stricta* had the highest cover at all sites, making up 73.26% of the total area covered by this community. One can see also that *S. americanus* and *E. rostellata* formed an important part of the cover only locally.

The comparison of basal area of species described in Table 42 gives a clearer account of vegetation relations than would a comparison of densities. The reason is that *D. stricta* had a relative density of 50.77% and *S. pectinata* only 18.34%, but the cover of *D. stricta* was much lower because it is a much smaller plant and has smaller culms than *S. pectinata.*

The soils in the eastern part of the area at site 10 had a pH of 8.0-8.5, an average saturation percentage of 56%, a fairly high organic content of 17.9% and a soil texture classified as a sandy, clay loam in the surface 10 cm. and sand at the 60 cm. level. The total salinity was 0.20-0.63% and the chlorinity 0.09-0.36% in the surface 10 cm. The vegetation relations are in Table 41.

TABLE 41. Transect analysis at soil sample site 10. Density, 87.

Species	Relative Density %	Basal Area %	B. A. % Total %	Height cm.
Distichlis stricta	69.00	2.10	35.13	35-42
Spartina pectinata	28.70	3.75	62.71	90-100
Scirpus paludosus	2.30	.13	2.17	68-73
		5.98		

TABLE 42. A comparison of the basal area of species at ten transect sites within the *Spartina pectinata-Distichlis stricta* Community. B. A. is expressed as a percentage of the actual cover.

	Transects									
Species	1	2	3	4	5	6	7	8	9	10
Spartina pectinata	3.75	4.50	3.86	3.93	2.33	2.20	1.95	1.80	.90	1.57
Distichlis stricta	2.10	3.74	1.24	1.68	1.13	.56	.96	1.10	1.05	3.07
Scirpus americanus	......	2.40	2.66	......	......	......	......	.07	.93	.66
Eleocharis rostellata	......	......	......	......	......	2.40	2.06	1.70	......	......
Poa arida	......	......	......	......	.23	.07	.07	......	.63	.33
Scirpus paludosus	.13	......	......	......	.13	......	......	......	......	......
Juncus Torreyi	......	......	......	......	.23	......	......	.07	......	......
Juncus interior	......	.35	......	......	......	......	......	......	......	......
Apocynum sibiricum	......	.10	.16	......	......	......	......	......	......	......
Total	5.98	11.09	7.90	5.61	4.05	5.23	5.04	4.74	3.61	5.63

At site 12 in the western part of the community the soils at the 10 cm. level had a pH of 8.1-8.6, a saturation percentage of 64%, an organic content of 10.1%, and a soil texture classified as sandy, clay loam and as a sand at the 60 cm. level. The total salinity was 0.27-1.00% and the chlorinity 0.14-1.46%. Tables 3-6 provide more complete data on soil relations, and Table 43 gives the vegetational relations at soil sample site 12.

TABLE 43. Transect analysis at soil sample site 12. Density, 147.

Species	Relative Density %	Basal Area %	B. A. % Total %	Height cm.
Distichlis stricta	62.16	3.74	33.72	40- 50
Spartina pectinata	19.28	4.50	40.58	100-130
Scirpus americanus	12.85	2.40	21.64	100-120
Apocynum sibiricum	.71	.10	.90	42- 44
Juncus interior	5.00	.35	3.16	76- 80
		11.09		

TABLE 44. Analysis of the *Scirpus americanus-Eleocharis rostellata* Community. A 15 transect summary. Density, 1599.

Species	Relative Density %	Basal Area %	B. A. % Total %	Frequency %
Eleocharis rostellata	60.22	3.99	42.35	93.24
Scirpus americanus	22.24	4.05	42.99	100.00
Eleocharis tenuis	5.46	.28	2.97	13.32
Distichlis stricta	4.07	.21	2.23	6.66
Agrostis alba	2.83	.17	1.81	59.94
Carex praegracilis	1.06	.14	1.49	13.32
Juncus torreyi	.87	.06	.64	39.96
Panicuc lanuginosum	.65	.04	.43	6.66
Carex lanuginosa	.64	.05	.53	26.64
Scirpus lineatus	.50	.07	.74	26.64
Fimbristylis castanea	.40	.02	.21	6.66
Juncus interior	.30	.08	.85	33.30
Apocynum sibiricum	.25	.12	1.27	33.30
Cicuta maculata	.13	.06	.64	13.32
Agropyron smithii	.10	.02	.21	6.66
Sphenopholis obtusata	.07	.003	.03	6.66
Panicum virgatum	.05	.01	.11	6.66
Lippia lanceolata var. *recognita*	.05	.006	.06	6.66
Carex annectans var. *xanthocarpa*	.05	.004	.04	6.66
Vernonia fasciculata	.04	.008	.08	6.66
Liatris lancifolia	.02	.03	.32	6.66
		9.421		

Scirpus americanus-Eleocharis rostellata COMMUNITY

The most western margin of the marsh contained a sedge-meadow type vegetation in which the dominants were *S. americanus* and *E. rostellata.* This community was bordered on the east either by a *D. stricta-S. depressa* or a *S. pectinata-D. stricta* Community type. To the west of the sedge-meadow, forming the western limits of the marsh, were the typical sandhills of the Great Bend Prairie. There was some infiltration of sandhill species on the western border, some of which were *Rosa arkansana, Vitis riparia, Polygonum convolvulus, Cucurbita foetidissima, Galium aparine, Lactuca ludoviciana,* and *Oenothera rhombipetala.*

A 15 transect survey, made in the north-western corner of the community during June and July, indicated (Table 44) that the average basal area was 9.42%. *Eleocharis rostellata,* the short dominant in this zone, was 30-70 cm. tall, had a relative density of 60.22%, a frequency of 93.24%, and a basal area of 3.99% or 42.35% of the total. *Scirpus americanus,* the tall dominant, was 70-160 cm. tall, had a relative density of 22.24%, a frequency of 100.00%, and a basal area of 4.05%, or 42.99% of the total. These two species had a combined relative density of 82.46% and covered 85.34% of the total vegetated area, clearly indicating their dominance in this vegetation type.

Distichlis stricta, which was not one of the characteristic species, had a relative density of 62.68% in the most north-eastern transect where the community bordered upon the *D. stricta-S. depressa* Community. This transect was probably through an ectone between the latter, which had a higher soil salinity, and the Sedge-Meadow Community. *D. stricta* was not present in any other transect.

Another species of some local importance in the northern part of the transected area was *Eleocharis tenuis,* which had at one site a relative density of 77.88% and a basal area of 48% of the total. Other species with a wide distribution and a fairly high frequency included *Agrostis alba,* 59.94%, *Juncus torreyi,* 39.96%, *Juncus interior,* 33.30%, *Apocynum sibiricum,* 33.30%, *Carex lanuginosa,* 26.64%, and *Scirpus lineatus,* 26.64%. Data on the remainder of the species with lower frequencies are in Table 44, which summarizes the vegetational relations.

A comparison of the basal area relations of the species in Table 45 clearly indicates the dominance of *S. americanus* and *E. rostellata.* The total basal area at all transect sites in this zone was 6.88-13.37%, while that of *E. rostellata* was 0.36-6.27% and *S. americanus* 1.50-8.00%. Only two other species comprised any appreciable part of the basal area, and these were only locally important. The first of these, *D. stricta,* had a basal area of 3.23% in transect 10 and was codominant there, whereas *E. tenuis* had a basal area of 3.81% at site 9 and was one of the controlling species at that location.

The vegetational relations at soil sample site 14 are in Table 46. Surface

TABLE 45. A comparison of the basal area of species at ten transect sites within the *S. americanus-E. rostellata* Community. B. A. is expressed as a percentage of the actual cover.

Species	Transects 1	2	3	4	5	6	7	8	9	10
Scirpus americanus	8.00	5.63	5.86	3.10	2.93	4.50	4.12	3.02	3.23	5.70
Eleocharis rostellata	1.87	5.50	5.22	3.43	3.33	4.13	4.76	5.36	.36	......
Eleocharis tenuis	......	......	.40	......	......	......	......	......	3.81	......
Distichlis stricta	......	......	......	......	......	......	......	......	......	3.23
Agrostis alba	......	.03	1.16	.25	.23	.16	.16	.07	.35	......
Carex praegracilis	.25	......	......	......	......	......	......	......	......	......
Apocynum sibiricum	.10	......	......	.13	......	......	......	.83	......	......
Juncus Torreyi	......	......	......	.10	.10	.20	......	......	......	......
Juncus interior	.04	......	.12	.06	......	.33	......	......	......	......
Scirpus lineatus	......	......	.51	......	......	......	......	.05	.08	......
Cicuta maculata	......	......	......	......	.16	......	......	.80	......	......
Carex lanuginosa	.05	.34	.10	......	......	......	......	.30	......	......
Panicum lanuginosum	......	......	......	......	......	......	......	......	......	......
Fimbristylis castanea	......	......	......	......	......	......	......	......	......	......
Liatris lancifolia	......	......	......	......	......	.50	......	......	......	......
Agropyron smithii	......	......	......	......	......	.40	......	......	......	......
Panicum virgatum	......	......	......	......	......	......	......	......	......	......
Vernonia fasciculata	......	......	......	......	.13	......	......	......	......	......
Lippia lanceolata var. *xanthocarpa*	.10	......	......	......	......	......	......	......	......	......
Carex annectans var. *xanthocarpa*	......	.06	......	......	......	......	......	......	......	......
Sphenopholis obtusata	......	......	......	......	......	......	......	......	.05	......
Total	10.41	11.56	13.37	7.07	6.88	10.22	9.04	10.43	7.88	8.93

soils in the area were the darkest of any on the marsh, due to their high organic content of 23.4%. The pH in the surface 10 cm. was 7.6-7.9, the saturation percentage 151%, and the soil texture was a sandy loam and a loamy sand at the 60 cm. level. The salinity in the surface soil was 0.18-

TABLE 46. Transect analysis at soil sample site 14. Density, 144.

Species	Relative Density %	Basal Area %	B. A. % Total %	Height cm.
Eleocharis rostellata	71.53	3.43	48.54	30- 50
Scirpus americanus	21.53	3.10	43.86	100-120
Agrostis alba	3.47	.25	3.52	80- 82
Juncus interior	1.39	.06	.84	75
Apocynum sibiricum	1.39	.13	1.83	54
Juncus torreyi	.69	.10	1.41	75
		7.07		

0.68% and the chlorinity 0.03-0.23. One reason for the extremely high water holding capacity of this soil is the high organic content. In addition, the extensive root and rhizome systems of the sedges made the soil surface highly absorptive.

Grazed-sandhill COMMUNITY

The portion of the Grazed-sandhill Community studied quantitatively was located on a sandy beach ridge which formed the southern border of the salt flats. A ten transect analysis of this area during July indicated that the average basal area was 2.88% and that forbs, common to sandy soil, reached their peak in diversity in this community. A total of 36 species were found, 19 of which had a frequency of only 10%, indicating that they occurred at only one location and were not widely distributed.

The species maintaining the highest frequency percentages were *Paspalum ciliatiforium, Eriogonum annuum, Strophostyles leiosperma, Ambrosia psilostachya* var. *coronopifolia, Monarda citriodora,* each with a 60% frequency, and *Festuca octoflora* and *Argemone polyanthemos* with frequencies of 50%.

The species which had the highest relative densities were *F. octoflora, P. ciliatifolium, E. annuum, A. psilostachya* var. *coronopifolia, M. citriodora, Setaria geniculata, Conyza canadensis, Cenchrus longispinus,* and *A. polyanthemos* in order of abundance. This group of nine species comprised 67.59% of the total density and had a combined basal area of 1.51% or 65.99% of the total.

Table 47 provides a more detailed analysis of the species relations, and Fig. 17 and 18 illustrate two aspects of the community.

A summary of the basal area relations in this community (Table 48) indicates that no one or two species made up the greatest part at all transect sites. A combination of two or three species at each site, such as *P. ciliatifolium* and *F. octoflora* at site 5, comprised the greatest part of the basal cover, 67%, but at other sites other combinations of species formed the greater portion.

The vegetation at the soil sample site in this community is described in Table 49. The soils in this area are made up of loose sand and had a pH of 6.5, a total salinity of .007% and a chlorinity of .001%. This analysis, made in July, is quite similar to the soil relations found in the Sandhill Mixed Prairie Community. The soils in the latter community are also sandy. They had a pH of 6.5 and a low salinity and chlorinity. The fact that the dominant prairie grasses play such a small part in the species relations in this Grazed-Sandhill Community must not be attributed to soil relations but to the heavy grazing which occurs throughout the growing season.

TRANSECTS BORDERING THE SALT FLATS AND SALINE PONDS

North of the east-west road bisecting the marsh a series of transects were

TABLE 47. Analysis of Grazed Sandhill Community. Ten transect summary. Density, 312.

Species	Relative Density %	Basal Area %	B. A. % Total %	Frequency %
Festuca octoflora	18.21	.18	7.87	50.00
Paspalum ciliatifolium	9.21	.35	15.30	60.00
Briogonum annuum	7.68	.33	14.43	60.00
Ambrosia psilostachya var. *coronopifolia*	7.02	.16	6.99	60.00
Monarda citriodora	6.82	.13	5.68	60.00
Setaria geniculata	6.45	.12	5.24	20.00
Conyza canadensis	4.70	.09	3.93	30.00
Cenchrus longispinus	3.95	.11	4.81	20.00
Bouteloua gracilis	3.66	.03	1.31	10.00
Strophostyles leiosperma	3.64	.05	2.19	60.00
Argemone polyanthemos	3.55	.14	6.12	50.00
Oenothera laciniata var. *grandiflora*	2.38	.08	3.50	30.00
Hordeum pusillum	2.05	.03	1.31	10.00
Andropogon gerardi	1.76	.03	1.31	10.00
Bromus tectorum	1.64	.02	.87	10.00
Euphorbia dentata	1.46	.02	.87	10.00
Chloris verticillata	1.39	.06	2.62	20.00
Chenopodium leptophyllum	1.28	.01	.44	10.00
Salsola kali var. *tenuifolia*	1.23	.06	2.62	10.00
Euphorbia glyptosperma	1.23	.02	.87	10.00
Plantago purshii	1.17	.01	.44	20.00
Haplopappus divaricatus	1.12	.05	2.19	20.00
Bouteloua curtipendula	1.06	.02	.87	10.00
Leptoloma cognatum	.92	.03	1.31	10.00
Lepidium virginicum	.92	.01	.44	20.00
Croton glandulosus var. *septentrionalis*	.82	.009	.39	20.00
Panicum scribnerianum	.80	.02	.87	10.00
Cirsium undulatum	.71	.04	1.75	10.00
Amaranthus tamariscinus	.59	.02	.87	10.00
Cycloloma atriplicifolium	.53	.01	.44	10.00
Asclepias speciosa	.48	.01	.44	10.00
Commelina erecta var. *angustifolia*	.36	.01	.44	10.00
Helianthus petiolaris	.35	.01	.44	10.00
Sporobolus asper	.30	.006	.26	10.00
Solanum rostratum	.28	.01	.44	20.00
Cyperus strigosus	.27	.003	.13	10.00
		2.288		

TABLE 48. A comparison of the basal area of species at ten transect sites within the Grazed Sandhill Community. B. A. is expressed as a percentage of the actual cover.

	Transects									
Species	1	2	3	4	5	6	7	8	9	10
Eriogonum annuum	......	......	.80	.66	.23	......	......	.16	.26	1.23
Paspalum ciliatifolium	1.40	.16	.13	.50	1.10	......	......	.23	......	......
Festuca octoflora	.69	.47	......	.15	.43	......	......	.13	......	......
Ambrosia psilostachya var. *coronopifolia*	.08	.71	......	.13	.06	......	......	.31	.33	......
Monarda citriodora	.21	.06	......	......	......	.21	.30	.08	......	.48
Setaria geniculata	......	......	......	......	......	......	......	......	.40	.80
Cenchrus longispinus	......	......	......	......	......	......	.46	......	.73	......
Conyza canadensis	.06	......	......	......	......	.78	.10	......	......	......
Argemone polyanthemos	.46	......	.16	.20	......	......	......	......	.46	.13
Oenothera laciniata	.16	......	......	......	......	......	.56	......	......	.08
Chloris verticillata	.53	......	.10	......	......	......	......	......	......	......
Salsola kali var. *pestifer*	......	......	.66	......	......	......	......	......	......	......
Haplopappus divaricatus	......	......	......	......	......	.30	......	......	.20	......
Strophostyles leiosperma	......	.06	.10	......	......	.06	......	.13	.18	.06
Cirsium undulatum	......	......	......	......	......	.40	......	......	......	......
Bouteloua gracilis	......	......	......	......	......	......	.33	......	......	......
Hordeum pusillum	......	......	.30	......	......	......	......	......	......	......
Andropogon gerardi	......	......	......	......	......	.33	......	......	......	......
Leptoloma cognatum	......	......	......	.33	......	......	......	......	......	......
Cyperus strigosus	......	.03	......	......	......	......	......	......	......	......
Bromus tectorum	......	......	.20	......	......	......	......	......	......	......
Euphorbia dentata	......	......	......	......	......	......	......	.20	......	......
Euphorbia glyptosperma	......	......	.23	......	......	......	......	......	......	......
Bouteloua curtipendula	......	......	......	......	......	.20	......	......	......	......
Panicum scribnerianum	......	.21	......	......	......	......	......	......	......	......
Amaranthus tamariscinus	......	......	......	......	.26	......	......	......	......	......
Chenopodium leptophyllum	......	......	......	......	......	......	......	......	.11	......
Plantago purshii	......	.06	......	......	.10	......	......	......	......	......
Lepidium virginicum	.03	......	......	......	......	......	.13	......	......	......
Cycloloma atriplicifolium	......	.10	......	......	......	......	......	......	......	......
Asclepias speciosa	......	......	......	......	......	......	......	.16	......	......
Commelina erecta var. *angustifolia*	......	......	......	......	......	......	.13	......	......	......
Helianthus petiolaris	......	......	......	......	......	......	......	......	......	.13
Solanum rostratum	.06	......	.13	......	......	......	......	......	......	......
Croton gladulosus var. *septentrionalis*	......	......	......	.06	......	.03	......	......	......	......
Sporobolus asper	......	......	......	......	.06	......	......	......	......	......
Total	3.68	1.86	2.81	2.03	2.24	2.31	2.01	1.40	2.67	2.91

set up. The first station was located 29 meters east of the road leading north from the east-west road in the center of the marsh and each of the following three was 100 meters east of the preceding. The first station ten meters north of the road was on bare ground. A transect one meter south had a *Distichlis stricta* basal area of 2.60%, and a second one three meters south had a basal area of 6.00%.

The second transect station was located 100 meters east of the first and five and one-half meters north of the east-west road, on bare ground. A half meter south of the barren area the basal area of *D. stricta* was 1.50%, and one and one-half meters south the basal area was 5.20%. In this series, salinity tests were made and the total salt content was 2.46% on bare ground, 2.12% a half meter south, and 1.05% one and one-half meters south in the upper 10 cm. of soil. A chloride analysis showed closed correlation with the total salt analysis and was 1.13%, 1.01%, and 0.61% for each of these sites respectively.

The third series of transects was initiated on bare ground 100 meters east of the second and 12.5 meters north of the east-west road. A transect one meter south of the bare ground had a *D. stricta* cover of 0.89%, and three meters south was a transect with a cover of 9.86, with *D. stricta* making up 9.80% and *P. arida* 0.06%.

TABLE 49. Transect analysis at site of soil sample. Density, 52.

Species	Relative Density %	Basal Area %	B. A. % Total %
Festuca octoflora	48.06	.69	18.74
Paspalum ciliatifolium	21.52	1.40	38.05
Chloris verticillata	9.62	.53	14.41
Monarda citriodora	5.60	.21	5.71
Argemone polyanthemos	5.60	.46	12.50
Ambrosia psilostachya var. *coronopifolia*	1.92	.08	2.17
Solidago altissima	1.92	.06	1.63
Lepidum virginicum	1.92	.03	.81
Solanum rostratum	1.92	.06	1.63
Oenothera laciniata var. *grandiflora*	1.92	.16	4.35
		3.68	

The fourth station was 100 meters east of the third and 19 meters north of the east-west road on bare ground. One meter south the *D. stricta* cover was 0.16%, and six meters south it was 7.23%. In this series, salinity and chloride analyses were also made in the surface 10 cm. of soil and the results were similar to those described earlier. The salinity of the barren salt flat was 2.74%, 1.45% one meter south and 0.72% six meters south. Again the chlorinity analysis showed a close correlation with the total salt analysis and was 1.68%, 0.78% and 0.40% for each of the sites respectively.

These transects indicate the great fluctuation in vegetation which occurred at short distances from the bare salt flats. The salinity relations of the two series of transects show a close correlation with vegetational cover. There was little variation in the species cover, but the basal area of *D. stricta* was greatly reduced in the area of highest salinity, close to the salt flats. The reduced salinity in areas closest to the road is caused by the leaching action of water flowing through drainage ditches.

Two transects were run on the eastern border of pond site 8 in a dense *D. stricta* Community, and Table 50 presents the results of these transects. The salinity in this area (0.28-1.26%) was at least partially determined by the lake waters since they flood this area during wet periods. The transect data indicate that the vegetation of this area is closely associated with that of the Tall *D. stricta* Community.

An area bordering pond site 9 was studied with a series of 12 transects. This area was very variable in composition, and had all types of vegetation from bare areas to the Tall *D. stricta* type represented. This last community developed in areas of greater moisture and lower salinity. A summary of the vegetation in this community is in Table 51.

TABLE 50. Results of a two transect analysis of the eastern border of pond site 8. Density, 288.

Species	Relative Density %	Basal Area %	B. A. % Total %	Height cm.
Distichlis stricta	90.68	6.39	96.23	50-62
Scirpus paludosus	9.32	.25	3.77	60-70
		6.64		

TABLE 51. Results of a twelve transect analysis of the vegetation bordering pond site 9. Density, 871.

Species	Relative Density %	Basal Area %	B. A. % Total %	Frequency %
Distichlis stricta	95.29	3.80	95.00	91.63
Scirpus paludosus	.83	.09	2.25	24.99
Suaeda depressa	1.60	.02	.50	24.99
Poa arida	2.28	.09	2.25	8.33
		4.00		

Salicornia rubra was found in an open salt flat in the southwestern part of this area. Some other species, besides those mentioned in Table 51, found in areas of high moisture and lowered salinity were *Polygonum hydropiperoides, Polygonum lapathifolium* and *Xanthium pennsylvanicum.*

SUMMARY OF QUANTITATIVE RELATIONS

The following pages provide a brief, comparative description of the quantitative relations of species in the major plant communities on the marsh. From a comparison of the relative density, basal area, and frequency of species within the areas (Tables 52-54), it can be clearly seen that many species were found in only one transect area, some in two, but only a very small number in more than two communities. The actual occurrence of species at transect sites within the various plant communities were one species in six communities, one species in four communities, three species in three communities, 15 species in two communities, and 52 species in one community. Species listed in Table 8, which describes the seasonal and zonal aspect of the vegetation, were either extremely rare or in some cases did not occur during the period of these quantitative studies.

Distichlis stricta was the most widely spread and one of the more important species in four of the seven communities in which it occurred. It was found in soil which varied in salinity from a low of 0.04% in the *S. airoides* area to a high of 2.52% in the *D. stricta-S. depressa* Community. It reached its best growth in the Tall *D. stricta* Community where it had a relative density of 94.46%, a frequency of 100%, and a basal area of 92.65% of the total. The salinity in this area was 0.29-0.94%. *D. stricta* did not occur in the Sandhill Mixed Prairie or Grazed Sandhill communities which had lower salinities than the marsh communities, nor did it occur in the *S. depressa* area which occupied parts of the open salt flats.

In the *D. stricta* and *D. stricta-S. depressa* zones, *D. stricta,* can be considered the dominant of a unistratal community, whereas, in the *S. paludosus-D. stricta* and *S. pectinata-D. stricta* areas it must be considered the dominant of the lower strata of a bistratal community. *S. paludosus* in the former and *S. pectinata* in the latter made up the greater part of the upper strata in these areas. *D. stricta* was also found in the lower strata of the *S. americanus-E. rostellata* and the *S. airoides* communities, but in it was of much less importance than in those previously described. Billings (1945) also mentions the ability of *D. stricta* to exist in a unistratal or multistratal community and that it could be found in almost any saline soil except the very driest.

Another species of fairly wide distribution was *Scirpus paludosus.* This species seemed to favor the moist and slightly saline areas but sometimes was found in areas where the salinity reached slightly over 1%. The range of salinity under which it ocurred was 0.22-1.10% in the surface 10 cm. of soil. It was one of the dominants of the *S. paludosus-D. stricta* Community, with a relative density of 31.80%, a frequency of 100%, and a basal area which was 54.99% of the total. *S. paludosus* occurred also in the Tall *D. stricta* Community, where it was only of local importance, and in the *D. stricta-S. depressa* Community it was very widely scattered and not of local importance. In all of the communities it was found in, except *S. pectinata-D. stricta,* it was a member of the upper strata. In this zone and in its rare occurrence in the *S. americanus-E. rostellata* Community, it was a member of one of the lower strata. *S. paludosus* did not occur in the most saline salt flats or in the very dry communities.

The next three species were each found in three of the major communities on the marsh. The first of these, *Suaeda depressa,* reached its greatest abundance in the more saline areas of the marsh. In the *S. depressa* community it had a relative density of 100%, a frequency of 30%, and a basal area which accounted for 100% of the total. This community had the lowest basal area on the marsh, 0.06%, and *S. depressa* was the only species found on the transects. Two other species, *Sesuvium verrucossum* and *Salicornia rubra,* were found also locally in this general area, but they composed an extremely small portion of the total basal area. *S. depressa* was also of some importance in the *D. stricta-S. depressa* Community, where it was quite prevalent and had a relative density of 13.13%, a frequency of 62.37%, and a basal area which was 13.50% of the total. It was also found in small quantities in the Tall *D. stricta, S. airoides, S. americanus-E. rostellata* and *S. pectinata-D. stricta* communities.

The remaining two species occurring in three communities, *Ambrosia psilostachya* var. *coronopifolia* and *Juncus interior,* were not of major importance in any community in which they occurred. The former species was found on relatively dry, nonsaline soils, while the latter occupied the moister portions of the communities in which it occurred.

Of the 15 species found in two communities only *A. gerardi, E. rostellata, S. americanus, P. scribnerianum, S. pectinata* and *S. airoides* were dominants in at least one of the communities in which they occurred.

Andropogon gerardi and *Panicum scribnerianum* were most important in the Sandhill Mixed Prairie Community, but they also occurred in the Grazed Sandhill Community, where they comprised only a very small part of the total vegetation. These two species were limited to the drier sandy areas of the marsh and were not found in wet or saline areas. In the Prairie Community, *A. gerardi* had a relative density of 8.53%, a frequency of 12.50%, and a basal area which was 16.73% of the total, whereas, in the Grazed Sandhill Community it composed only 1.76% of the total density, had a frequency of 10%, and a basal area which was 1.31% of the total. The basal area covered by this species and other tall grasses such as *S. nutans* and *P. virgatum* was greatly reduced in the heavily grazed areas. *P. scribnerianum* had a relative density of 19.78%, a basal area of 14.88% of the total, and a frequency of 100% in the prairie area. It must be considered one of the major dominants in the lower strata of this community, whereas, in the grazed sandhill area it was of much less importance and had a relative density of only 0.80%, a frequency of 10%, and a basal area which was 0.87% of the total.

Eleocharis rostellata and *Scirpus americanus* were codominants in the Sedge-Meadow Community and were also present and of some local importance in the *S. pectinata-D. stricta* Community. These species reached their peak abundance in the *S. americanus-E. rostellata* area, where the soil retains a great deal of moisture and the salinity was 0.18-.68%. In this area the two species had a combined relative density of 82.46%, a frequency of 93.24% and 100%, and a basal area which comprised 85.34% of the total, whereas, in the *S. pectinata-D. stricta* Community they were of less importance, having a combined relative density of 25.28%, a basal area of 21.94% of the total, and frequencies of 30% and 50% for each species respectively. The great reduction in basal area and relative density and frequency which these species had in the *S. pectinata-D. stricta* Community showed they were of less importance here than in the *S. americanus-E. rostellata* Community. The reason for this is probably the higher salinities reached in the former community.

Spartina pectinata, as mentioned earlier, was the tall dominant in the *S. pectinata-D. stricta* Community. In this area it had a relative density of 18.34%, a frequency of 100%, and a basal area which accounted for 45.08% of the total. Its wide distribution and high basal cover were the factors which made it the most characteristic plant of a community. It also occurred scattered in wetter parts of the Sandhill Mixed Prairie, the *S. americanus-E. rostellata* and in less saline areas of the *D. stricta-S. depressa* communities, but in these areas it was only of minor importance and made up only a very small part of the total cover.

Sporobolus airoides was found in two main community types and was also scattered in hummocks on the open salt flats. It reached its greatest abundance in the *S. airoides* Community, where it had a relative density of 90.50%, a frequency of 100%, and a basal area which accounted for 88.21% of the total. It also occurred on the western border of the prairie, but here it comprised only 6.24% of the total density, had a basal area of 11.21% of the total, and a frequency of 25%. This species appeared to make its best growth in those areas which had only moderate salinity and low moisture, but it was also found on the open salt flats in the areas of highest salinity and higher moisture.

The species found in only one community and of more general importance where they occurred include *Bromus japonicus* and *Festuca octoflora*. *B. japonicus* was found in areas of low salinity and moisture, including the sandy hummocks and the Sandhill Mixed Prairie Community. In the prairie it had a relative density of 27.79%, a frequency of 87.50%, and a basal area which accounted for 14.38% of the total. Unexpectedly, as discussed earlier, this species was one of the more conspicuous plants in the lower strata of both the prairie and hummock communities.

Festuca octoflora had a relative density of 18.21%, a frequency of 50%, and a basal area which made up 7.87% of the total in the Grazed Sandhill Community. It was also found in the Prairie Community but was never very important there. This species was most characteristic of dry, sandy, non-saline areas, and during the early spring it was fairly characteristic of the lower strata of the Grazed Sandhill Community.

Species in the prairie, grazed sandhill, sedge-meadow and other areas of the Big Salt Marsh which were of some importance but not mentioned here are described in more detail in some of the earlier sections. An account of their quantitative relations are in Tables 52-54, and their seasonal and zonal distribution are in Table 8.

Salt Tolerance of Marsh Species

Table 55 contains a list of plants found on the Big Salt Marsh which either were growing on saline soils or had been listed by Fernald (1950), Rydberg (1932), or others as occurring on them. In addition to the species list, Table 55 contains the range of salinity, in the upper 10 cm. and at the 60 cm. level of the soil, under which the various species has been found growing. The majority of species listed for the *S. americanus-E. rostellata* (Sedge-Meadow) and *S. pectinata-D. stricta* communities have not been included in this list because their salinity relations were described earlier and many of these species, as cited in Table 8, reached their highest salinity tolerance in these areas, indicating that they were typical of fresh water areas or those of only the lowest salinities.

Agropyron smithii, which occurred in the prairie, sedge-meadow, and on sandy hummocks, has been listed by Hitchcock (1898) and Weaver and Albertson (1956) as being tolerant of brackish soils. In this study it was found to have reached its greatest abundance in the Prairie Community which had the lowest salinity, 0.003-.02% in the surface 10 cm. As noted in Tables 8, 44, and 45, it was also found in the Sedge-Meadow Community where the salinity was 0.18-0.68%. *A. smithii* did not occur in areas of higher salinities on the marsh and, though it is tolerant of traces of salt, it should not be considered an indicator of saline soils.

Aster ericoides (A. multiflorus Ait.) has been listed by Schaffner (1898) as a successful invader of saline soils. This species was found in a wide variety of vegetation types, including Prairie, Tall *D. stricta* Meadow, Sandy Hummock, and *S. airoides* communities. The salinity in the *S. airoides* Community was 0.04-0.19%, and the total range of salinity in the surface 10

TABLE 52. A comparison of the relative density (%) of species within the major study areas.

1—*Suaeda depressa*, 2—Tall *Distichlis stricta*, 3—*Sporobolus airoides*, 4—Sandhill Mixed Prairie, 5—*Scirpus paludosus-Distichlis stricta*, 6—*Distichlis stricta-Suaeda depressa*, 7—*Spartina pectinata-Distichlis stricta*, 8—*Scirpus americanus-Bleocharis rostellata*, 9—Grade Sandhill.

Species	Transect Area								
	1	2	3	4	5	6*	7	8	9
Achillea lanulosa	......	......	......	.35	......	......	......	......	......
Agropyron smithii	......	......	......	7.28	......	......	......	.10	......
Agrostis alba	......	......	......	......	......	......	......	2.83	......
Agrostis hiemalis	......	......	......	3.37	......	......	......	......	......
Amaranthus tamariscinus	......	......	......	......	......	......	......	......	.59
Ambrosia psilostachya	......	......	2.08	.79	......	......	......	......	7.02
Andropogon gerardi	......	......	......	8.53	......	......	......	......	1.76
Apocynum sibiricum	......	......	......	......	......	......	.31	.25	......
Argemone polyanthemos	......	......	......	......	......	......	......	......	3.55
Artemesia ludoviciana	......	......	......	4.33	......	......	......	......	......
Asclepias speciosa	......	......	......	......	......	......	......	......	.48
Aster ericoides	......	......	1.16	......	......	......	......	......	......
Bouteloua curtipendula	......	......	......	......	......	......	......	......	1.06
Bouteloua gracilis	......	......	......	......	......	......	......	......	3.66
Bromus japonicus	......	......	......	27.97	......	......	......	......	......
Bromus tectorum	......	......	......	......	......	......	......	......	1.64
Carex annectans	......	......	......	......	......	......	......	.05	......
Carex lanuginosa	......	......	......	......	......	......	......	.64	......
Carex praegracilis	......	......	......	......	......	......	......	1.06	......
Cenchrus longispinus	......	......	......	......	......	......	......	......	3.95
Chenopodium leptophyllum	......	......	......	......	......	......	......	......	1.28
Chloris verticillata	......	......	......	......	......	......	......	......	1.39
Cicuta maculata	......	......	......	......	......	......	......	.13	......
Cirsium undulatum	......	......	......	......	......	......	......	......	.71
Commelina erecta	......	......	......	......	......	......	......	......	.36
Conyza canadensis	......	......	......	......	......	......	......	......	4.70
Croton glandulosa	......	......	......	......	......	......	......	......	.82
Cycloloma atriplicifolium	......	......	......	......	......	......	......	......	.53
Cyperus strigosus	......	......	......	......	......	......	......	......	.27
Distichlis stricta	......	94.46	5.85	......	63.60	86.56	50.77	4.07	......
Eleocharis rostellata	......	......	......	......	......	......	18.92	60.22	......
Eleocharis tenuis	......	......	......	......	......	......	......	5.46	......
Elymus canadensis	......	......	.41	.48	......	......	......	......	......
Erigeron strigosus	......	......	......	.14	......	......	......	......	......
Eriogonum annuum	......	......	......	......	......	......	......	......	7.68
Euphorbia dentata	......	......	......	......	......	......	......	......	1.46
Euphorbia glyptosperma	......	......	......	......	......	......	......	......	1.23
Festuca octoflora	......	......	......	......	......	......	......	......	18.21
Fimbrystilis castanea	......	......	......	......	......	......	......	.40	......
Haplopappus divaricatus	......	......	......	......	......	......	......	......	1.12
Helianthus petiolaris	......	......	......	......	......	......	......	......	.35

	Transect Area								
Species	1	2	3	4	5	6*	7	8	9
Hordeum pusillum	......	......	......	......	......	......	......	......	2.05
Juncus interior	......	......	......	.12	......	......	.49	.30	......
Juncus torreyi	......	......	......	......	......	......	.56	.87	......
Lepidium virginicum	......	......	......	.29	......	......	......	......	.92
Leptoloma cognatum	......	......	......	......	......	......	......	......	.92
Liatris lancifolia	......	......	......	......	......	......	......	.02	......
Lippia lanceolata	......	......	......	......	......	......	......	.05	......
Monarda citriodora	......	......	......	.41	......	......	......	......	6.82
Oenothera laciniata var. *grandiflora*	......	......	......	......	......	......	......	......	2.38
Oxalis stricta	......	......	......	.25	......	......	......	......	......
Panicum lanuginosum	......	......	......	......	......	......	......	.65	......
Panicum scribnerianum	......	......	......	19.78	......	......	......	......	.80
Panicum virgatum	......	......	......	7.28	......	......	......	.05	......
Paspalum ciliatifolium	......	......	......	......	......	......	......	......	9.21
Plantago purshii	......	......	......	3.63	......	......	......	......	1.17
Poa arida	......	.16	......	......	......	......	3.80	......	......
Polygonum ramosissimum	......	......	......	......	3.80	......	......	......	......
Salsola kali	......	......	......	......	......	......	......	......	1.23
Scirpus americanus	......	......	......	......	......	......	6.36	22.24	......
Scirpus lineatus	......	......	......	......	......	......	......	.50	......
Scirpus paludosus	......	5.38	......	......	31.80	.28	.45	......	......
Setaria geniculata	......	......	......	......	......	......	......	......	6.45
Solanum rostratum	......	......	......	......	......	......	......	......	.28
Sorghastrum nutans	......	......	......	8.47	......	......	......	......	......
Spartina pectinata	......	......	......	......	......	.03	18.34	......	......
Sphenopholis obtusata	......	......	......	......	......	......	......	.07	......
Sporobolus airoides	......	......	90.50	6.24	......	......	......	......	......
Sporobolus asper	......	......	......	......	......	......	......	......	.30
Strophostyles leiosperma	......	......	......	......	......	......	......	......	3.64
Suaeda depressa	100.00	......	......	......	.80	13.13	......	......	......
Tradescantia occidentalis	......	......	......	.29	......	......	......	......	......
Vernonia fasciculata	......	......	......	......	......	......	......	.04	......

* Data for this community have been compiled as an average of five separate analyses within this vegetation type.

cm. was 0.003-0.94%. Its broad range of salinity tolerance indicates that it might be an important species in areas with a fairly wide salinity range. In face, however, this species always was widely scattered to rare in occurrence and was never found invading the open salt flats or any communities directly adjacent to it. Its only occurrence in these areas was on the margins of sandy hummocks where the salinity was greatly reduced. Schaffner (1898) mentions that *A. ericoides* was only occasional in occurrence in the northern Kansas salt marshes which he studied.

Aster exilis was found in the Prairie, Tall *D. stricta* Meadow, Sedge-

TABLE 53. A comparison of the percentage of total basal area covered by species found in the major study areas.

1—*Suaeda depressa*, 2—Tall *Distichlis stricta*, 3—*Sporobolus airoides*, 4—Sandhill Mixed Prairie, 5—*Scirpus paludosus-Distichlis stricta*, 6—*Distichlis stricta-Suaeda depressa*, 7—*Spartina pectinata-Distichlis stricta*, 8—*Scirpus americanus-Eleocharis rostellata*, 9—Grazed Sandhill.

	Transect Area								
Species	1	2	3	4	5	6*	7	8	9
Achillea lanulosa	......	......	......	.83	......	......	......	......	......
Agropyron smithii	......	......	......	11.21	......	......	......	.21	......
Agrostis hiemalis	......	......	......	.83	......	......	......	......	......
Agrostis alba	......	......	......	......	......	......	......	1.81	......
Amaranthus tamariscinus	......	......	......	......	......	......	......	......	.87
Ambrosia psilostachya	......	......	9.08	.83	......	......	......	......	6.99
Andropogon gerardi	......	......	......	16.73	......	......	......	......	1.31
Apocynum sibiricum	......	......	......	......	......	......	.34	1.27	......
Argemone polyanthemos	......	......	......	......	......	......	......	......	6.12
Artemesia ludoviciana	......	......	......	5.85	......	......	......	......	......
Asclepias speciosa	......	......	......	......	......	......	......	......	.44
Aster ericoides	......	......	.72	......	......	......	......	......	......
Bouteloua curtipendula	......	......	......	......	......	......	......	......	.87
Bouteloua gracilis	......	......	......	......	......	......	......	......	1.31
Bromus japonicus	......	......	......	14.38	......	......	......	......	......
Bromus tectorum	......	......	......	......	......	......	......	......	.87
Carex annectans	......	......	......	......	......	......	......	.04	......
Carex lanuginosa	......	......	......	......	......	......	......	.53	......
Carex praegracilis	......	......	......	......	......	......	......	1.49	......
Cenchrus longispinus	......	......	......	......	......	......	......	......	4.81
Chenopodium leptophyllum	......	......	......	......	......	......	......	......	.44
Chloris verticillata	......	......	......	......	......	......	......	......	2.62
Cicuta maculata	......	......	......	......	......	......	......	.64	......
Cirsium undulatum	......	......	......	......	......	......	......	......	1.75
Commelina erecta	......	......	......	......	......	......	......	......	.44
Conyza canadensis	......	......	......	......	......	......	......	......	3.93
Croton glandulosa	......	......	......	......	......	......	......	......	.39
Cycloloma atriplicifolium	......	......	......	......	......	......	......	......	.44
Cyperus strigosus	......	......	......	......	......	......	......	......	.13
Distichlis stricta	......	92.65	1.91	......	43.04	86.53	27.46	2.23	......
Eleocharis rostellata	......	......	......	......	......	......	10.45	42.35	......
Eleocharis tenuis	......	......	......	......	......	......	......	2.97	......
Elymus canadensis	......	......	.18	.33	......	......	......	......	......
Erigeron strigosus	......	......	......	.11	......	......	......	......	......
Eriogonum annuum	......	......	......	......	......	......	......	......	14.43
Euphorbia dentata	......	......	......	......	......	......	......	......	.87
Euphorbia glyptosperma	......	......	......	......	......	......	......	......	.87
Festuca octoflora	......	......	......	......	......	......	......	......	7.87
Fimbrystilis castanea	......	......	......	......	......	......	......	.21	......
Haplopappus divaricatus	......	......	......	......	......	......	......	......	2.19
Helianthus petiolaris	......	......	......	......	......	......	......	......	.44

Species	Transect Area 1	2	3	4	5	6*	7	8	9
Hordeum pusillum	......	......	......	......	......	......	......	......	1.31
Juncus interior	......	......	......	.05	......	......	.51	.85	......
Juncus torreyi	......	......	......	......	......	......	.51	.64	......
Lepidium virginicum	......	......	......	.06	......	......	......	......	.44
Leptoloma cognatum	......	......	......	......	......	......	......	......	1.31
Liatris lancifolia	......	......	......	......	......	......	......	.32	......
Lippia lanceolata	......	......	......	......	......	......	......	.06	......
Monarda citriodora	......	......	......	.13	......	......	......	......	5.68
Oenothera laciniata var. *grandiflora*	......	......	......	......	......	......	......	......	3.50
Oxalis stricta	......	......	......	.16	......	......	......	......	......
Panicum lanuginosum	......	......	......	......	......	......	......	.43	......
Panicum scribnerianum	......	......	......	14.88	......	......	......	......	.87
Panicum virgatum	......	......	......	11.88	......	......	......	.11	......
Paspalum ciliatifolium	......	......	......	......	......	......	......	......	15.30
Plantago purshii	......	......	......	1.50	......	......	......	......	.44
Poa arida	......	.08	......	......	......	......	2.24	......	......
Polygonum ramosissimum	......	......	......	......	1.84	......	......	......	......
Salsola kali	......	......	......	......	......	......	......	......	2.62
Scirpus americanus	......	......	......	......	......	......	11.49	42.99	......
Scirpus lineatus	......	......	......	......	......	......	......	.74	......
Scirpus paludosus	......	7.27	......	......	54.99	1.78	1.20	......	......
Setaria geniculata	......	......	......	......	......	......	......	......	5.24
Solanum rostratum	......	......	......	......	......	......	......	......	.44
Sorghastrum nutans	......	......	......	8.70	......	......	......	......	......
Spartinata pectinata	......	......	......	......	......	.19	45.08	......	......
Sphenopholis obtusata	......	......	......	......	......	......	......	.03	......
Sporobolus airoides	......	......	88.21	11.21	......	......	......	......	......
Sporobolus asper	......	......	......	......	......	......	......	......	.26
Strophostyles leiosperma	......	......	......	......	......	......	......	......	2.19
Suaeda depressa	100.00	......	......	......	.13	11.50	......	......	......
Tradescantia occidentalis	......	......	......	.33	......	......	......	......	......
Vernonia fasciculata	......	......	......	......	......	......	......	.08	......

* Data for this community have been compiled as an average of five separate transect analyses within this vegetation type.

Meadow, and Hummock communities. It occurred in a broad range of salinity relationships of 0.003-0.94% in the surface 10 cm., just as in *A. ericoides*. Hitchcock (1898), in his brief survey of the Big Salt Marsh, mentioned this species as being salt tolerant, and Keith (1958) cites it as occurring in an area where the salinity was 0.26-0.50%. Information accumulated on its distribution in this study indicates that it is able to tolerate salinities below 1% in the moister areas. *A. exilis* was not of great abundance on the Big Salt Marsh, varying from rare to widely scattered, and it should not be considered a species indicative of areas of high salinity.

Atriplex argentea (*A. expansa* Watson) was listed by Hitchcock (1898)

TABLE 54. A comparison of the frequency (%) of species within the major study areas.

1—*Suaeda depressa,* 2—Tall *Distichlis stricta,* 3—*Sporobolus airoides,* 4—Sandhill Mixed Prairie, 5—*Scirpus paludosus-Distichlis stricta,* 6—*Distichlis stricta-Suaeda depressa,* 7—*Spartina pectinata-Distichlis stricta,* 8—*Scirpus americanus-Eleocharis rostellata,* 9—Grazed Sandhill.

	Transect Area								
Species	1	2	3	4	5	6*	7	8	9
Achillea lanulosa	......	......	......	25	......	......	......	......	......
Agropyron smithii	......	......	......	25	......	......	......	6.66	......
Agrostis hiemalis	......	......	......	12.50	......	......	......	......	......
Agrostis alba	......	......	......	......	......	......	......	59.94	......
Amaranthus tamariscinus	......	......	......	......	......	......	......	......	10
Ambrosia psilostachya	......	......	40	12.50	......	......	......	......	60
Andropogon gerardi	......	......	......	12.50	......	......	......	......	10
Apocynum sibiricum	......	......	......	......	......	......	20	33.30	......
Argemone polyanthemos	......	......	......	......	......	......	......	......	50
Artemesia ludoviciana	......	......	......	37.50	......	......	......	......	......
Asclepias speciosa	......	......	......	......	......	......	......	......	10
Aster ericoides	......	......	30	......	......	......	......	......	......
Bouteloua curtipendula	......	......	......	......	......	......	......	......	10
Bouteloua gracilis	......	......	......	......	......	......	......	......	10
Bromus japonicus	......	......	......	87.50	......	......	......	......	......
Bromus tectorum	......	......	......	......	......	......	......	......	10
Carex annectans	......	......	......	......	......	......	......	6.66	......
Carex lanuginosa	......	......	......	......	......	......	......	26.64	......
Carex praegracilis	......	......	......	......	......	......	......	13.32	......
Cenchrus longispinus	......	......	......	......	......	......	......	......	20
Chenopodium leptophyllum	......	......	......	......	......	......	......	......	10
Chloris verticillata	......	......	......	......	......	......	......	......	20
Cicuta maculata	......	......	......	......	......	......	......	13.32	......
Cirsium undulatum	......	......	......	......	......	......	......	......	10
Commelina erecta	......	......	......	......	......	......	......	......	10
Conyza canadensis	......	......	......	......	......	......	......	......	30
Croton glandulosa	......	......	......	......	......	......	......	......	20
Cycloloma atriplicifolium	......	......	......	......	......	......	......	......	10
Cyperus strigosus	......	......	......	......	......	......	......	......	10
Distichlis stricta	......	100	40	......	100	96.82	100	6.66	......
Eleocharis rostellata	......	......	......	......	......	......	30	93.24	......
Eleocharis tenuis	......	......	......	......	......	......	......	13.32	......
Elymus canadensis	......	......	10	25	......	......	......	......	......
Erigeron strigosus	......	......	......	12.50	......	......	......	......	......
Eriogonum annuum	......	......	......	......	......	......	......	......	60
Euphorbia dentata	......	......	......	......	......	......	......	......	10
Euphorbia glyptosperma	......	......	......	......	......	......	......	......	10
Festuca octoflora	......	......	......	......	......	......	......	......	50
Fimbrystilis castanea	......	......	......	......	......	......	......	6.66	......
Haplopappus divaricatus	......	......	......	......	......	......	......	......	20
Helianthus petiolaris	......	......	......	......	......	......	......	......	10

					Transect Area				
Species	1	2	3	4	5	6*	7	8	9
Hordeum pusillum	......	......	......	......	......	......	......	......	10
Juncus interior	......	......	......	12.50	......	......	10	33.30	......
Juncus torreyi	......	......	......	......	......	......	20	39.96	......
Lepidium virginicum	......	......	......	12.50	......	......	......	......	20
Leptoloma cognatum	......	......	......	......	......	......	......	......	10
Liatris lancifolia	......	......	......	......	......	......	......	6.66	......
Lippia lanceolata	......	......	......	......	......	......	......	6.66	......
Monarda citriodora	......	......	......	25	......	......	......	......	60
Oenothera laciniata var. *grandiflora*	......	......	......	......	......	......	......	......	30
Oxalis stricta	......	......	......	25	......	......	......	......	......
Panicum lanuginosum	......	......	......	......	......	......	......	6.66	......
Panicum scribnerianum	......	......	......	100	......	......	......	......	10
Panicum virgatum	......	......	......	25	......	......	......	6.66	......
Paspalum ciliatifolium	......	......	......	......	......	......	......	......	60
Plantago purshii	......	......	......	75	......	......	......	......	20
Poa arida	......	10	......	......	......	......	50	......	......
Polygonum ramosissimum	......	......	......	......	60	......	......	......	......
Salsola kali	......	......	......	......	......	......	......	......	10
Scirpus americanus	......	......	......	......	......	......	50	100	......
Scirpus lineatus	......	......	......	......	......	......	......	26.64	......
Scirpus paludosus	30	......	......	100	5.71	20	......	......	......
Setaria geniculata	......	......	......	......	......	......	......	......	20
Solanum rostratum	......	......	......	......	......	......	......	......	20
Sorghastrum nutans	......	......	......	25	......	......	......	......	......
Spartina pectinata	......	......	......	......	......	1.42	100	......	......
Sphenopholis obtusata	......	......	......	......	......	......	......	6.66	......
Sporobolus airoides	......	......	100	25	......	......	......	......	......
Sporobolus asper	......	......	......	......	......	......	......	......	10
Strophostyles leiosperma	......	......	......	......	......	......	......	......	60
Suaeda depressa	30	......	......	......	10	62.37	......	......	......
Tradescantia occidentalis	......	......	......	12.50	......	......	......	......	......
Vernonia fasciculata	......	......	......	......	......	......	......	6.66	......

* Data for this community have been compiled as an average of five separate transect analyses within this area.

and Schaffner (1898) as being a successful invader of saline soils. Schaffner (1898) mentioned that it was rare in occurrence in the more saline areas but occasional in less saline ones. This species was extremely rare on the Big Salt Marsh, being found only once bordering a small salt flat north of the Tall *D. stricta* area. It was associated with *S. airoides, S. paludosus, P. ramosissimum* and *D. stricta.* No salinity measurement was made in this area, but areas with the same vegetation complement had a salinity of 0.22-1%.

Atriplex patula var. *hastata* has been mentioned by Coupland (1950) and Rawson and Moore (1944) as being found in the most saline places border-

TABLE 55. Range of salt tolerance of species on the Big Salt Marsh.

Species	10 cm. Min. %	10 cm. Max. %	60 cm. Min. %	60 cm. Max. %
Agropyron smithii	.003	.68	.002	.07
Aster ericoides	.003	.94	.002	.65
Aster exilis	.003	.94	.002	.65
Atriplex argentea	.22	1.10	.28	.45
Atriplex patula var. *hastata*	.003	1.10	.28	.45
Baccharis salicina	....	.50	....	.20
Cycloloma atriplicifolium	....	.007	....	....
Distichlis stricta	.04	2.52	.01	1.09
Eleocharis acicularis	.22	1.26	....	....
Eleocharis rostellata	.18	1.00	.07	.49
Eustoma grandiflora	.18	1.00	.07	.49
Eustoma grandiflora f. *Fischeri*	.18	1.00	.07	.49
Fimbristylis castanea	.18	.68	.03	.07
Flaveria campestris	.18	1.00	.07	.49
Haplopappus phyllocephalus subsp. *annuus*	.003	.50	.002	.20
Heliotropium curassavicum	.22	1.10	.28	.45
Hordeum jubatum	.003	1.10	.002	.45
Hordeum pusillum	.003	.02	.002	.009
Iva annua	.003	1.00	.002	.49
Lippia lanceolata var. *recognita*	.18	.68	.03	.07
Muhlenbergia asperifolia	.003	.50	.002	.20
Myosurus minimus	.02	.05	....	....
Panicum virgatum	.003	.68	.002	.07
Pluchea purpurascens	.22	.63	.18	.49
Poa arida	.04	1.60	.01	.65
Polygonum lapathifolium	.18	.68	.03	.07
Polygonum ramosissimum	.27	1.10	.28	.45
Potamogeton foliosus	.22	1.26	....	....
Rumex maritimus var. *fueginus*	.22	.63	.18	.49
Salicornia rubra	1.16	2.75	.67	1.29
Scirpus americanus	.18	1.00	.03	.49
Scirpus paludosus	.18	1.10	.03	.65
Sesuvium verrucossum	.82	2.75	.67	1.29
Setaria geniculata	.003	.68	.002	.07
Spartina pectinata	.18	1.00	.03	.49
Sporobolus airoides	.003	1.60	.002	.34
Sporobolus pyramidatus	....	.85	....	.34
Sporobolus texanus	.003	.50	.002	.20
Suaeda depressa	.04	2.75	.01	1.29
Tamarix gallica	.72	1.45	.27	.76
Typha angustifolia	.25	.52	....	....
Typha latifolia	.02	.52	....	....

ing saline lakes in Canada. This species has been mentioned in many works on coastal marshes (Harshberger, 1911; Ganong, 1903) as having a wide range of salinity tolerance. On the Big Salt Marsh it was found in a wide variety of communities, including the Prairie, Sandy Hummock, Tall *D. stricta, S. airoides,* and the *S. paludosus-D. stricta. A. patula* var. *hastata* was very rare to rare in occurrence, but as its salinity range, 0.003-1.10%, indicates, it is capable of a fairly broad distribution. In this area it could not be considered one of the primary indicators of high salinity since it was rarely found invading the open salt flats or areas of highest salinity.

Schaffner (1898) and Penfound (1953) did not mention this species as being one of the important invaders of areas of high salinity. On this marsh, however, when the *S. paludosus-D. stricta* or one of the other communities in which it occurred bordered the open salt flats, some greatly dwarfed forms (up to 10 cm.) which appeared to be *A. patula* var. *hastata* were found. These dwarfed forms never developed flowers and died soon after germination.

Baccharis salicina was found only on two low hummocks on the marsh. Gates (1940) and Harrington (1954) among others have listed this species as occurring on saline soil. The surface soil on one of the hummocks in which it occurred had a salt content of 0.50% during July, but this value probably fluctuates throughout the growing season. Since this species was found in only two extremely small areas, it should not be considered one of the primary indicators of saline soils. It was never found invading or encroaching upon the bare salt flats, and, as discussed earlier, the vegetation in the area in which it occurred (Fig. 19) was of the *D. stricta-S. depressa* type.

Cycloloma atriplicifolium (*C. platyphyllum* (Michx.) Moq.) has been reported by Harshberger (1911) as being prevalent in saline areas in southern Kansas. This species was found growing in the area but only in widely scattered patches in the Grazed Sandhill Community. The soils in this area were sandy with a salinity of 0.007%, and were among the least saline areas on the marsh.

Distichlis stricta (*D. spicata* (L.)) has been cited by numerous authors including Harshberger (1911), Kearney *et al.* (1914), Flowers (1934), and Billings (1945), as one of the controlling species in large parts of inland salt flats and salt marshes. Many workers including Hilgard (1914), Harris (1920), Richards *et al.* (1954) and some of those mentioned above have pointed out that this species has a very wide range of salt tolerance. On the Big Salt Marsh *D. stricta* was found in the wetter parts of the Prairie, the Tall *D. stricta,* Sedge-Meadow, *S. pectinata-D. stricta, S. airoides, S. paludosus-D. stricta,* and *D. stricta-S. depressa* communities. The total salinity range under which it existed, as noted in Table 55, was 0.04-2.52%.

It reached its most robust growth and highest basal area in the Tall *D. stricta* Community where the salinity was 0.29-0.94%. In the *D. stricta-S. depressa* Community, where this species entered areas of salinity of 0.49-2.52%, it was definitely stunted in growth. Schaffner (1898) mentioned this stunted growth form of *D. stricta* in the more saline zones of vegetation he described. The mere presence of this species, as other authors have stated, does not necessarily indicate high salinities, but when it is found covering large areas, with a low basal area and a stunted growth form, the salinity of the soil is invariably high.

This species spreads easily by underground rhizomes (Fig. 10). These are shallow, usually occurring within the surface 10 cm. of soil; however, the roots coming off the rhizomes are deeper penetrating and during soil sampling, root material was found at the 60 cm. level. This point is of some interest for in the *D. stricta-S. depressa* Community one finds the deeper rooted *D. stricta* and its codominant *S. depressa* which has a short taproot that rarely penetrates much below the 15 cm. level. These facts would seem to negate the ideas of some authors that plants tend to have their roots situated above or below the layers of greatest salt concentration because *D. stricta* had its rhizomes in the saline area and roots at a lower depth where the salinity was still fairly high, 0.27-1.09%. At germination, however, both species would be subjected to the higher range of soil salinity which occurs at the surface.

Shantz and Piemiesel (1924), Aldous and Shantz (1924), and Weaver (1954) among others have mentioned that *D. stricta* grows well in an area containing a shallow water table as well as a high salt content. This is also true on the Big Salt Marsh where the water table is particularly shallow, and during wet periods parts of the Tall *D. stricta* area, where this species makes its best growth, is under as much as 15 cm. of water.

Eleocharis acicularis was found growing at the bottom of shallow saline lakes. It is not found listed as a salt tolerant species, but Gates (1942), Flowers (1934), and Rydberg (1932) did list it as occurring in wet areas. As the lakes dry up large numbers of this species are observed covering extensive areas, but the plants are so small, 1-10 cm. tall on this marsh, that it seems insignificant and can easily be overlooked. The salt content in the two lakes in which it was definitely observed was 0.22-1.26%. This clearly indicates that *E. acicularis* must be tolerant of at least fairly high salinities or it could not exist in these saline lakes.

Eleocharis rostellata has not been cited as a common species of inland salt marshes, but Fernald (1950) mentioned it as occurring in brackish or saline lakes, and Miller and Egler (1950) cite it for a coastal marsh in Connecticut. This species is the codominant in the Sedge-Meadow Community of this marsh, and it is also prevalent, but in greatly reduced numbers, in the *S.*

pectinata-D. stricta Community. The salinity of the former locality was 0.18-0.68% and in the latter 0.20-1.00%, but if it appears to occupy more saline areas it can always be associated with increased local moisture or drainage ditches where the salinity is greatly reduced. From its distribution it could be said that *E. rostellata* is tolerant of salinities below 1%, but was most abundant between 0.18% and 0.68%. When present at higher salinities, the plants did not flower or fruit.

Eustoma grandiflora and *E. grandiflora* f. *fisheri* have not been mentioned in the literature as being particularly tolerant of high salinities. This species was found, however, under similar conditions as *Flaveria campestria.* The bulk of this species was located in the western part of the *S. pectinata-D. stricta* Community, where the salinity was 0.27-1.00%, while some specimens were found in the Sedge-Meadow and other moist non-saline areas of the marsh. *E. grandiflora* and its white form were never found in any areas more saline than that mentioned above, and one should not consider it an inhabitant of the most saline areas but rather a species which reaches its maximum salt tolerance in the *S. pectinata-D. stricta* Community.

Penfound and Hathaway (1938) and Kurz and Wagner (1957) have indicated that *Fimbristylis castanea* has been found growing in a wide range of salinity conditions on certain coastal marshes, but no record of its occurrence on inland salt marshes has been found. On this marsh it was limited to the Sedge-Meadow Community, where the salinity was 0.18-0.68%. It was not found invading more saline areas and can not be considered as indicator of the more highly saline soils.

Flaveria campestris (*F. angustifolia* of manuals) has been listed by Hitchcock (1898), Harirs (1920), Harrington (1954), and Jantzen (1960) as being present in saline soils. On the Big Salt Marsh *F. campestris* was found in the Sedge-Meadow, Fresh Water Seep, *S. pectinata-D. stricta* communities, and in other areas bordering drainage ditches. In actuality, this species does not invade the open salt flats of this marsh as mentioned by Jantzen (1960), but it does border these places along drainage ditches and other moist sites with a lowered salinity. *F. campestris* is widely scattered in these areas during the late summer and fall months. The actual salinity in the areas of its occurrence was 0.18-1.00%, with 1.00% being about the maximum in any area in which it might occur. It is definitely capable of entering areas with a salinity below 1.00% but should not be considered one of the primary invaders of the bare salt flats.

Haplopappus phyllocephalus subsp. *annuus* is cited by Hall (1928) as a taxon which occurs in saline areas. This species occurred only in a single location on the Big Salt Marsh at the base of a sandy hummock, where it was associated with *A. exilis* and *A. ericoides.* The majority of specimens were high up on the sandy hummock, but a few plants were found lower down and their bases were covered with a salt crust. The salinity in this area was 0.003-0.05‰. Seed germination studies, described later, indicate that this species can germinate in salinities up to 2‰ at 20°C.

Heliotropium curassavicum, a succulent with a shallow taproot, was located in the *S. paludosus-D. stricta* Community and was found also along the east-west road bisecting the marsh. This species is cited by Fernald (1950) as occurring in saline marshes. On this marsh its chief occurrence was in the *S. paludosus-D. stricta* Community where the salinity was 0.22-1.10‰. It was found also in the more saline *D. stricta-S. depressa* area. This species is tolerant of brackish conditions, but does not usually occur in situations where the salinity is appreciably over 1‰.

Hordeum jubatum, has been cited by Schaffner (1898), Kearney *et al.* (1914), Coupland (1950), Ganong (1903), and Weaver and Albertson (1956) as being present in certain saline soils. Kearney *et al.* (1914) describe it as occurring in a community dominated by *D. stricta,* and Schaffner (1898) reports it as being found in a community in which species less characteristic of halophytic regions are trying to gain a foothold. On the Big Salt Marsh it occurred in many communities including the Sandhill Mixed Prairie, Tall *D. stricta,* Hummock, Sedge-Meadow, *S. pectinata-D. stricta* and *S. paludosus-D. stricta.* The total range of salinity under which it was found was 0.003-1.10‰, but it was most abundant in the Tall *D. stricta* Community and wetter saline areas where the salinity was 0.29-0.94‰. Figure 6 shows a colony of *H. jubatum* scattered through an area south of the sandhill region occupied by *D. stricta* and *S. airoides,* where the salinity on August 19, 1960 was 0.85‰ in the surface 10 cm., 34‰ at 60 cm., and the chlorinity was 0.53‰ and 0.19‰. This species was widely scattered through wetter saline areas, but it was never particularly abundant in any one place and did not invade communities with salinities much over 1‰.

Hordeum pusillum is considered a member of slightly saline communities by Parodi (1930), Ragonese and Covas (1947), and Hitchcock (1950). It was found in the Sandhill Mixed Prairie, Grazed Sandhill, and Hummock communities of the Big Salt Marsh, where the salinity range was extremely low. In the Grazed Sandhill Community where it was most prevalent the salinity was 0.007‰, whereas in the prairie area it was 0.003-0.02‰. The occurrence of *H. pusillum* in only the least saline communities of this marsh indicated that, at least in this local area, the species was not tolerant of a wide range of salinity.

Iva annua (*Iva ciliata* Willd.) has been cited by Schaffner (1898) as occurring along with *D. stricta* and *S. depressa* in saline communities, but only in rare instances. On this marsh it was found bordering the Prairie Community, in the *S. pectinata-D. stricta* Community, and bordering the *D. stricta-S. depressa* Community in one area where the former comes in contact with it. The total salinity in the areas in which this species exists was 0.003-1.00%, but it was found mainly in the part of the *S. pectinata-D. stricta* area in which the salinity was 0.27-1.00%. This species was extremely rare on the marsh and only a few patches of 10-20 individuals were found. It was not commonly present in areas with a salinity higher than 1% and should not be considered one of the important indicators of high salinity in this area.

Muhlenbergia asperifolia has been cited by Gates (1936) as being found in saline areas. This species was located only in the sandy hummock areas, seepage area, and along roadsides where the salinity was 0.003-0.50% in the surface 10 cm. It was definitely not an indicator of highly saline ground, and its extremely rare occurrence did not provide a great amount of information to judge its entire range of distribution.

Stone (1959) reported that *Myosurus minimus* exists in soils which are from moderately to highly alkaline. It was found on this marsh only in the seepage area on the sides of small, 15-30 cm. high mud ridges. The waters in this area of the marsh have the lowest salinity, 0.02-0.05%, of any pond site. The low salinity of these waters indicates that *M. minimus* grows well in areas of fresh water and the lack of its appearance in or around any of the more saline ponds demonstrates that, at least in this area, it has not been successful in spreading into saline soils.

Panicum virgatum has been listed by Penfound and Hathaway (1938) and Kurz and Wagner (1957) as being found under a wide range of salinity conditions on certain coastal marshes. However, there are no reports of it in saline inland marshes. On the Big Salt Marsh, it was found in the Prairie, Sandy Hummocks, and Sedge-Meadow communities. It reached its greatest abundance in the Prairie and Sandy Hummocks where the salinity was 0.003-0.02% and was sparsely scattered through the sedge-meadow area where the salinity was 0.18-0.68%. This species showed no signs of being especially salt tolerant and was not found entering highly saline areas on this marsh.

Pluchea purpurascens has been considered an inhabitant of brackish and saline marshes by Fernald (1950) and Gates (1940). This species was found in the northern sector of the Tall *D. stricta* Meadow Community, bordering a large lake. The lake waters which overflow into this area had a salinity of 0.22-0.48% and the soils 0.29-0.63%. Only a single plant was found at this location and since it was observed in only one other place along a drainage ditch, this species must be considered tolerant of only the lowest salinities.

Poa arida has been cited by Hitchcock (1950) as a member of saline communities. On this marsh it occurred in the Tall *D. stricta, S. pectinata-D. stricta*, Sedge-Meadow, *S. airoides, S. paludosus-D. stricta* and the *D. stricta-S. depressa* communities. It was not very abundant and only of local importance even though it occurred in many communities and in a fairly wide salinity range. As noted in Table 55, the total range of salinity in the surface 10 cm. which it tolerated was 0.04-1.60‰; however, at the location where it was most abundant, the Tall *D. stricta* Community, the salinity was 0.29-0.94‰.

This plant is a perennial and is the first species to be found flowering in the saline areas of the marsh. After flowering in May, it again begins vegetative growth and by fall new culms develop. This is probably advantageous and allows it to flower early in the spring. *P. arida* is of secondary importance in most of the areas in which it occurs and, depending on the species which accompany it, it can be considered a fair indicator of moderate salinities.

Polygonum lapathifolium has not been reported as being particularly salt tolerant, but it did occur in some wet, saline areas of this marsh. It was found in the sedge-meadow area and in a wet *D. stricta* Community in the southern part of the marsh, where the salinity was 0.18-0.68‰. This species is definitely not an indicator of high salinities, but, as with many others which occurred in the Sedge-Meadow Community, it reached its peak of salinity tolerance in this area.

The next species, *Polygonum ramosissimum*, has been cited by Schaffner (1898) as a characteristic species of the barren salt flat. On the Big Salt Marsh it occurred in the Sandy Hummock, *S. paludosus-D. stricta*, and *D. stricta-S. depressa* communities, and at times when these bordered the open salt flats it was associated with *S. depressa*. In the main areas in which it was growing, the salinity was 0.27-1.10‰, and at the sites where it entered more open areas the salinity was slightly higher. *P. ramosissimum* should not be considered one of the main invaders of the open salt flats in this area because it occurred chiefly in the communities mentioned above and only in one area did it invade the *S. depressa* community.

Potamogeton foliosus occurred in a few of the shallow saline lakes on the marsh. Only a few widely scattered plants were found in the lake bottoms and it was usually rare. It is cited by Muenscher (1944) as occurring in brackish lakes and ponds. The waters it occurred in on this marsh had a salinity of 0.22-1.26‰, which indicates that it can tolerate fairly high salinities.

Rumex maritimus var. *fueginus* has been cited by Fernald (1950) as being an inhabitant of salt marshes. This species was found in the same locality as *P. purpurascens*, bordering a large lake in the northern part of the Tall *D. stricta* Community. As in the case of *P. purpurascens*, it was extremely rare. The salinity in this area was 0.22-0.63‰, and, as mentioned earlier, the salinity of the lake waters which flood it was 0.22-0.48‰. Since *R. maritimus* var. *fueginus* was not found entering more saline areas it must be considered tolerant of only the lowest salinities.

Salicornia rubra has been cited by numerous authors, including Aldous and Shantz (1924), Kearney *et al.* (1914), Flowers (1934), Weaver and Clements (1938), Shreve (1942), Rawson and Moore (1944), Billings (1945), and Coupland (1950), as occurring in inland areas containing extremely high salinities. Flowers (1934) described it as one of the pioneer species of the halosere of the Great Salt Lake and Kearney *et al.* (1914) cite it as one of the most salt resistant species in Tooele Valley, Utah. Schaffner (1898), Hitchcock (1898), and Penfound (1953) do not mention it as occurring in the Kansas or Oklahoma marshes they studied. Prior to this study the only known collection of this species in Kansas was made by Carleton in 1892 in Stafford County, but no habitat or exact locality data were found with the herbarium specimen. *S. rubra* was not listed by Waterfall (1952) as occurring in Oklahoma, indicating, as is also cited in Muenscher (1944), that in the central states it reached its southern limits of distribution at this collection site in Kansas.

If one considers that this species is one of the primary invaders of open salt flats in Utah and Canada (Flowers (1934); Coupland (1950)), and while in this area it is found in only one extremely small locality, it becomes clear that it cannot spread as rapidly as it does in other areas.

As mentioned by Kearney *et al.* (1914) *S. rubra* is a shallow-rooted annual with a taproot that usually does not penetrate deeper than 30 cm. It was found at only one location on the marsh where the salinity was 1.16-2.75%. Accompanying it were two other halophytic species, *Suaeda depressa* and *Sesuvium verrucosum*. The high salinities in these salt flat areas indicate clearly that species located in them are definitely halophytic. The fact that *S. rubra* does not spread can be explained by the fact that no viable seed are produced and none were found as late as September 1959. If this is always true, *S. rubra* must be brought into this area anew, at intervals, by birds in their migration flights. Another reason for the latter assumption is that the 1959 colony could not be found again in 1960. A second possibility might be that germination of seeds is delayed and only during certain years are conditions just right for germination.

Scirpus americanus has been reported by Rydberg (1932), Flowers (1934), Taylor (1938), and Penfound (1953) as occurring in saline marshes. Miller and Egler (1950) mention it as forming a community with *E. rostellata* in a Connecticut coastal marsh, just as it does in Kansas. This species was found in the Sedge-Meadow and *S. pectinata-D. stricta* communities, along drainage ditches, and in patches on wetter, less saline, parts bordering the *D. stricta-S. depressa* Community. The range of salinity under which it was growing was 0.18-1.00% in the surface 10 cm. and the range in the Sedge-Meadow Community where it was one of the major dominants was 0.18-.68%. At times when this species was found in salinities above 0.80%, the plants were greatly stunted and produced no fruit, indicating that it can exist in areas of moderate but not high salinity.

Scirpus paludosus (*S. campestris* Britt.), has been described by Penfound (1953), Schaffner (1898), and Flowers (1934) as occurring in slightly saline areas. On the Big Salt Marsh this species occurred in the Tall *D. stricta*, Sedge-Meadow, *S. pectinata-D. stricta*, *D. stricta-S. depressa*, and the *S. paludosus-D. stricta* communities. It was found also along drainage ditches and bordering some of the saline lakes. As mentioned by Flowers (1934), this species usually occurs in areas where the salinities are low or reduced. The total range of salinity under which *S. paludosus* grew was 0.18-1.10%, and it reached its highest basal area in a single transect of the Tall *D. stricta* Community (Table 14), where the salinity was 0.29-0.94%. As mentioned above, *S. paludosus* was found also in the more saline *D. stricta-S. depressa* Community, but when found there it was usually associated with some source of added moisture that tended to alleviate the high salinities. In some cases it was found in areas of higher salinity in this community, but no fruit was produced and the plants were greatly stunted. This species, as well as the previously mentioned *S. americanus*, spreads by underground rhizomes which gives it some advantage in occupying saline areas.

Sesuvium verrucosum has been cited by Gates (1940) and Penfound (1953) as occurring on highly saline soils. This species is succulent in habit and is one of the primary invaders of the open salt flats. It was considerably more abundant and more widely scattered than *Salicornia rubra* but must be considered rare in comparison to *Suaeda depressa*. The total salinity range in the salt flat areas in which it grew was 1.16-2.75%. Occasionally a few scattered individuals were in parts of the *D. stricta-S. depressa* Community where the salinity was 0.82-2.45%. The salinities which this species tolerated clearly indicate that it is halophytic. It is listed as a perennial by Rydberg (1932), but for all practical purposes it acts as an annual when occupying the open salt flats. It, as well as *S. rubra* and *S. depressa*, have a shallow taproot which does not survive from one season to the next. One factor that tends to eliminate *S. verrucossum* is that it can not stand submergence for long periods, whereas, in the areas in which it occurs it has to contend with this factor at some time during the growing season.

Hitchcock (1936) and Gates (1950) have indicated that *Setaria geniculata* occurs in salt marshes. On this marsh it was always rare, but it was found in the Sandhill Mixed Prairie, Sedge-Meadow, Grazed Sandhill, and Sandy Hummock communities. The total salinity in the surface 10 cm. of the areas in which it occurred was 0.003-0.68% and in the area where it was most prevalent, the Grazed Sandhill, the salinity was 0.003-0.02%. The appearance of *S. geniculata* in many non-saline communities indicated that 0.68% was probably the highest salinity tolerated by this species on the marsh. Since it did not occur in areas of higher salinity, it should not be considered an indicator of highly saline soils in this locality.

Spartina pectinata has been mentioned by Hitchcock (1950), Muenscher (1944), and Fassett (1957) as being a member of brackish coastal communities. It was found mainly in the *S. pectinata-D. stricta* Community, but it occurred also in the Sedge-Meadow Community, on sandy hummocks, in wetter parts of the prairie, bordering the most northern saline lake along drainage ditches, and in the wetter and less saline portions of the *D. stricta-S. depressa* Community. The salinity in the areas where it occurred was 0.18-1.00%. All salinities over 1% the plants were greatly stunted and usually did not produce fruit. *S. pectinata* was characteristic of a wet, slightly saline community, but in no instances did it occur in the bare salt flats or areas with a continuously high salinity throughout the growing season.

Sporobolus airoides has been cited as an occupant of inland saline areas by many authors, including Kearney *et al.* (1914), Harris (1920), Shreve (1942), Penfound (1953), Aldous and Shantz (1924), and Hilgard (1914). Its distribution on the Big Salt Marsh was limited to the Sandhill Mixed Prairie, *S. airoides,* open salt flats, and the grazed area south of the sandhills. The total range of salinity under which this species grew was 0.003-1.60%. In the *S. airoides* Community where it was very abundant and had a high basal area, the salinity was 0.04-0.19%. It was common also in parts of the southern grazed area where the salinity was 0.85% on August 19, 1960. A small portion of this area is illustrated in Fig. 6.

The fact that this species was capable of establishing itself on the open salt flats indicates that it is tolerant of high salinities. Fig. 20 illustrates one of the hummocks formed by *S. airoides* in an open salt flat habitat.

Another species on the marsh, *Sporobolus pyramidatus,* has been cited by Ragonese and Covas (1947) and Hitchcock (1950) as occurring in saline soils. This species occurred in one location in the southern grazed area, just south of the sandhills proper. It was extremely rare and found only at the site of Fig. 6, where it was associated with *S. airoides, D. stricta* and *H. jubatum*. The salinity in this area was 0.85% in the upper 10 cm. A fuller account of other soil relations are in Table 55 and in the description of *H. jubatum* in this section. It is definitely tolerant of moderate salinities, but its rare occurrence and complete absence from any of the ungrazed saline communities indicate that it would not be useful as a primary indicator of saline conditions in this area.

Sporobolus texanus has been cited by Schaffner (1898) as being a successful invader of saline areas in the northern Kansas marshes which he studied. It was found only in the sandy hummock area and bordering roadsides on the Big Salt Marsh. The salinity in these areas usually was 0.003-0.50%. This low salinity range combined with the fact of its low abundance demonstrates that this species should not be considered an indicator of salinity on the marsh.

Suaeda depressa (*S. erecta* (S. Wats.) A. Nels.) has been reported by many authors, including Kearney *et al.* (1914), Flowers (1934), Gates (1940), Rawson and Moore (1944), Coupland (1950), and Keith (1958) as being a salt tolerant species. On this marsh it was found in the Tall *D. stricta* Meadow, *S. depressa, D. stricta-S. depressa, S. paludosus-D. stricta, S. pectinata-D. stricta, Sedge Meadow,* and *S. airoides* communities. The total range of salinity in the surface 10 cm. of the area it grew in was 0.04-2.75%, whereas, in the *S. depressa* Community, where it was one of the primary invaders of the open salt flats, the salinity was 1.16-2.75%.

According to Flowers (1934) and Kearney *et al.* (1914) *S. depressa* is less tolerant of alkali than *S. rubra,* but in this marsh it comprised the greatest part of the vegetation in the areas of highest salinity, indicating that it is as salt tolerant as *S. rubra* in this locality.

A seed germination study, discussed in fuller detail later, indicated that seeds of *S. depressa* could germinate in salinities ranging from distilled water to 4% sodium chloride. This may explain its wide range of distribution and its occurrence in the highly saline communities. One possible explanation for its lack of ability to spread out in the less saline communities might be its inability to compete for light and moisture in these areas. Schimper (1903) has stated that the competition of more vigorous plants excludes halophytes from all localities except the saline.

A study of root penetration was made on 100 specimens of the depressed form of *S. depressa* on September 23, 1960. The depth of penetration at this time averaged 10.59 cm., varying within the colony from 6-15 cm. and at no time during the course of this study was root material of this species found penetrating below the 30 cm. level. The specimens found in this colony seemed to have developed from recently germinated seed, and they appeared less robust and slightly smaller than the depressed forms which appeared earlier in the season. These data and observations made earlier during the growing season indicate that *S. depressa* has a shallow rooting taproot.

As cited in Table 5, the extensive areas covered by the *D. stricta-S. depressa* vegetation type had a salinity of 0.49-2.52%. These species have two distinct habits of growth. *S. depressa* is a succulent with a shallow taproot, while *D. stricta* is a deeper penetrating grass which spreads by rhizomes. The broad distribution of the two species demonstrates that these two life forms are exceptionally favorable for widespread distribution in highly saline soils.

Suaeda depressa wilts when submerged and finally dies off after long periods of submergence. This factor as well as the extremely high salinities which develop are probably the main reasons why it does not establish itself on certain portions of the open salt flats.

Tamarix gallica has been cited as being tolerant of soils containing some salinity (Gates, 1940; Penfound, 1953; Hopkins and Tomanek, 1957). On the Big Salt Marsh it occurs on certain hummocks, and along with *D. stricta* (Fig. 11), bordering the barren salt flats. The soil salinity in the latter area was 0.72-1.45%.

When Hitchcock (1898) visited this area he did not report *T. gallica,* a fairly conspicuous species, as growing in saline soils, and conversations with local residents indicate that it is of more recent introduction in the area. It was not found actively spreading until the summer of 1960, when a group of 10-30 seedlings were found along a natural drainage channel in the northeastern part of the marsh.

Seed germination studies directed by Tomanek (1957) indicate that this species can germinate almost as well at salinities of 0.50-1.00% as it did at 0.01-0.05%. Germination at high salinities allows *T. gallica* to spread out through this area; however, it has not spread rapidly and if one considers the entire marsh area it must be considered rare in occurrence. As Merkel and Hopkins (1957) have stated, this species can produce both a superficial lateral root system and a deeply penetrating primary root which would allow it to reach all the available water at both levels, but even with these advantages it exhibited a low abundance on this marsh.

McMillan (1959), Penfound and Hathaway (1938), Taylor (1939), and Gates (1940) have indicated that *Typha angustifolia* occurs in saline areas. On the Big Salt Marsh it was limited to drainage ditches, including those which bordered the *S. pectinata-D. stricta* and Sedge-Meadow communities, and it was found growing also along the margins of one or two of the saline ponds. The salinity in the areas in which it occurred was 0.25-0.52%. *T. angustifolia* was not widely distributed on the marsh and occurred in areas of only moderate salinity, as reported by Flowers (1934) in his work in Utah, so it should not be considered a characteristic species of highly saline areas. McMillan (1959) has indicated that the species is more restricted in its distribution to saline areas than *T. latifolia.* In this area the two species occurred very close together and for most of their distribution had a similar range of salinity tolerance.

Typha latifolia has been described as a member of saline communities by Rawson and Moore (1944), Penfound and Hathaway (1938), and McMillan (1959). This species occurred along drainage ditches bordering the Sedge-Meadow and *S. pectinata-D. stricta* communities, on the margin of saline ponds, and also in the seepage area of the marsh. It was found in areas where the salinity was 0.02-0.52%, which indicates that it has a slightly broader range of distribution than *T. angustifolia.* McMillan (1959) has reported that *T. latifolia* has a broad distribution in eastern Nebraska, whereas, *T. angustifolia* seems to be chiefly confined to saline areas. The areas on the marsh occupied by these species were low to non-saline.

SEED GERMINATION

Seeds of *Bromus japonicus, Suaeda depressa,* and *Haplopappus phylocephalus* subsp. *annuus* were grown in petri dishes on two sheets of filter paper. Two dishes containing 50 seeds or a total of 100 seeds were used for each salt concentration in each study. The dishes containing the seeds were placed in a dark room and allowed to germinate for thirty days. No special treatment was given the seed of *B. japonicus* or those of *H. phyllocephalus* subsp. *annuus,* but it was found from preliminary studies that the seeds of *S. depressa* would only germinate after their seed coats were ruptured. Seeds of all species studied were considered to have germinated when the plumule reached one centimeter in length or when the plumule and radicle had both developed.

The species chosen for this study occupied different habitats. *S. depressa* was almost always found in the most saline areas, *H. phyllocephalus* subsp. *annuus* was found on the border of a sandy hummock which was marginal in position between saline and non-saline soil, and *B. japonicus* was never found on any but the most non-saline soils. The salinity in the upper 10 cm. of soil in which these species were found was 0.04-2.75% for *S. depressa,* 0.003-0.50% for *H. phyllocephalus* subsp. *annuus,* and 0.003-0.02% for *B. japonicum.* Table 56 shows the germination ability of these species at different salt concentrations.

TABLE 56. Percent germination after thirty day period.*

	Sodium chloride concentration								
Species	0.0	.25	.50	.75	1	2	3	4	5
S. depressa 20°C.	27	31	53	37	38	23	21	19	—
Room Temp.	48	52	72	46	48	28	30	X	—
B. japonicus R. T.	63	46	31	4	—	—	—	X	X
H. phyllocephalus subsp. *annuus* 20°C.	40	36	25	14	12	3	—	X	X

* X = no test made, — = no germination.

The results of these studies indicated that *S. depressa* reached its optimum germination percentages, 53 and 72%, in a 0.50% sodium chloride solution and that seeds of this species were able to germinate at all salt concentrations up to 4%. The seeds of *B. japonicus* and *H. phyllocephalus* subsp. *annuus* acted like most glycophytes in that they had the optimum germination in distilled water and at all other salt concentrations there was a continuous drop in germination with a rise in salinity. This reduction in germination with increased salinity was also reported by Poma (1922) and others.

The seeds of *B. japonicus* which did not germinate in a 1, 2 or 3% salt solution were placed in distilled water and after thirty days these yielded germination values of 83, 89, and 90%, indicating that the high salt concentrations main effect was osmotic and not a toxic effect of the sodium or chlorine ions. The same procedure was carried out with seeds of *S. depressa* which did not germinate in a 5% sodium chloride solution, and in this case 50% of the seeds germinated. MacKay and Chapman (1954), in their study of seed germination of *Suaeda australis* Moq. var. *novazelandica* and *Mesambryanthemum australe* Sol. ex Forst., have reported also that high salt concentrations were not toxic and that a transfer of seeds to tap water, from high salt concentrations, would allow them to germinate.

S. depressa, one of the primary invaders of the bare salt flats, could germinate in salinities ranging from that of distilled water up to 4% sodium chloride, but its actual distribution was limited mainly to areas where the salinity was 0.49-2.75%, and only in extremely rare cases was it found at lower salinities.

The germination rates obtained for *S. depressa* at all salt concentrations up to 4% indicated that this species can germinate in a much wider range of salinities than other species of *Suaeda* studied by Chapman (1947, 1947a) and MacKay and Chapman (1954). Chapman (1942, 1947, 1947a, 1960) reached the conclusion that many marsh species did not germinate until the salinity was reduced.

PIONEER HALOPHYTIC VEGETATION IN INLAND SALT MARSHES

Chapman (1960) has stated that areas which have a *Distichlis* or *Suaeda* community occupying the most saline areas in the interior of North America should be considered salt marsh, whereas the drier areas in the interior containing a primary community of *Salicornia* or *Allenrolfea* should be considered salt desert. In the study of the literature concerning these communities, and as Chapman himself has indicated, it seems that this division is more arbitrary than real.

The saline areas of north-central Kansas described by Schaffner (1898) were bordered by a *Distichlis stricta* area and he cited *D. stricta, Suaeda depressa* and *Polygonum ramosissimum* as the characteristic plants of bare areas. On the Big Salt Marsh *S. depressa, Sesuvium verrucosum,* and rarely *Salicornia rubra* occurred on the barren salt flats, while the next most saline areas were dominated by a *D. stricta-S. depressa* Community. In Oklahoma marshes, Penfound (1953) listed *S. verrucosum* as forming the pioneer community on the salt flats and *D. stricta* as marginal. Pound and Clements (1900) have stated that *D. stricta, Suaeda depressa, Salicornia rubra, Atriplex hastata, A. argentea* and *P. ramosissimum* occurred in saline areas of Nebraska. Rawson and Moore (1944), Coupland (1950) and Keith (1958) all have cited *D. stricta, S. depressa,* and *S. rubra* as occurring in the most saline areas of the Canadian marshes which they studied. Flowers (1934) and Kearney *et al.* (1914) have listed *S. rubra* as one of the most important invaders of the bare salt flats and *D. stricta* and *S. depressa* in slightly less saline communities. This would seem to indicate that in the northern and western areas studied, *S. rubra* is always one of the most important invaders of the bare salt flats. In Kansas this species is of little importance, but *S. depressa* becomes extremely important, while in Oklahoma *S. verrucosum* seems to be the pioneer species.

In all the studies reviewed, *D. stricta* covers a large part of the highly saline areas and should be considered one of the most characteristic species of the inland salt marshes and deserts of the United States and Canada. The fact that many workers such as Billings (1945), Hilgard (1914), Keith (1958), Flowers (1958), and others, including this author, have cited it as occurring under a wide range of salinity conditions indicate that it is not always a good indicator of highly saline soils. However, as mentioned earlier in this paper and by Schaffner (1898), this plant is dwarfed under conditions of high salinity, and in this study it was found to have a very low basal area under these conditions. Another helpful factor in determining whether the area is highly saline is the associated species. If these are succulents such as *S. depressa* and *S. verrucosum*, this indicates a high salinity. Kearney *et al.* (1914) also diagrammed *Suaeda as* being a dwarfed form when occupying salt flat areas.

Sporobolus airoides has been cited as occurring in moderately saline areas by Flower (1934), Kearney (1914) in Utah, Penfound (1953) in Oklahoma, and by the present author in this study, but no mention of it has been made in the works on Canadian marshes. Other species listed as being of some importance in Oklahoma marshes are *Tamarix gallica*, *Scirpus americanus* and *S. paludosus*. The first of these was of little importance on the Big Salt Marsh, but it did occur in areas where the salinity reached 1.45%. *S. americanus* was limited mainly to fresh water or only brackish areas on the marsh and *S. paludosus* was found in slightly more saline areas, but, as Flowers (1934) and Penfound (1953) have mentioned, it is also usually limited to brackish areas and is not found in localities of the highest salinity. Other species play important parts locally in these areas, but the taxa mentioned above and in the former section on the salt tolerance of species have the broadest distribution in the United States and Canada.

SUCCESSIONAL RELATIONS

From the vegetational relations discussed earlier, possible trends of succession can be described, based on the present conditions of vegetation distribution.

One can see from the successional relations of the vegetation suggested in Fig. 21 and in the previous analyses that two main trends appear to exist. One leads toward a line with a reduced salinity, but a retention of a high amount of soil moisture and a *Scirpus americanus- Eleocharis rostellata* Community. The second main trend occurs with a building up of soil, a reduction in moisture and salinity and the formation of a mesic state in which the Sandhill Mixed Prairie Community is predominant. According to the climatic conditions in this area of Kansas one would expect this type of community to develop. However, for this to occur in the area of the salt marsh the soil must be built up and the salinity and moisture content reduced considerably.

A building up of soil occurs when vegetation occupies the more saline or wetter flat areas, causing an accumulation of organic matter and wind blown soil particles. One species which is tolerant of high salt content and is important in raising the ground level is *Sporobolus airoides*. The raised mounds formed by this and other species accumulate blowing soil from the surrounding sand-dunes and raise the general level of the land.

It must be remembered that the successional trends delineated in Fig. 21 may never occur. The reason for this, as Polunin (1960) has mentioned, is that the conditions in these saline areas may never change and if they do the tendency would probably be toward an increase in salinity. This would make these communities static successional units since no successional changes could take place without a lowering of salinity or soil moisture. The reason for this is that the sedge-meadow plants can not tolerate the extremely high salinities of the salt flats and also by and large the prairie species can not generally occupy areas of higher moisture or higher salinities.

Flowers (1934) has stated that *Salicornia rubra* tolerated higher salt concentrations than most other species and that *Suaeda depressa* is also prominent in invading the strand. On the Big Salt Marsh *S. rubra* was extremely rare and found only in a single colony of 50-100 individuals, associated with *S. depressa* and *Sesuvium verrucosum*. It would seem, then, that in this area *S. depressa* in both its erect and depressed forms is definitely the primary invader of the bare salt flats, where the salinity was 1.16-2.75%. Another succulent, *S. verrucosum*, is of secondary importance and formed small, widely scattered colonies on the open salt flats, sometimes being associated with *S. depressa* and in only one instance with *S. rubra*.

Distichlis stricta, as mentioned by Flowers (1934), Kearney *et al.* (1914), Hilgard (1914), and Billings (1934) is very versatile, being able to live under a wide variety of salinity relations, 0.29-2.52% on the Big Salt Marsh. Flowers (1934) has stated that *D. stricta* does not seem to allow many other plants to enter areas which it dominates. The Tall *D. stricta* Meadow Community on this moderately saline and highly moist marsh was almost completely dominated by dense stands of the species and only a few scattered plants of other species were present. The *D. stricta-S. depressa* Community occupied very large areas of the marsh with a salinity averaging lower than the barren salt flats but in all cases over 1%.

All other marsh communities seemed to radiate out from the *S. depressa* Community mentioned above, but *D. stricta* and not *S. depressa* was one of the major vegetational elements in many of these communities. As mentioned in the quantitative discussion, an *S. airoides* Community developed along the eastern margin of the marsh, forming a rather abrupt boundary to the Tall *D. stricta* community. The change can be best expressed by the quantitative results, for, in the Tall *D. stricta* area, *D. stricta* had a relative density of 94.46% and a basal area of 11.35% or 92.65% of the total, whereas, in the adjoining *S. airoides* Community it was much sparser, having a relative density of 5.85% and a basal area of 0.10% or 1.81% of the total. This *S. airoides* Community then blends into the Sandhill Mixed Prairie area, which indicates, as noted in Fig. 21, that the development of the prairie need not pass through a *S. americanus-E. rostellata* Community.

The *D. stricta* Community, besides having the relations discussed above, seemed to be transitional to many of the other major communities. As illustrated in Fig. 21, it leads to a *S. americanus-E. rostellata* area on the western margin of the marsh or to a *Spartina pectinata-Distichlis stricta* community first and then to the former.

In one area it leads directly to a prairie community and in other areas located on the salt flats, a *D. stricta* or a *D. stricta-S. depressa* Community blends into a *Scirpus paludosus-Distichlis stricta* Community.

CLIMAX RELATIONS

In the Big Bend area of Kansas the dominant natural vegetation is of the Sandhill Mixed Prairie type. Under normal conditions, the climate of Stafford County, Kansas, with low rainfall, low humidity and drying winds would produce a Mixed Prairie Climax Association. In this localized area, however, a salt marsh vegetation develops which has several communities occupying different salinity ranges.

Under the system of plant community classification described by Clements (1920), the salt marsh communities would not be considered on an equal level with the Sandhill Mixed Prairie Climax Association but must be considered a sub-climax since the Sandhill Mixed Prairie was the one considered to be in harmony with the climate in the area. The subclimax communities are produced by the local deposits of excess salts.

An application of the continuum approach described by Curtis (1955, 1959) to the communities on the Big Salt Marsh reveals that one can find a gradual change in species composition between two distinct areas in many cases, but in other instances the changes in community structure are abrupt and the distribution is definitely discontinuous. An example of a continuous relation exists between the species of the *Scirpus americanus-Eleocharis rostellata* and the *Spartina pectinata-Distichlis stricta* communities, whereas an extreme discontinuity exists the Sandhill Mixed Prairie or the *Sporobolus airoides* and Tall *Distichlis stricta* communities. Goodall's (1954) statement that all vegetational classifications are more or less arbitrary may be true, but as he himself stated, some areas must be considered discontinuous and if no attempt is made to separate areas of different structure the results of vegetational analysis would lead to great confusion.

The evidence seems to indicate that this should not be considered a Salt Marsh Climax Association, but rather a series of subclimax associes caused by the more or less permanent presence of excess salts. It seems clear that if the salts and excess water were removed, by changes in one or more of the edaphic factors discussed, the salt marsh vegetation would disappear and the Sandhill Mixed Prairie type would predominate.

FACTORS CONTROLLING COMMUNITY DISTRIBUTION

A good introduction to this subject is a statement advanced by Clements (1920): "Every plant is a measure of the conditions under which it grows. To this extent it is an index of the soil and climate, and consequently an indicator of the behavior of other plants and animals in the same spot." This statement is undoubtedly true and an attempt will be made here to explain the controlling factors in each of the marsh communities. The distribution of communities on this marsh clearly indicates that it was the upper limit of salinity that determined the species complement.

For the most highly saline areas which included bare ground, the *Suaeda depressa* stands, and the *Distichlis stricta-Suaeda depressa* Community where the salinities reached 2.96%, 2.75% and 2.52%, there was a direct correlation between decreased salinity and increase in species number and cover. The community with the next highest salinity was the Saline Pond which has a high 1.17% and only two species of vascular plants, but in this case the moisture factor was decisive, since many species which are not aquatic, could not enter. However, saline conditions are also important in deciding species presence, as evidenced by the fact that the fresh water seep, with the lowest average salinity (0.03%), of any pond tested, had a completely different complement.

The next three communities were fairly closely related by salinity conditions. The Tall *D. stricta* Community had an average salinity of 0.59% and a high of 0.94%. There was no great increase in species number in this area; however, there was a great increase in basal area, and this community had the highest, averaging 12.25%, of any community on the marsh. The *Scirpus paludosus-Distichlis stricta* Community had an average salinity of 0.45% and a high of 1.10%. It contained only nine species, all of which must be considered at least slightly halophytic, indicating that the salt concentration was the factor which prevented the invasion of the area by glycophytic species. The final community in this group, the *Spartina pectinata-Distichlis* *stricta,* had an average salinity of 0.51% and high of 0.63% and 1.00%. This community had an increase in species and cover over all the more saline areas except the Tall *D. stricta* which had a higher cover, indicating that the reduction of salinity allowed for the invasion of glycophytes and species of low salt tolerance. The former area was bordered by the highly saline soils of the *D. stricta-S. depressa* Community, and this accounts for the high salinity reached at the margin. The *S. pectinata-D. stricta* area also had a higher organic content than the *S. paludosus-D. stricta* area.

The *Scirpus americanus-Eleocharis rostellata* Community indicated a low to non-saline wet habitat. Furthermore, there was an abrupt reduction in species number as well as cover when this community bordered a more saline area. In this area the average salinity was 0.40% and the highest 0.68%, indicating that the salinity was low.

The *Sporobolus airoides* community reached its best development in an area where the salinity averaged 0.12% and the high was 0.19%, but in the southern grazed area of the marsh it was found growing perfectly well in dense colonies at a location where the salinity was 0.85% and on the salt flats in an area where the salinity reached 1.60%. This community is only a good indicator of high salinity when *S. airoides* is associated with other halophytes.

The prairie and grazed sandhill areas are a culmination of this line of development because they have the lowest salinity and moisture of any community on the marsh. The differences in species composition between these two communities must be ascribed chiefly to grazing and not to any soil factor.

This brief summary indicates that for the more saline communities in this area there is no difficulty in distinguishing the limiting factor as salinity, but in areas of low salinity, soil moisture and the associated factor of aeration play an important role. An example of this would be the completely different floras which develop in the prairie and sedge-meadow communities; soils in both communities are low in salinity, but the sedge-meadow has a fairly high water content, whereas the prairie is comparatively well drained.

Good (1953), Steiner (1934), Harshberger (1909), and many others have also pointed out that salinity is the most important factor in determining the distribution of plants in a salt marsh habitat. In many communities, including the Sandhill Mixed Prairie, *S. americanus-E. rostellata* and *S. pectinata-D. stricta,* a reduction in salinity was accompanied by a large increase in species number.

Others, as mentioned earlier in this paper, have mentioned that pH and soil moisture may be important factors controlling halophyte distribution. On this marsh all areas were fairly moist, and it would be extremely difficult to use this as a separating factor. Standing water and lakes do play some part in preventing the succulent halophytes from invading certain highly saline areas, but when this surface moisture is gone these plants are able to enter. The pH factor, as mentioned earlier, showed little variation in the saline communities and from this study it can not be considered very important.

Adjustments to great variations in osmotic concentration of the soil solution must be made by the roots of species such as *S. depressa, Sesuvium verrucossum, Salicornia rubra* and *D. stricta* to allow them to survive. Some of these species as mentioned by Frey-Wyssling (1935) and Warming (1925) have special mechanisms which aid them. In the case of *Suaeda, Salicornia* and *Sesuvium* it is succulence, whereas, in *Distichlis* and some other grasses salts are excreted through specialized glands.

SUMMARY

1. The soil and water relations of the Big Salt Marsh, Stafford, Kansas have been described and discussed.
2. A complete description of the seasonal and zonal distribution of the marsh species of plants was worked out.
3. Quantitative studies of the marsh plant communities indicated density, basal area, and frequency relations within the various communities.
4. It was found that the principal factor affecting the qualitative and quantitative relations of distribution was soil salinity, but in the low and non-saline areas soil moisture played an important role.
5. The salt tolerance of marsh species has been indicated. This demonstrated that it was the upper limit of salinity that was most potent in species distribution.
6. Seed germination studies with three species, *Bromus japonicus, Haplopappus phyllocephalus* subsp. *annuus*, and *Suaeda depressa* indicated that the first two species behaved as glycophytes and the latter as a halophyte. All species were found to germinate in a wider range of salinity conditions than their distribution indicated.
7. The species which were found to have the greatest salt tolerance were *Suaeda depressa, Sesuvium verrucosum, Salicornia rubra,* and *Distichlis stricta.* The latter species was the most versatile on the marsh. Of the remaining, *S. depressa* was the most abundant on the open salt flat, *S. verrucosum* was widely scattered and only of local importance, and *S. rubra* was found in only one very localized area.

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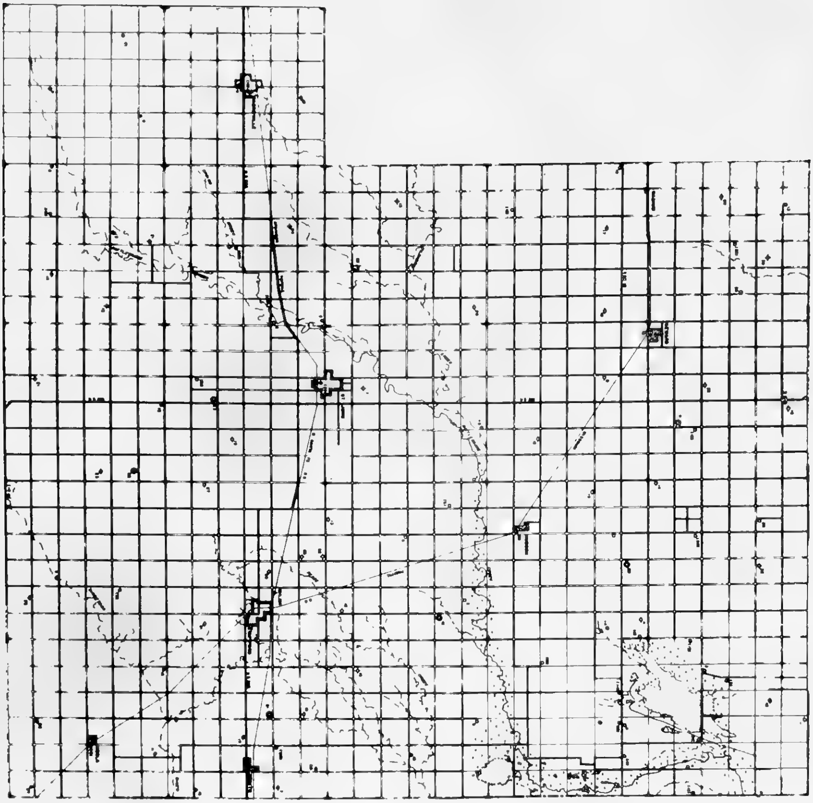

FIG. 1. Location of the study area in the northeastern corner of Stafford County. (State Geological Survey of Kansas Map). County is divided into sections which are a mile square.

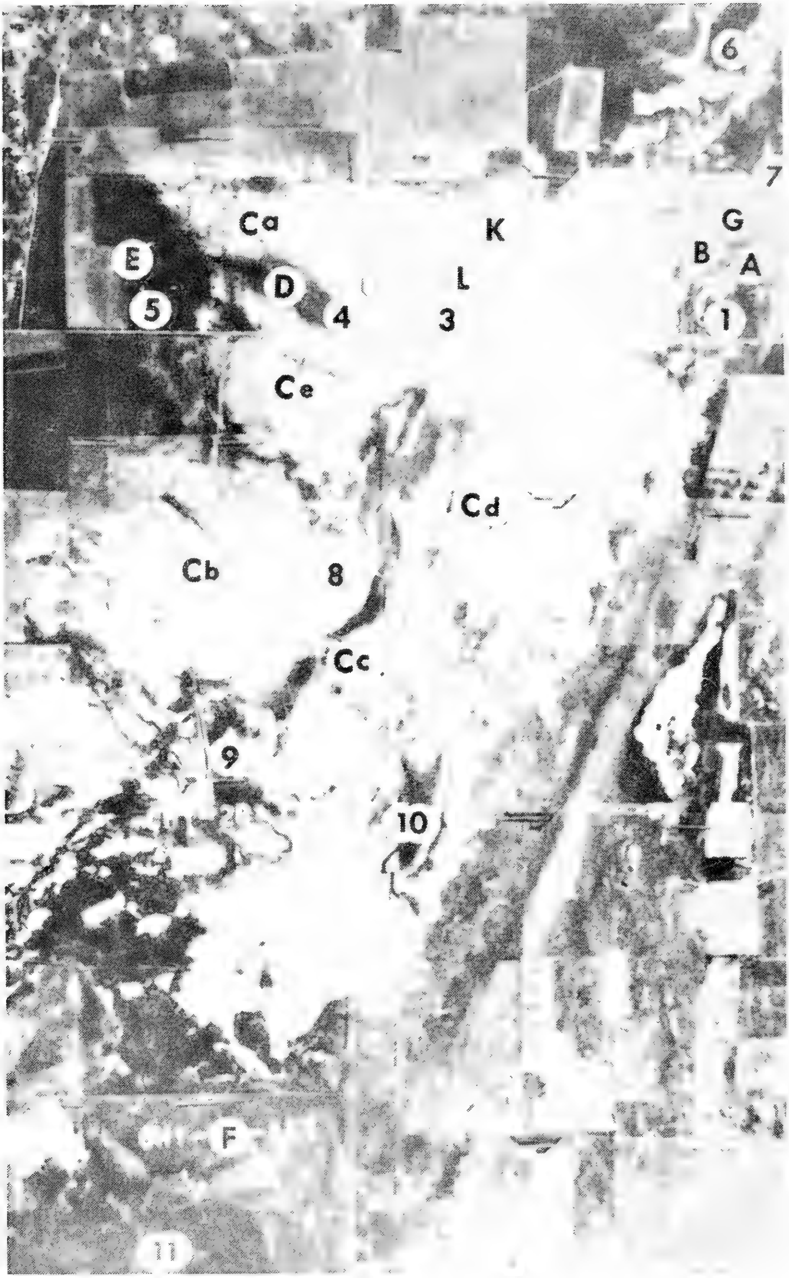

FIG. 2. Aerial photograph showing sites of quantitative vegetation sampling and water samples. 1-11 Water sample sites (see Table 2). A-L Vegetation sites (see Tables 8, 27, 28, 29, 30 and 31). (U.S. Dept. Agric. photograph). One mile—41 millimeters

FIG. 3. Tall *Distichlis stricta* community. This area has the highest basal cover on the marsh.

FIG. 4. *Scirpus paludosus-Distichlis stricta* community. The tall species in this figure is *S. paludosus.*

FIG. 5. Early summer view of the Sandhill Mixed Prairie Community. Tall grasses are beginning to develop.

FIG. 6. Saline area south of sandhills. Species present include *Hordeum jubatum, Distichlis stricta, Sporobolus pyramidatus* and *S. airoides.*

FIG. 7. Upright form of *Suaeda depressa* on the open salt flats. Light meter case is 11 cm. high.

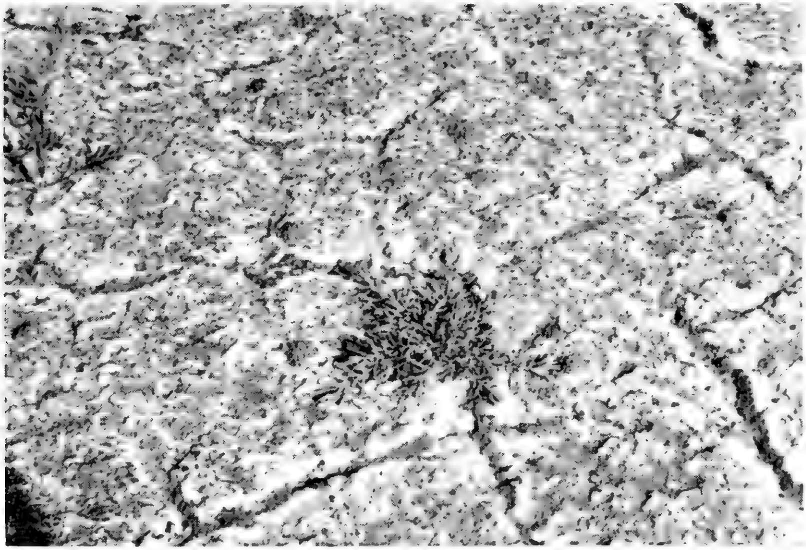

FIG. 8. Depressed form of *Suaeda depressa* on the open salt flats.

FIG. 9. *Distichlis stricta-Suaeda depressa* community. The cover is very low and the plants are dwarfed.

FIG. 10. This excavated section shows the rhizomatous growth habit of *Distichlis stricta.*

Fig. 11. *Tamarix gallica* is shown here invading a highly saline soil. The undergrowth is a dense cover of *Distichlis stricta*.

Fig. 12. *Spartina pectinata-Distichlis stricta* community.

FIG. 13. Spring aspect of the *Scirpus americanus-Eleocharis rostellata* community.

FIG. 14. Summer aspect of the *Scirpus americanus-Eleocharis rostellata* community. *Cicuta maculata* is the most characteristic plant of this period.

Fig. 15. Fresh Water seep community. Some of the more characteristic species of this summer aspect are *Typha latifolia*, *Sagittaria latifolia*, and *Scirpus validus*.

Fig. 16. A saline pond filled with a dense growth of *Chara* spp.

FIG. 17. Late spring aspect of parts of the Grazed Sandhill community. The most characteristic species in this area is *Monarda citriodora.*

FIG. 18. Early summer aspect of the Grazed Sandhill community. Flowering is *Argemone polyanthemos.* Other species in this vicinity are *Eriogonum annuum* and *Conyza canadensis,* but these are still in vegetative condition.

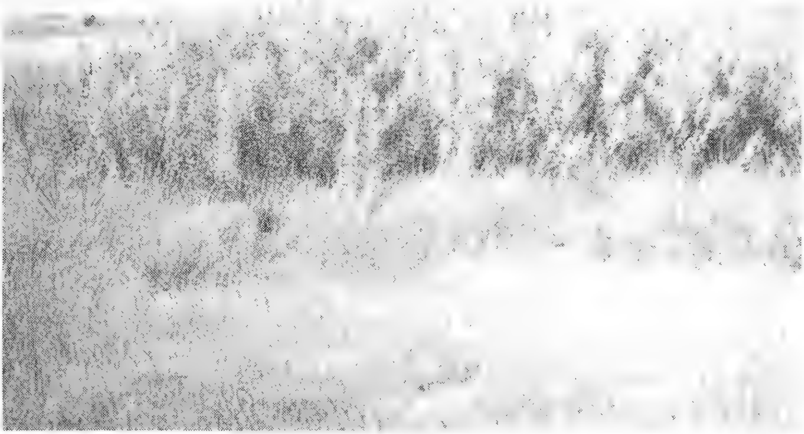

Fig. 19. A low hummock covered with a dense colony of *Baccharis salicina*.

Fig. 20. A *Sporobolus airoides* hummock on the open salt flat. The dense root and rhizome system of this species forms the raised area.

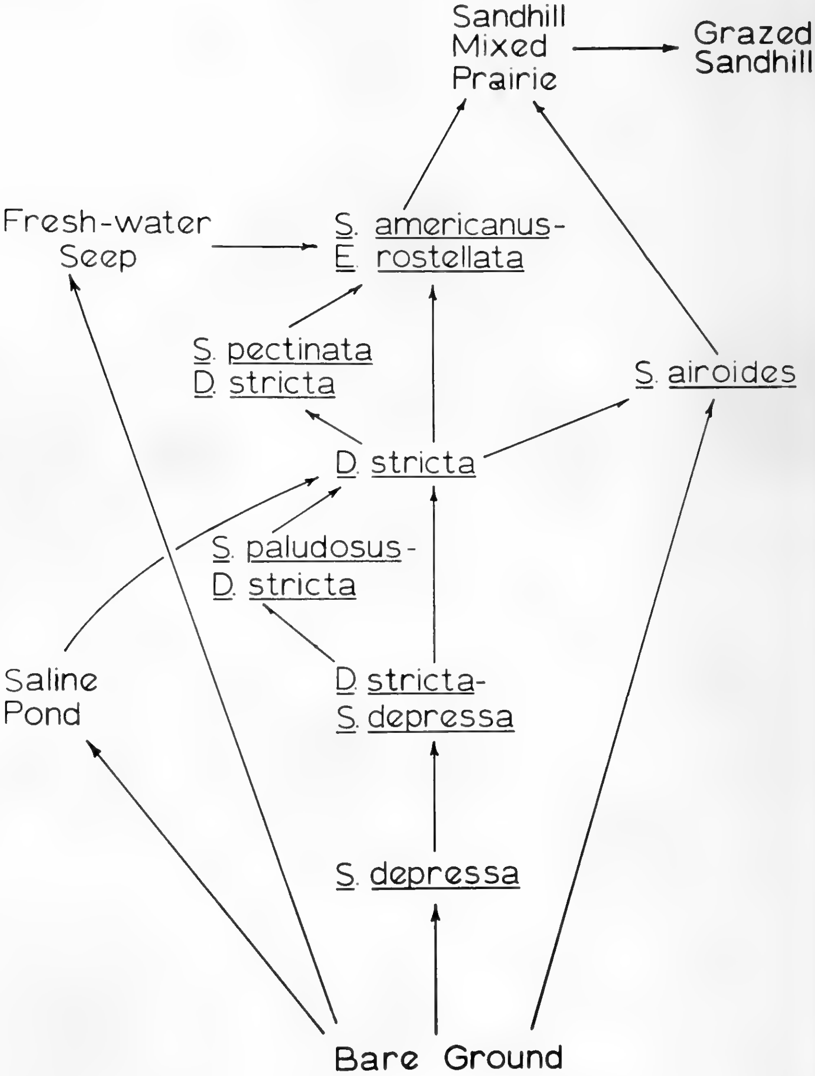

FIG. 21. A hypothetical scheme of the major successional trends on the Big Salt Marsh.

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FOSSORIAL ADAPTATIONS IN THE BANK SWALLOW, *RIPARIA RIPARIA* (LINNAEUS)

By

Abbott S. Gaunt

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Fossorial Adaptations in the Bank Swallow, *Riparia riparia* (Linnaeus)[1]

By

ABBOTT S. GAUNT[2]

ABSTRACT

The Bank Swallow is the only North American swallow that characteristically excavates a nesting cavity. This habit seemingly is incongruous with the delicate structure that swallows have evolved, partly as an adaptation to aerial foraging. Behavioral and morphological studies were made to determine what, if any, modifications for digging have evolved in Bank Swallows.

A key adaptation is behavior in burrowing. Unlike many burrowing birds, Bank Swallows do not excavate by thrusting a strong bill into the substrate in drill-like fashion, but instead they use a rapid, lateral slashing motion. This technique engenders torque around the long axis of the bill and around the midpoint of the frontonasal hinge.

Various proportions based on measurements of the Bank Swallow's skull were compared with similar proportions in skulls of six other species of North American swallows. The Bank Swallow's bill was shown to be smaller than bills of other swallows relative to cranial and sternal measurements, and more nearly circular in cross-section. The supports of the bill, though not enlarged, are functionally larger by virtue of the bill's small size. Length of the skull compared to dry weights of the five paired muscles that control digging motions showed that these muscles are about as massive as would be expected in a swallow the size of a Bank Swallow. Structure and placement of these muscles do not vary significantly among the swallows studied.

The small size and conical shape of the Bank Swallow's bill probably represent departure from the ancestral condition. Such changes confer the following advantages: (1) reduction of stress upon supports of the bill, (2) reduction of fractural stress, (3) creation of a structure capable of slashing into substrata in a variety of directions, and (4) slight increase in mechanical advantage. Seeming lack of change in either mass or structure of the muscles studied indicates that

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these are preadapted to a slashing mode of excavation; that is to say, the action of slashing is judged to require the same muscles as those used in feeding motions.

For the Bank Swallow, energy considerations alone demand that modifications of the bill or associated structures be such as to allow continued efficiency in feeding; such modifications meanwhile must also tend toward increasing efficiency in digging. Thus, these swallows, notably successful as burrowers, must either have evolved modifications that confer substantial gain in efficiency of digging with a minimum of change in the original structure, or they must have been preadapted to burrowing. The Bank Swallow shows both osteologic change and myologic preadaptation.

The Rough-winged Swallow also nests in burrows but is restricted to use of pre-existing burrows or natural cavities. It is capable of modifying these but seems not to be sufficiently effective in digging to justify the expenditure of energy required to excavate an entire burrow.

Swallows in general are faced with a paucity of suitable nesting sites. The use of burrows (probably beginning with use of burrows abandoned by other animals), seems to be an adaptation to increase the numbers of available nesting sites. The evolution of burrowing species is a consequence of this adaptation.

INTRODUCTION

The past two years have seen a blossoming of work in avian functional anatomy. In 1961, Bowman published his *opus magnus* on adaptations in the Galapagos finches. The year 1962 saw the publication of both Zusi's work on the head and neck of the Black Skimmer and the studies of Goodman and Fisher on the feeding apparatus in waterfowl. Taken together with Forbes' (1882) classic study on the neck of darters, Burt's (1930) studies of modifications in woodpeckers, and Beecher's work on American orioles, American blackbirds, and honey creepers (1950; 1951a; 1951b), these papers represent almost every possible approach to the field. Forbes' paper presents the simplest approach, analysis of the functional adaptation of a given structure, the Donitz bridge. The work of Zusi is an extension of Forbes' approach. Here the functional import of several structures is studied in relation to the highly specialized feeding behavior of the Black Skimmer. Burt studied the adaptations of a group in which all members are more-or-less specialized for the same ecologic role, that is, drilling into a solid substrate. Bowman's interest lay in the evolution of divergent adaptations within a small, closely related group. Goodman and Fisher undertook an analysis of adaptations for a general function within an extremely large group. Beecher's studies have a distinctly phylogenetic orientation.

This paper presents an approach differing from all of the above. I have attempted an analysis of adaptations pertinent to a specific, seemingly implausible, pattern of nesting behavior in a single species of a highly specialized group.

The diverse genera and species of the family Hirundinidae may be regarded as minor variations on a single morphological theme. They are all, without exception, highly specialized for feeding upon airborne arthropods. So stringent are the adaptive requirements for occupancy of this niche that the resemblance in external morphology of all the birds exploiting it is remarkable. The great degree of morphological similarity amongst the swallows and the taxonomic difficulties attendant thereto have been remarked by Mayr and Bond (1943). In their attempt to order the genera in this family, they were forced to rely on patterns of nest construction as much as, if not more than, on morphological characters.

Among the adaptations shared by airborne aerial feeders are long wings, short neck, short legs, relatively weak feet, large gape, and short, flat bill. None of these seems conspicuously well-suited to the task of burrowing. Yet, the trait of burrowing nesting cavities into soil has arisen independently in three genera of swallows: *Riparia* (4 species, 2 confined to Africa, 1 African and Asiatic, 1 African and Holarctic), *Pseudhirundo* (1 African species), and *Cheramoeca* (1 Australian species). In addition, it is probable that at least some of the species of *Psalidoprocne* (11 African species) dig their nesting burrows (Serle, 1950). It is evident that any fossorial modifications must have evolved within the rigid morphological restrictions set by aerial feeding. The advantages of maintaining light weight seemingly have precluded such possible adaptations as massive bills or feet. Therefore, the question of just what modifications may be developed presents an intriguing problem to the functional anatomist and student of evolution.

The fact that no extensive modifications are probable, if, indeed, possible, suggests that the digging swallows may have evolved behavioral techniques for the utilization of existing anatomical structures with little or no morphological modification. If so, then analysis of the situation might provide additional information about morphological preadaptation. The problem encountered with the Bank Swallow closely parallels the situation suggested for study by Davis (1949): "The most promising situation for detecting morphological preadaptation should be in a form or group of related forms showing some specialized habit or other environmental relation that would be reflected in its morphology. The generic or family levels are most likely. . . . A further requirement is that the adapted type belong to a taxonomic group large enough to exhibit a range of morphological variation, i.e., large enough that the basic morphological plan of the group as a whole can be determined. Finally, knowledge of the ecological relations of both the adapted type and its unadapted or differently adapted relatives must be sufficiently intimate to reveal the functional relations of the preadaptation." The last criterion is, perhaps, not met as well as might be wished. This failing is balanced by the fact that "the basic morphological plan" of the swallows is both obvious and restricted.

As an object of study in relation to the posed problem, the North American Bank Swallow, *Riparia riparia riparia*, presents a number of advantages. Its natural history has been intensively studied by a number of authors, and, consequently, considerable information about its digging habits is available; it is common in Kansas, thereby facilitating the collection both of study specimens and of additional data on digging; moreover, the Museum of Natural History at The University of Kansas possesses a good series of skeletons of *Riparia* and other North American swallows.

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FIELD STUDIES

The natural history and behavior of the temperate zone swallows have been generally well documented. Concerning the Bank Swallow, the observations of Petersen (1955), coupled with the voluminous and detailed work of Stoner (*esp.* 1936), could provide virtually all the field information requisite to the present study. In view of these extensive works, a detailed report of my field work would be redundant here, but a discussion of certain points is vital to the theme of this work.

The field work in connection with this study was undertaken with three objectives in view: (1) to gain a personal acquaintance with the behavior of the birds; (2) to corroborate observations of previous authors in the light of a different emphasis; (3) to compare the Bank Swallow with the Rough-winged Swallow *(Stelgidopteryx ruficollis)*. Observations were made in the springs and summers of 1960 to 1962.

Colonies Studied

Two nesting sites were studied, one along the banks of a sand pit, the other in a bank of the Kansas River. The former site provided nesting area for both *Riparia* and *Stelgidopteryx*; the latter was occupied primarily, if not exclusively, by *Riparia*.

The Holliday Sandpits comprise a roughly kidney-shaped pond, the north-west end of which is the site of sand dredging operations. The "hilus" of the pond is bordered by sand banks from one to eight feet high. All nests of *Riparia* and the majority of those of *Stelgidopteryx* were tunneled into these banks. The eastern and southern margins of the pond are partially composed of earthen banks. A few *Stelgidopteryx* nests were found there. This site provided nesting area for about 100 pairs of birds in the years 1960 and 1961. In 1962, it was largely destroyed by flooding and was abandoned by the birds.

Three and one-half miles east of Lawrence and about one and one-half miles southeast of the sand pits there is a long curve in the bed of the Kansas River. The south shore here is a sand bank about twelve feet high at normal spring and early summer river levels. Of this, about eight to ten feet are vertical and suitable for nesting. In the years 1959 to 1961, this bank afforded nesting sites for a Bank Swallow colony of about 100 to 300 pairs. In 1962, possibly as a result of the destruction of the sand pit site, two colonies were established at the river. Combined, these colonies included about 700 breeding pairs.

I observed Rough-winged Swallows at the river site several times, but none was ever found nesting there. However, it is possible that some nests were built in abandoned Bank Swallow burrows. On several occasions, birds flushed from the banks showed the flashing display of white under-tail coverts characteristic of *Stelgidopteryx*.

Burrows

The Bank Swallow and the Rough-winged Swallow are the only North American swallows that characteristically nest in burrows, although the habit is not uncommon in certain other hirundinids. Despite the similarity in physical appearance, the nesting habits of the two species differ markedly. There are few credible reports of North American Bank Swallows nesting in other than burrows of their own construction, although the European Sand Martin is reported by Rennie (*in* Burns, 1924) to nest in crevices, masonry, and tree cavities, by Henson and Johnson (1955) to occupy artificial burrows, and by Hickling (1959) to nest in drainage pipes. Stockard (1905) reports finding a Bank Swallow's nest in Mississippi that was "placed in a deserted Kingfisher's tunnel." Considering that the rough-wing is more common in Mississippi, the great similarity of the eggs of the two species, and the fact that the Bank Swallow is highly colonial, this may be a case of mistaken identity. Such is almost certainly the case of the bird reported by Hammond (Coues, 1876) as nesting behind a loosened weather board of a saw mill.

The Rough-winged Swallow is known to nest in a wide variety of sites. Lunk (1962) lists 11 categories of nesting sites used by this bird.

The question of whether or not the rough-wing digs its own hole has been open for many years. Opinions ranged from Dingle's (1942) flat affirmative ("Burrows, excavated . . . by the birds themselves, are the usual nesting sites of the roughwing.") to Allen's (1933) equally positive denial ("the Roughwings . . . never dig burrows."). In relatively few reports is there any indication that the author actually saw the birds dig. Bailey (1913) describes the "drilling of the hole, which is made by the birds using their feet to scratch with, and push the dirt backward out of the tunnel. Unlike the Kingfisher, their beak plays a secondary part in the drilling of their home." Burns (1924) also mentions that the rough-wing "is perhaps more apt to use its feet in scratching out the dirt" than the Bank Swallow. Eliot (1932) reported a pair which "began to excavate a hole . . . but gave up." The hollowing of decayed roots by the rough-wing is described by van Fleet (1876). Sutton and Pettingill (1942) rather ambiguously reported the beginning of "nest-digging." Weydemeyer (1933) bluntly stated, "I have observed them [rough-wings] digging burrows in banks of clay, of sand, and of gravel." Lunk (1962) recorded rough-wings "kicking out a few spurts of sand" from Bank Swallow holes. He then continues: "Otherwise, however, my evidence is entirely negative. The activity just described was quite out of the ordinary, and of a most desultory character. It appears that during my studies no Rough-wing nest, of nearly a hundred built in the area, was in a hole excavated by the birds themselves. Without exception, burrows were known, or could be presumed, to be unused or abandoned holes of other species. At certain times and places suitable holes were evidently at a premium—yet not even then did the Rough-wings exhibit the slightest tendency to do any burrowing for themselves. I have no evidence that they even deepened or enlarged any existing burrow before building."

Most authors seem to have assumed that any bird found nesting in a hole must have dug the hole. The majority of rough-wing nests I have observed were in evidently abandoned Bank Swallow burrows. I have never observed rough-wings digging, although two pairs nested in banks avoided by Bank

Swallows. While these tunnels may have been excavated by rough-wings, it is here assumed that some hole already existed. It is most probable that Bank Swallows had used these banks in previous years and for some reason, possibly texture of the substrate, had abandoned them. Also, slumping of these banks frequently exposed rodent burrows, and other holes were left by the falling of clay nodules that suffuse the area. Such holes might easily be adapted by rough-wings; Dawson (1923) remarked that the rough-wings "prefer some natural lead,—an old Kingfisher's burrow, a hole left by a rotten root or a fallen stone, or something of that sort." Tyler (1913) stated: "I believe that only in exceptional cases do the birds excavate their own nest cavity, as the hard formation of the [San Joaquin River] banks would seem to make such a task very difficult." Strangely, the burrows I observed that were most likely dug or modified by rough-wings were in harder, less sandy banks than those in which I have found Bank Swallows digging.

In summary, I concur with Lunk that it would be improvident to state that rough-wings never perform any extensive excavation of their own. However, the activity would appear to be unusual. For this reason the bird is treated as a non-burrowing swallow in later analyses.

There have been several attempts to distinguish between holes of *Riparia* and *Stelgidopteryx* by the shape of the entrance. In reality, there is no question that both species may use either round or elliptical entrances. In the event that the rough-wing has used a previously existing tunnel, the problem becomes meaningless. I have noticed, however, that *Riparia* burrows that were probably enlarged by *Stelgidopteryx* tended to be modified more extensively laterally than vertically. I will show that the rough-wing's bill and musculature are, if anything, more suited to lateral than to vertical excavation.

Two methods, neither completely satisfactory, were used by Dr. R. F. Johnston and myself to measure the depths of several hundred Bank Swallow burrows. The first method, simply digging them out, was usually employed when it was desirous to obtain data on clutch size. This method has the advantage of revealing which holes contain nests, but is tiring, slow, and necessitates an estimate rather than an accurate measurement of the depth. Moreover, it is occasionally impossible to dig out the deepest holes. The mean depth obtained by this method for 28 tunnels containing nests was 27.7 inches with a range of 15 to 48.

The second method involved the use of a calibrated aluminum rod. This method is fast, accurate, and permits measurement of both very deep and hard to reach holes. Unfortunately, it does not reveal which holes contain nests. Therefore, it was necessary to pick some minimum depth for purposes of calculating the mean depth. Stoner (1936) reported a minimum of 14 inches and Petersen (1955) a minimum of 16 inches for completed burrows in the colonies they studied. Cooper (1955) reported a Sand Martin burrow only 3.5 inches deep and with no entrance tunnel. He was "quite certain that the hole had not been interfered with by human beings." One wonders if a natural slump may not have been involved. I have observed swallows continuing to use nests the tunnels to which had been completely eliminated by minor slumping of the bank. The minimum depth that I have observed for an entire, completed burrow was 15 inches. As this depth is exactly intermediate between those reported by Stoner and Petersen, I chose it as the minimum depth for calculations. It is obvious, however, that many incomplete holes were measured, and the data, therefore, are biased toward shallowness. Using the rod technique, 122 tunnels yielded a mean of 27.2 inches and a range of 15 to 51 inches. Combining the measurements of all tunnels 15 inches or more in depth, including some that were dug out but did not contain nests, I found 161 burrows yielded a mean of 27.3 inches and a range of 15 to 51 inches.

EXCAVATION

The excavatory behavior of the Bank Swallow is central to the theme of this study. Most of the salient points have been suitably described by Stoner (1936) as follows:

> "When starting a burrow it appears that the birds first cling to some slight projection on the face of the bank from which they can reach the point of attack, either with the claws or bill or both. After a time a slight concavity is formed, its sides creased with the marks of claws and bill. As the work proceeds, the ceiling takes on a distinctly arched form, while the floor is practically flat.
>
> "Observations indicate that the more deeply scarred appearance of the inner or apical part of the cavity is due to the use of the bill. The bird clings to the walls and dislodges the particles of sand or gravel by pecking with a rapid side-to-side movement of the head. As soon as a shelf has resulted the feet with their long sharp claws are brought into action. Both bill and claws of captured individuals were sometimes caked with moist earth. In digging, the tail is frequently used as a support, as in woodpeckers."

He continues:

> "With the deepening of the excavation the dislodged materials fall to the floor of the shallow burrow whence they are ejected by frequent vigorous kicks accompanied by a kind of wriggling movement of the body. In this action the wings also are 'shuffled' rapidly in a backward and forward direction as well as from side to side, thus aiding in whipping the sand out behind the bird."

A number of important points are to be noted in this description. Paramount is the lateral motion of the bill. The Bank Swallow does not probe into the substrate in the manner of a woodpecker or kingfisher. Rather, the head is moved through a series of arcs to alternate sides. The resulting cavity, thus, is carved, rather than drilled. In suitable substrate, the roof of the tunnel and nesting cavity bears a scalloped design. In 1962, a rise in the level of the river undercut the bank below the colonies. The subsequent slumping neatly sectioned several completed cavities, clearly revealing the tell-tale slashing pattern. The same pattern may be seen in newly begun holes (Figs. 8, 9).

After the entrance to the tunnel has been formed, the beak becomes the major, if not the sole, instrument of digging. The feet may be used in excavation, especially in the lower portion of the tunnel; but, aided by the wings, they are more important in kicking the loosened sand out of the tunnel. In consequence, the swinging motion of the head prescribes an arched roof, while the wings and feet scrape out a floor that is usually flat or slightly concave. Sometimes the bird may kick so vigorously that twin grooves are cut into the floor. The entire process defines a tunnel that varies from almost round to elliptical in cross-section.

Although he mentions it elsewhere, Stoner (1925) says nothing in the above account to substantiate the fable that the Bank Swallow carries loosened sand from its burrow in its bill. To anyone who has seen the sand jet from the opening of a burrow, the relative inefficiency of the by-the-billful method is obvious. Perhaps, as Petersen suggested (1955), the legend may be attributed to observations of the birds picking up bits of sand, a habit in which they, as well as other swallows, frequently indulge. Petersen also mentioned that the bird has a predilection to pick up something upon leaving the burrow. If a fecal sack is not available, a grain of sand or small pebble may be picked up. This habit probably explains Stoner's earlier observations.

In contradistinction to the situation with the Bank Swallow, there is no detailed description of a rough-wing using its bill to dig. Rather, all mention the use of the feet, in the same manner as those of the Bank Swallow, to remove loose sand from the burrow. Whether the loose sand is of natural origin or a product of scratching or pecking is not clear. The best that can be found concerning the use of the bill are the remarks of Bailey and Burns cited previously. This is further evidence that the skull of the rough-wing is appropriately considered with the skulls of non-burrowing swallows.

Before leaving the subject of excavation, there is one more point to be considered. Hickling (1959) described a community digging display of the Sand Martin at the time of burrow-excavation. He described the birds circling and hovering in front of the cliff face in a "progressive series of 'movements' or elements building up to a climax. . . . The actual digging occurs only at this climax." He describes the communal nature of the display as follows:

"The communal nature of these displays is best seen if a well-defined group of holes is watched closely. At one display a group of birds—three or four commonly, but quite often five or six—may be seen to be active at one hole while neighbouring holes are left unattended. During the next display quite different holes may be used for excavation. Up to three birds often enter one hole to dig, and there may be other birds sitting at the entrance ready to take the place of those already in the hole. Again, birds may be watched moving from hole to hole, excavating at several in succession. Yet fighting and aggressive posturings are sporadic only, and seem to me to be accidental squabbling arising out of the jostling in a crowd, rather than strictly territorial defense."

Such an approach to the problem of community housing is, to say the least, unusual in swallows. The North American Bank Swallows appear to be clearly territorial, and their behavior in this respect has been well documented by Petersen (1955). He observed that "groups of several or a dozen or more birds move along the bank in hovering flight," but interpreted this behavior as a part of territory formation. Hickling's observations were of birds at a sand pit, and he remarked that "the behaviour described may not be typical of colonies of other kinds." He noted that Petersen's observations were made at river colonies. I have observed periodic or cyclic hovering similar to that described at both types of sites. I have not, however, observed any instance in which more than the members of a presumably mated pair were involved in excavating a given tunnel. Digging is performed also in the absence of any such "display." I have also witnessed Cliff Swallows hovering before Bank Swallow burrows in the described manner, both in the presence and absence of the owners. Such "displays" as I have observed appear to be hovering by birds that are strongly attracted to the holes but for some reason cannot or will not enter them. Among the Bank Swallows, many hovering birds may be unemployed members of mated pairs awaiting their turns to dig. Tooby (1947) suggested that hovering might be "an advertisement flight of the male Sand Martin." While the performance may serve some social function, I doubt that it has any direct sexual significance or that only males are involved. If the behavior described by Hickling is usual for English Sand Martins, then they would seem to be behaviorally distinct from their North American relatives. The English birds would seem to have evolved closer than the American members of the species to true community nesting.

OSTEOLOGY

Various osteological measurements were made from specimens of seven species: *Tachycineta thalassina* (20: 11 ♂♂, 5 ♀♀, 4 ?), *Iridoprocne bicolor* (26: 8 ♂♂, 17 ♀♀, 1 ?), *Riparia riparia* (16: 7 ♂♂, 9 ♀♀), *Stelgidopteryx ruficollis serripennis* (8: 3 ♂♂, 4 ♀♀, 1 ?), *Hirundo rustica*

(24: 12 ♂♂, 11 ♀♀, 1 ?), *Petrochelidon pyrrhonota* (33: 13 ♂♂, 17 ♀♀, 3 ?), and *Progne subis* (8: 3 ♂♂, 5 ♀♀). Three additional specimens, which were not suitable for measuring, were used for studies of the process of ossification in each of the three following species: *I. bicolor*, *H. rustica*, and *P. pyrrhonota.* Two specimens of *R. riparia* from New Mexico and two of *S. r. psammochrous* from Arizona were found to differ markedly in size from the specimens from Kansas. These, too, were used for studies of ossification, but were not included in the calculations.

Except for *Tachycineta*, the majority of specimens used for calculations were from Kansas. The exceptions are as follows: *Tachycineta*, 1 from Washington, 19 from New Mexico; *Riparia*, 1 from Colorado; *Hirundo*, 2 from Nebraska, 1 from Missouri, and 1 from New Mexico; *Petrochelidon*, 1 from California; and *Progne*, 1 from Missouri, 1 from Arizona. The Arizona specimen of *Progne* was from Pima County and may represent *P. s. hesperia.* However, the measurements of this specimen cannot be distinguished from those of *P. s. subis*, and it was treated as such.

CHARACTERS STUDIED

The following is a list of the characters studied and of the linear measurements used in the analysis with a brief definition of each (see Fig. 1 for detail).

Skull Length: from the tip of the bill to the most posterior point of the cranium (does not include the rhamphotheca).

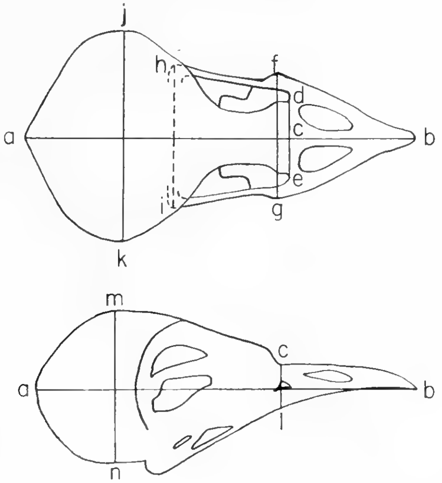

FIG. 1. Characters studied. Dorsal and lateral views of skull of *Riparia*, slightly diagrammatic. a-b, Skull Length; a-c, Cranial Length; c-b, Bill Length; d-e, Frontonasal Width; f-g, Maxillary Width; h-i, Interquadratic Width j-k, Cranial Width c-l, Bill Depth m-n, Cranial Depth.

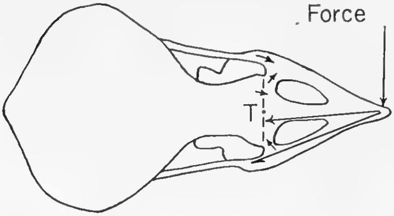

FIG. 2. Pattern of forces impinging on bill supports in *Riparia* when digging. Lateral force will create torque around midpoint of frontonasal hinge (T). Arrows indicate direction of net stress.

Bill Length: from the tip of the bill to a transverse line across the most anterior portion of the rostral border of the frontals (does not include the rhamphotheca).

Cranial Length: Skull Length less Bill Length.

Frontonasal Width: transverse distance across the frontonasal hinge.

Maxillary Width: greatest width between the external margins of the maxillaries. This measurement is approximately equal to the gape of the bird.

Interquadratic Width: greatest width between the external margins of the quadratojugals.

Cranial Width: greatest width of cranium not including the circumorbital ridge.

Bill Depth: from the top of the bill at the level of the frontonasal hinge to a transverse line across the bottom of the maxillaries.

Cranial Depth: from the highest point on the cranium to a median sagittal line along the parasphenoid rostrum.

Sternal Plate Length: in the midline from the anterior border of the dorsal lip of the coracoid sulcus to the posterior edge of the sternal plate.

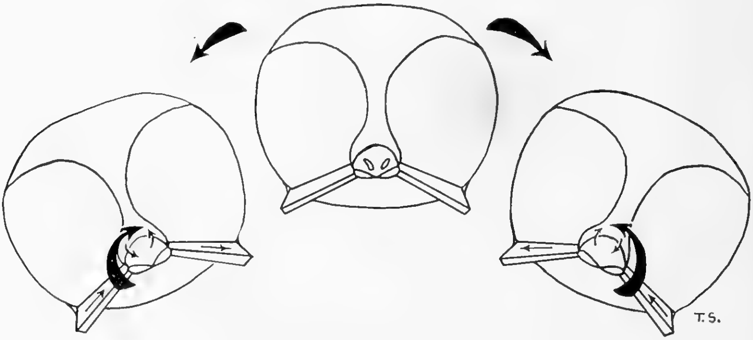

FIG. 3. Pattern of forces on bill of *Riparia* during slashing in an arc. Torque is created around Small arrows on lateral skulls indicate direction of stress and torque around midpoint of frontonasal hinge; large arrows direction of torque around long axis of bill.

Method

Before an analysis can be made, it is necessary to consider briefly the forces acting upon the skull of the Bank Swallow in the process of digging. Stress will result from the resistance of the substrate to the cutting edge of the bill in a direction opposite to that of the head's movement. Since the Bank Swallow excavates by carving, primarily with a lateral or dorso-lateral motion, the forces impinging upon the bill will contain a large lateral component. Vertical and posterior components are also present (Figs. 2, 3). Stresses resulting from digging will be directly upon the bill and the points of its attachment to the cranium. Therefore, if any modifications to resist stress are present, they should be found in one or more of three critical sites: (1) the bill itself; (2) the frontonasal hinge; and (3) the quadratojugal articulation.

Analysis of the skull must deal with proportions of one measurement relative to another, for it is obvious that linear measurements cannot be compared directly across generic lines. The use of proportions involves several risks. One is that both structures used for measurements may have been modified, which could obscure indications of those very modifications. Another is that the organism that is being used as a standard may itself be modified from the "basic morphological plan" of the group in one or more characters. Both these hazards may be avoided if one of the characters used as a basis for comparison is of a structure not likely to have been modified by selection for digging with the bill, and which, moreover, is likely to maintain proportional stability throughout the group. The discovery of such a character might well prove worthy of a study in its own right. However, one can choose certain characters that meet the first criterion and appear, *a priori*, to satisfy the second to a reasonable degree. The length of the sternal plate appears to be such a character. It is divorced from the influences pertinent to the skull and is not so likely to be influenced by differences in flight technique as is the depth or length of the keel. Another check is to look for consistency in the direction of the deviation. A character that consistently appears larger (or smaller) in comparison with a series of other characters, or in comparison with the same character in several species, is more likely to have been modified than one that deviates extensively but in only a few instances. Again, comparison with a series of species or genera is more likely to show a real deviation from "swallowness" than comparison with a single standard species or genus. Both these checks have been used in this study.

Proportions were compared directly by setting the mean proportion of measurements of two characters (*N.B.: not* the proportion of the means of two measurements) of *Riparia* equal to 100 and dividing this into the mean proportions of the same characters obtained in the other genera. The results are expressed as a percentage of the proportion obtained for *Riparia*.

Two sources of possible error have been introduced into this analysis as a consequence of lumping the data. All specimens of a given species were considered together, regardless of possible age or sex differences. The error introduced through differences in age is probably minimal. In all skulls used for measurements, the cranial sutures had completed fusion and there was extensive pneumatization of the cranial vault. Fusion of cranial sutures may be considered as the indication of termination of linear growth. Differences in the degree of pneumatization might well affect measurements of skull weight or volume, but have little significance in regard to linear measurements. In none of the species studied was there clear-cut sexual dimorphism so far as the features under consideration are concerned; in all instances there was extensive overlap in the range of measurements of both sexes. Females generally averaged somewhat smaller, but in most instances the difference was extremely slight and never approached statistical significance. Even in *Stelgidopteryx*, in which there is noticeable sexual dimorphism in a number of external measurements, the sample size at hand did not permit detection of any significant differences between the skulls of males and females. Indeed, in some measurements, the females averaged slightly larger. In view of this, it seemed permissible to lump all specimens in order to obtain larger samples. Considering the small size of some samples, the lumping may have, at worst, slightly increased the variance of the sample.

ANALYSIS

Bill.—Table 1 shows the relationship of the Bill Length to four other measurements of the skull and to the Sternal Plate Length. In four of the five comparisons, the mean proportions of measurements for *Riparia* are consistently equal to or smaller than those of the other species. The constant

TABLE 1. Percentage Comparisons of Bill Length.*

	$\frac{\text{Bill Length}}{\text{Cranial Length}}$	$\frac{\text{Bill Length}}{\text{Sternal Plate Length}}$	$\frac{\text{Bill Length}}{\text{Interquadratic Width}}$	$\frac{\text{Bill Length}}{\text{Frontonasal Width}}$	$\frac{\text{Bill Length}}{\text{Maxillary Width}}$
Tachycineta	103.7	102.9	104.5	113.0	107.9
Iridoprocne	105.9	98.7	102.5	112.1	105.5
Stelgidopteryx	106.5	102.6	105.2	100.0	96.8
Hirundo	121.8	117.7	113.0	124.2	98.6
Petrochelidon	103.5	102.4	101.2	98.6	94.1
Progne	140.1	121.5	116.7	112.5	105.9
Mean	113.6	107.6	107.2	110.1	101.5
Riparia	100.0	100.0	100.0	100.0	100.0

* In this table the figures presented represent a percentage of the mean proportion for *Riparia*. Except where noted, the measurement to be tested is used as the numerator, and percentages greater than 100 indicate that this measurement is smaller in *Riparia*.

TABLE 2. Percentage Comparisons of Bill Depth.*

	Bill Depth	Bill Depth	Bill Depth	Bill Depth	Bill Depth
	Cranial Depth	Sternal Plate Length	Frontonasal Width	Bill Length	Maxillary Width
Tachycineta	106.2	107.0	120.1	102.0	117.6
Iridoprocne	108.0	100.6	116.2	98.6	111.6
Stelgidopteryx	98.2	93.0	93.2	89.0	64.8
Hirundo	110.3	103.2	113.3	88.0	90.4
Petrochelidon	104.5	102.5	103.1	100.7	97.2
Progne	153.1	127.2	120.1	103.8	113.6
Mean	113.4	105.6	111.0	97.0	99.2
Riparia	100.0	100.0	100.0	100.0	100.0

* For explanation of figures see Table 1.

factor being the length of the bill, it may be concluded that, compared with the other species, the bill is relatively shorter in *Riparia*. The column in which *Riparia* is not consistently smaller is that comparing Bill Length with Maxillary Width, another measurement of the bill. Here the value obtained for *Riparia* is seen to be median in the series, with three of the other species being larger and three smaller.

If comparisons are now taken by species, we see that the greatest deviation from *Riparia* lies in comparison with *Hirundo* and *Progne*, two species with relatively long bills. Note that the discrepancy of *Riparia* with *Petrochelidon* lessens, and even changes direction in measurements involving width. The Cliff Swallow's skull is noticeably short and wide; this can be detected by simple visual comparison of the skull with that of any other species.

Table A-1 in the Appendix presents much the same information. In this table, the ratios, along with other data, are presented without conversion to

TABLE 3. Percentage Comparisons of Maxillary Width.*

	Cranial Width	Sternal Plate Length	Frontonasal Width	Bill Length	Bill Depth	Interquadratic Width
	Maxillary Width	Maxillary Width	Maxillary Width	Maxillary Width	Maxillary Width	Maxillary Width
Tachycineta	106.8	105.5	97.1	107.9	117.6	108.8
Iridoprocne	101.3	106.2	94.7	105.5	111.6	108.2
Stelgidopteryx ..	89.7	93.7	96.6	96.8	64.8	89.2
Hirundo	79.7	83.9	79.1	98.6	90.4	83.6
Petrochelidon ..	93.1	90.5	93.2	94.1	97.2	103.5
Progne	72.5	85.6	93.2	105.9	113.6	93.0
Mean	90.4	94.2	92.3	101.5	99.2	97.7
Riparia	100.0	100.0	100.0	100.0	100.0	100.0

* Note in this table that the measurement to be tested is used as the denominator. The figures still represent a percentage of the mean proportion for *Riparia*, but percentages greater than 100 indicate that Maxillary Width is larger in *Riparia*.

percentages of the value for *Riparia*. A similar table will be found in the Appendix for each of the textual tables.

Bill Depth at the level of the frontonasal hinge is considered in Table 2. Here it can be seen that the relative depth of the Bank Swallow's bill is consistently less than five of six species in three of five columns. *Stelgidopteryx* presents an outstanding exception, being considerably smaller than *Riparia* in all comparisons. Again, in those columns that do not show a consistent deviation, there is a comparison of two measurements of the bill. The relative flatness of the rough-wing's bill is probably significant and will be discussed later.

Table 3, in which Maxillary Widths are compared, can serve as a summary for all the tables concerned with characters of the bill. Maxillary Width has been used as the denominator rather than the numerator in this table, as

FIG. 4. Dorsal and lateral views of heads of *Riparia*, *Iridoprocne bicolor*, *Stelgidopteryx*, and *Hirundo*. Note the progressive widening and lengthening of bill in this series. Plumage patterns only suggested. Ca. life size.

well as in others. Thus, an increase in the value of the ratio signified either a *decrease* in Maxillary Width or an increase in the character used as the numerator. Therefore, a percentage of less than 100 indicates that Maxillary Width in that species is relatively greater than that of *Riparia*. As the situation in this table is the opposite of that in other tables, some care should be taken in the interpretation of these data.

In terms of Skull Width, Sternal Plate Length, and Frontonasal Width, Maxillary Width in *Riparia* is seen to be relatively smaller than in most other swallows. The pattern here, and in the preceding two tables, is clear. Whenever a character of the bill is compared with a non-bill character, the value of the proportion for *Riparia* is shown to be small. This relationship does not hold between any two characters of the bill. In such comparisons, the value for *Riparia* is found to be median within the range established for swallows. Thus, while maintaining its intrinsic proportions, the Bank Swallow's bill as a unit is relatively the smallest of those studied.

The tendency toward small bill-size in *Riparia* is least conspicuous in the first two columns of Table 3. Here two species, the Violet-green Swallow and the Tree Swallow, are seen to have values smaller than that of the Bank Swallow. The relatively small values obtained for *Tachycineta* and *Iridoprocne* may be the result of modifications of Maxillary Width and/or Skull Width and Sternal Plate Length in these species. It is also possible that this character is relatively less modified in *Riparia* than other characters of the bill. The bill of the Bank Swallow begins to widen at approximately the level of the frontonasal hinge. At the level of Interquadratic Width, the widening is sufficient to eliminate a clear pattern of exceptionally small size.

Analysis of the data presented in the above tables conveys little indication as to the over-all shape of the bill. The Bank Swallow's bill (Fig. 4) tends to be more nearly circular in cross-section, especially craniad, than the bills of

Table 4. Percentage Comparisons of Frontonasal Width.*

	Frontonasal Width	Frontonasal Width	Frontonasal Width	Frontonasal Width	Bill Length	Bill Depth
	Sternal Plate Length	Cranial Width	Cranial Length	Maxillary Width	Frontonasal Width	Frontonasal Width
Tachycineta	92.4	92.5	91.2	97.1	113.0	120.1
Iridoprocne	88.7	94.0	93.8	94.7	112.1	116.2
Stelgidopteryx ..	102.8	107.8	105.5	96.6	100.0	93.2
Hirundo	94.0	100.0	96.7	79.1	124.2	113.3
Petrochelidon ..	102.5	100.6	101.8	93.2	98.6	103.1
Progne	108.8	117.2	123.4	93.2	112.5	120.1
Mean	98.2	102.0	102.1	92.3	110.1	111.0
Riparia	100.0	100.0	100.0	100.0	100.0	100.0

* Note that in this table the measurement to be tested is used as the numerator in the first four columns, but as the denominator in the last two columns.

TABLE 5. Percentage Comparisons of Interquadratic Width.

	Interquadratic Width / Cranial Width	Interquadratic Width / Sternal Plate Length	Interquadratic Width / Skull Length	Interquadratic Width / Cranial Length	Interquadratic Width / Maxillary Width
Tachycineta	99.4	102.6	100.0	100.0	108.8
Iridoprocne	103.4	101.1	102.0	105.0	108.2
Stelgidopteryx	98.1	92.6	93.6	96.4	89.2
Hirundo	101.9	99.2	92.9	100.2	83.6
Petrochelidon	107.6	113.6	109.4	111.0	103.5
Progne	112.7	108.4	105.9	121.1	93.0
Mean	103.9	102.9	100.6	105.6	97.7
Riparia	100.0	100.0	100.0	100.0	100.0

Iridoprocne, *Stelgidopteryx*, and *Hirundo*. The difference in shape is least noticeable between *Riparia* and *Iridoprocne*, which, as noted, also has a relatively narrow gape. In both of these birds, the apparent rounding of the bill can be attributed to a relatively small flare in its proximal portion.

Frontonasal Hinge.—Table 4 presents much the same kind of information as Table 3. When compared with Sternal Plate Length or with other cranial characters, Frontonasal Width shows no tendency to deviate in any consistent manner. When compared with measurements of the bill, however, Frontonasal Width is consistently large (note that in the last two columns Frontonasal Width is the denominator). Thus, while the Bank Swallow's frontonasal hinge is no wider than would be expected in a swallow of that size, it is effectively larger in relation to the size of the bill than it is in other species.

Quadrates.—The Interquadratic Width represents a character that forms a bridge between measurements of the bill and of the cranium. This measurement tends to be relatively small in *Riparia* (Table 5). However, the tendency is not as distinct either in magnitude or in consistency as it is in other measurements of the bill. The tendency may not even be as strong as it appears. Cranial Width and Cranial Length in *Riparia* are relatively large (Table 6). Thus, the values in columns 1 and 4 of Table 5 may not be truly representative of the Interquadratic Width. Smaller values for Cranial Width and Cranial Length would increase the value of the ratios for *Riparia*, thereby lowering all the values in columns 1 and 4. It is, therefore, probable that Interquadratic Width for *Riparia* is small, but not exceptionally so for a species of its dimensions.

Miscellaneous characters.—Table 6 presents comparisons of Cranial Width, Cranial Length, and Skull Length. The data indicate that the skull of *Riparia*, including Bill Length, is about as long as would be expected, but that the cranium is wider than all but that of *Petrochelidon*, and tends to be somewhat elongate.

Cranial Width was used as a basis of comparison in Tables 3, 4, and 5. Its effect upon the last of these has already been discussed. The effect of narrower Cranial Width in column 1 of Table 3 would be to give a low value for the ratio found in *Riparia*, thereby emphasizing the apparent large size of *Tachycineta* and *Iridoprocne*, but bringing all other values more in line with those of columns 2 and 3. No change in interpretation is necessary. In column 2 of Table 4, the value for *Riparia* would be higher, and all percentages, consequently, lower. This would probably change the "sign" of the value for *Petrochelidon* and would make *Hirundo* somewhat smaller than, rather than exactly equal to, *Riparia*. Considering the small sample size for *Riparia* (13) in this comparison, and the fact that the standard error of the mean for *Riparia* (.032) is 16 times as great as that of *Hirundo* and eight times as great as that of *Petrochelidon*, I do not believe that any change in interpretation is necessary. The differences between these three species, in regard to this proportion, are extremely small (Table A-4).

Weights.—I have presented no data concerning comparative weights of the skulls of the seven species. Such data as are available are crude and subject to considerable error. They do indicate that, relatively, the skull of *Riparia* is among the more massive of swallows' skulls. Increased mass would be useful in the absorption of either sudden shock or continuous pressure. It must be remembered, however, that the avian skull completes its ossification rather slowly, owing to the process of pneumatization. Skulls at the Museum of Natural History indicate that the process is not wholly completed in swallows until midway through the second (first breeding) season. It is hardly probable that ossification of the sternum, which must withstand stress as soon as the birds begin to fly, is equally delayed. This introduces an age factor for which it is difficult to compensate. Moreover, slight damage to the skull, often unnoticed, can cause rather considerable change in the

TABLE 6. Miscellaneous Percentage Comparisons.

	Cranial Width / Sternal Plate Length	Skull Length / Sternal Plate Length	Cranial Length / Sternal Plate Length
Tachycineta	99.8	101.8	100.5
Iridoprocne	94.6	96.1	94.0
Stelgidopteryx	94.6	99.4	97.0
Hirundo	94.2	104.3	96.8
Petrochelidon	102.3	100.8	100.1
Progne	84.4	99.1	87.4
Mean	95.0	100.2	96.0
Riparia	100.0	100.0	100.0

weight. To have any real value, comparisons would have to be made among large series of skulls of equal degrees of pneumatization.

MYOLOGY

Myological studies were made of at least one specimen of eight species: *Tachycineta thalassina* (3 examined, only 1 suitable for dissection and weighing), *Iridoprocne albilinea* (2 dissected, both weighed), *I. bicolor* (2 dissected, both weighed, but Skull Length available for only 1), *Riparia riparia* (12 dissected, 9 weighed), *Stelgidopteryx ruficollis* (9 dissected and weighed), *Hirundo rustica* (6 dissected and weighed), *Petrochelidon pyrrhonota* (11 dissected and weighed), and *Progne subis* (8 dissected, 5 weighed). Greatest attention was given to five paired muscles: M. cucullaris, M. biventer cervicis, M. splenius capitis, M. rectus capitis lateralis, and M. rectus capitis ventralis. For reasons to be discussed below, the M. cucullaris and M. rectus capitis lateralis were treated as a single unit. These five pairs of muscles offer two advantages to the investigator. First, they are all large enough to be dissected free with reasonable assurance that the entire muscle has been obtained. Second, they are all involved in motions of the head that are critical to any digging movements.

METHOD

Each pair of muscles was dissected free as cleanly and completely as possible and stored in 70% alcohol in individual, labelled, two-dram vials. Upon

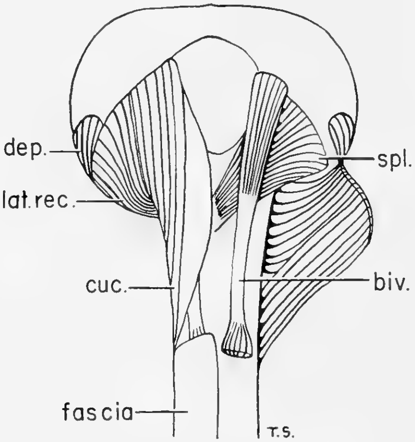

FIG. 5. Dorsal view of cervical musculature inserting on skull in *Riparia*. Skull tipped ventrad, muscles extended. Superficial muscles shown on left, dissected away on right. Biventer cervicis shown cut across anterior portion of second belly. Geniohyoidious removed. biv., biventer cervicis; cuc., cucullaris; dep., mandibular depressor, lat. rec., lateral rectus; spl., splenius cervicis. Ca. 3×.

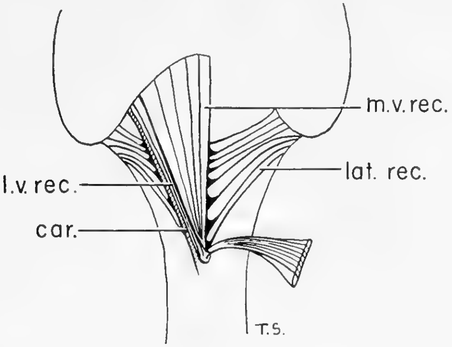

Fig. 6. Ventral view of cervical musculature inserting on skull in *Riparia*. Ventral rectus dissected always on right. car., carotid artery; l. v. rec., lateral portion of ventral rectus; m. v. rec., medial portion of ventral rectus. Other abbreviations as in Fig. 5. Ca. 3×.

completion of all dissections, the muscles were transferred for 1 week to a 1:1 mixture of methanol and ether at 7° C in order to reduce fat content. The mixture was then poured off and the muscles dried at 124° C for 24 hours. Each pair was then weighed on a Mettler model H-16 scale, weighing to 0.05 milligram and allowing a reasonably accurate estimate to 0.01 milligram.

The actions described for each muscle were determined from the morphology of the muscles and not from observations on living birds. It is entirely possible that the muscles may have slightly different actions under the influence of differential nerve impulses. Also, the action of a muscle may be modified in different ways when it acts in concert with various combinations of other muscles. Figures 5, 6, and 7 of *Riparia* may be used for reference.

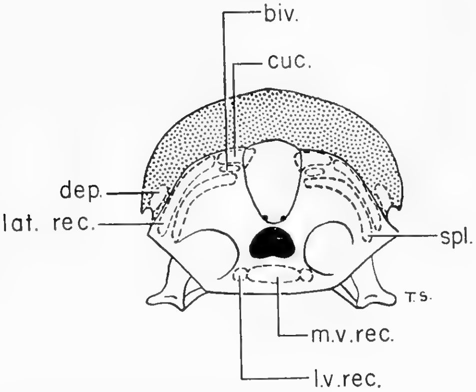

Fig. 7. Insertions of cervical musculature on skull in *Riparia*. Somewhat diagrammatic. Abbreviations as in Figs. 5 and 6. Ca. 4×.

DESCRIPTION OF MUSCLES

M. CUCULLARIS, caput portion

Origin: This muscle originates as fleshy fibers from the diapophyses of the fourth cervical vertebra. There is also extensive fascial involvement with other muscles in this area.

Insertion: Attachment is fleshy or by a very short aponeurosis across the dorsal edge of the occipital. Insertion begins at or near the midline and extends directly laterad or dorsad, then laterad, to the insertion of the M. rectus capitis lateralis, approximately one-half to one-third the distance from the midline to the median edge of M. depressor mandibulae. There is extensive fascial connection across the midline, especially in the most cephalad portion, between the two Mm. cucullarii.

Structure: The belly is broad, flat, and thin. The fibers diverge slightly from the origin, then remain parallel throughout the greater portion of the belly.

Action: Contraction of both members of this pair tilts the head upwards. Contraction of either unit singly also swings the head slightly to the side contracted.

Variation: The insertion of the M. cucullaris shows some variation. The insertions of the Mm. splenii capiti and Mm. biventer cervici fit into depressions on either side of the midline. The median portion of the occiput, therefore, appears as an inverted, tear-shaped bulge. In *Progne* and *Hirundo*, the insertions of the Mm. cucullarii extend across the bulge to meet, or nearly meet, at the midline. Before dissection, therefore, the insertion appears continuous and flush with the back of the skull. In *Iridoprocne*, the insertion appears to be continuous but lower on the occiput. In *Riparia*, and to a lesser extent in *Stelgidopteryx*, the two muscles insert beside the bulge and do not extend across it to the midline.

Remarks: Avian cervical musculature historically has been plagued with a plethora of names. Fortunately, a considerable degree of uniformity is found in most recent publications. Two names are in common usage for the muscle just described. I have followed the lead of Fisher and Goodman (1955) and Fisher (1958, 1961, 1962) in the use of M. cucullaris. It should be noted, however, that M. complexus is equally acceptable (Zusi, 1962).

M. RECTUS CAPITIS LATERALIS

Origin: This muscle arises from the hypopophyses of the second, third, and fourth cervical vertebrae. The attachment is aponeurotic or by numerous, short tendons.

Insertion: Attachment is fleshy or by a very short aponeurosis. The insertion begins at the lateral edge of the insertion of M. cucullaris, runs laterad to the medial border of M. depressor mandibulae, then turns ventrad to run along or just under the margin of the depressor as far as the exoccipital process. The lateral border of the insertion lies just above the insertion of M. splenius capitis.

Structure: The fibers are essentially parallel. The body of the muscle is broad and flat. The upper one-half to one-third of the muscle is closely associated with the M. cucullaris. At the point of insertion, the association is extremely intimate, and, in many specimens, the two muscles can be distinguished only with great difficulty.

Action: Contraction of both members of the pair tilts the head upward. Action of a single member will turn the head laterally and cause some dorso-ventral rotation of the head.

Variation: No significant variation was noted.

Remarks: According to Fisher and Goodman (1955:13 and Fig. 4, p. 16), the insertion of the lateral rectus in *Grus americana* is by a tendon to the exoccipital process and remote from the cucullaris. Burt (1930:515, Fig. 28) shows the lateral rectus extending well out onto the occiput of the Pileated Woodpecker. However, the arrangement of the other muscles that insert in the area is so different from the arrangement in passerines that the entire situation is questionably comparable. Boas (1929) describes the lateral rectus inserting lateral to the cucullaris on the exoccipital ridge in *Larus*, *Tetrao*, and *Anser*. His Plate 10 depicts a dorso-ventral orientation for the insertion with no lateral extension onto the occiput. Zusi (1962:76, Fig. 35; 86) figures and describes a similar insertion in *Thalasseus maximus*, *Geohelidon nilotica*, *Larus atricilla*, and *Rynchops nigra*. Schufeldt (1890:19, Fig. 4) shows the insertion of the rectus lateralis in *Corvus corax* meeting the edge of the cucullaris, but not extending onto the dorsal portion of the occiput. Palmgren (1949) describes the insertion in the seven species he studied (*Acrocephalus schoenobaenus*, *Carduelis flammea*, *Certhia familiaris*, *Parus atricapillus*, *Phoenicurus phoenicurus*, *Pyrrhula pyrrhula*, and *Regulus regulus*) as running from the insertion of the biventer to the neighborhood of the temporo-maxillary joint. His Figs. 1 to 4 show an insertion like that in the Raven for *Phoenicurus*, *Certhia*, and *Parus* but well out on the dorsal occipital ridge in *Carduelis*. It therefore appears that in some of the passerines, and perhaps the woodpeckers, the insertion of the lateral rectus has moved dorsad and laterad, perhaps assuming some of the function of the cucullaris and certainly increasing its ability to rotate the head.

M. BIVENTER CERVICIS

Origin: This muscle originates as a tendon arising from the neighborhood of the neural crest of the 14th (second thoracic) vertebra. The actual attachment is to the tendon of the M. spinalis cervicis.

Insertion: Fleshy fibers attach to the occipital directly beneath the insertion of the M. cucullaris.

Structure: This muscle is composed of two bellies connected by a tendon. The anterior belly extends from the insertion to the neighborhood of the fourth vertebra, approximately on a line with the posterior portion of the origin of the cucullaris. The posterior belly begins in the vicinity of the ninth vertebra and extends to the 13th vertebra. The fibers are parallel except for some pennateness in the regions of the tendons.

Action: Contraction of this muscle tilts the head upwards and draws the anterior portion of the neck toward the thorax. The posterior half of the central tendon and all of the posterior belly are covered by a thick fascia that acts as a pulley. Thus, the pull of the biventer is along the curve of the neck rather than directly back toward the thorax.

Variation: No significant variation was noted.

M. SPLENIUS CAPITIS

Origin: Fleshy fibers arise from the dorsal and lateral surfaces of the neural crest of the axis.

Insertion: The insertion is broad and fleshy, extending from the occipital bulge laterad beneath the insertions of M. biventer cervicis and M. rectus capitis lateralis to beneath the exoccipital process at the basitemporal process.

Structure: This muscle forms an almost perfect fan across the entire occipital area. The fibers diverge from the origin, but are never bipinnate.

Action: Again, combined action of both members of the pair results in a backward tilting of the head. It is probable that this is the lesser function. Action of a single member of the pair swings the head to the side.

Variation: No significant variation was noted.

M. RECTUS CAPITIS VENTRALIS

This muscle is conveniently divided into lateral and medial portions and should, perhaps, be considered as a complex. The dividing line approximates the line of the right and left dorsal carotid arteries except at the insertion, where the median portion spreads laterad. The relation between the two portions is only slightly more intimate than that between the dorsal portions of the cucullaris and lateral rectus.

Origin: The origin of the median belly is partially fleshy, partially tendinous. It arises in three heads from the hypopophyses of the axis, atlas, and third vertebra. The lateral belly arises by a short tendon from the hypopophysis of the fourth and sometimes fifth vertebra. The origins of all but the most anterior head of the medial portion are closely associated with the origin of M. rectus capitis lateralis.

Insertion: The median portion inserts fleshily over most of the area of the basitemporal plate. The anterior portion of the insertion forms an arc along the anterior and lateral borders of the basitemporal plate. The lateral portion inserts fleshily at the extreme latero-anterior corner of the arch formed by the median portion.

Structure: The fibers are rather loosely-associated, and the muscle tends to crumble readily. The fibers of the medial portion diverge from the points of origin, but are not bipinnate. The fibers of the lateral portion are essentially parallel except at the point of origin, where they converge to form the tendon.

Action: The medial portion of this muscle serves to tilt the head downward. The lateral portion serves this function also, but, in addition, can swing the head to the side if contracted singly.

Variation: Fisher and Goodman (1955:14 and Fig. 7, p. 22) describe the rectus ventralis as an asymmetrical muscle, with the left side extending farther caudad than the right. They attribute the asymmetry to the change in position of the trachea and pharynx. The situation in the swallows is somewhat ambiguous. There is no apparent difference amongst the species studied in the medial portion. The origins of the lateral portion seem to vary at the level of the individual. For those specimens inspected for asymmetry, the results are:

I. albilinea: left equal in both;
I. bicolor: left longer in one;
Stelgidopteryx: left longer in four, equal in one;
Riparia: left longer in three, equal in four;
Hirundo: left longer in one, equal in two;
Petrochelidon: left longer in two, equal in five; and
Progne: left equal in three.

In many cases in which the left was equal to the right, it appeared more robust. In most cases in which the left was longer, it originated from the fifth vertebra.

The area of insertion of the medial portion appears to be smaller in *I. bicolor*. In both specimens, it was confined to the area between the branches of the dorsal carotid arteries.

ANALYSIS

In analysing the relative size of muscles, it is necessary to find a measurement that will reflect expansion into three dimensions. Volume is, perhaps, the best measurement, but determining the volume of very small, irregularly shaped, absorbent structures presents rather complex technical problems, especially when a large portion of the volume to be measured consists of diffusible fluids. Weight appears to be the next best choice of measurement to document relative size. The major portion of the weight of a muscle consists of fluid, much of which is extracellular. Since the amount of fluid is quite variable, even from time to time in one muscle, it is necessary to eliminate this variable by thorough drying before weighing. Because weight varies as the cube of linear measurements, the cube root is used in comparisons of the weights with a linear measurement.

Note also that the mass (=weight) of a muscle represents only a crude approximation of its strength. Mass can be used as an index of strength only if there is little difference in the size and shape of the muscles compared. It has already been shown that there is little difference in the shapes of muscles in the species studied. The differences in mass also are small. The mean of the mass of any muscle in *Progne*, the largest species, is approximately five times the mean for the smallest species. In no other swallow is the mean mass for any muscle as much as twice as large as the mean for the smallest species.

Skull Length was chosen as the non-muscular measurement for use in comparisons. This character has been shown (Table 7) not to deviate proportionally in *Riparia*. It reflects, to some extent, the mass to be moved by the muscles studied and is easily measured on a partially dissected specimen. Unfortunately, when taking the measurement from alcoholic specimens, the rhamphotheca must be included. I have only one *Riparia* and no *Stelgidopteryx* skulls from Kansas with the rhamphotheca intact. Proportions based on the one *Riparia* skull indicate no change in direction from the proportions of the skulls without rhamphothecae.

Table 7 presents the myological data in the same manner in which the osteological data previously were presented. The data for *Tachycineta* and *I. bicolor* in Table 7 are from one specimen each. The Violet-green Swallow was mature. The Tree Swallow was probably a first-year bird. The data

TABLE 7. Comparisons of Cube Roots of Muscle Weights With Skull Lengths.

	Ventral Rectus / Skull Length	CLR-Complex / Skull Length	Splenius / Skull Length	Biventer / Skull Length	Total Mass / Skull Length
Tachycineta	98.2	94.6	97.0	98.1	97.0
I. albilinea	101.8	97.3	100.0	103.7	100.0
I. bicolor	94.5	90.5	93.9	103.7	95.0
Stelgidopteryx	94.5	91.9	100.0	98.1	96.0
Hirundo	94.5	94.6	100.0	100.0	98.0
Petrochelidon	107.3	104.0	103.0	103.7	105.1
Progne	112.7	108.1	107.6	109.2	109.8
Mean	100.5	97.3	100.2	102.4	100.1
Riparia	100.0	100.0	100.0	100.0	100.0

TABLE 8. Summary of Critical Proportions.

	Bill Length / Cranial Length	Bill Length / Interquadratic Width	Bill Length / Frontonasal Width	Bill Depth / Cranial Depth	Frontonasal Width / Maxillary Width
Tachycineta	103.7	104.5	113.0	106.2	97.1
Iridoprocne	105.9	102.5	112.1	108.0	94.7
Stelgidopteryx	106.5	105.2	100.0	98.2	96.6
Hirundo	121.8	113.0	124.2	110.3	79.1
Petrochelidon	103.5	101.2	98.6	104.5	93.2
Progne	140.1	116.7	112.5	153.1	93.2
Mean	113.6	107.2	110.1	113.4	92.3
Riparia	100.0	100.0	100.0	100.0	100.0

pertaining to these two birds differ markedly from those for the other swallows only in relation to M. splenius capitis, for which they appear somewhat small.

One of the intriguing aspects of the myological data, as seen in Table 7, is the absence of any clear pattern beyond the fact that both *Petrochelidon* and *Progne* are more heavily muscled than *Riparia*. There seems to be considerable variation in the proportions of the muscles relative both to Skull Length and to each other. This is especially true for *Stelgidopteryx*, *Hirundo*, *Petrochelidon*, and *Progne*, for which the samples are largest.

Although there is no over-all pattern, some pertinent facts are revealed by examination of individual columns. Perhaps most significant are the comparisons involving the total muscle mass. It appears that *Riparia* possesses cranial musculature that, although it approaches the limits of range of the muscle to skull length ratio for swallows, is not exceptionally large. Assuming that the first three values in this column do represent the species to a reasonable degree, then the total muscle mass for *Riparia* is relatively larger than four, smaller than two, and about equal to one of the other species. The data for the ventral rectus show about the same situation. The biventer appears to be somewhat small. There is apparently very little difference between the relative size of the splenius capitis in *Riparia* and the other swallows. The cucullaris-lateral rectus complex appears to be relatively large in *Riparia*, for it is comparatively larger than those of five of the seven other species, and in comparison with *Progne* it is the second largest muscle.

DISCUSSION

OSTEOLOGY

The most apparent fossorial modifications of the Bank Swallow are found in the structure of its bill. This structure, as a unit, is clearly smaller than the bills of other swallows relative to the size of the cranium and Sternal Plate Length. Those proportions that most clearly show this relationship are summarized in Table 8. Also, with the rhamphotheca in place, the Bank Swallow's bill is more conical than those of most other swallows (Fig. 4). As in other swallows, the bill of *Riparia* tapers to a slightly hooked point at the tip, but flares less proximally. Thus, in the intact bird, it appears to be more centrally placed relative to the shape of the head than in other swallows and resembles a short awl or nail projecting from the skull.

The shortening and reshaping of the bill confer a number of advantages. In the order of their probable importance, these are:

1. Reduction of tension and compression stress upon the supports of the bill, especially the frontonasal hinge;
2. Reduction of shearing stress across the bill;
3. Creation of a structure capable either of probing or of scratching in several directions with almost equal facility; and
4. A slight increase in mechanical advantage.

In the kinetic avian skull, the frontonasal hinge, as a flexible joint of thin bone, must be considered a primary weak spot. This is especially true in those cases in which strong forces must be transmitted through the joint from the bill to the cranium, or *vice versa*. In most avian activities, pressure through the hinge into the skull is directed either posteriorly from the tip of the bill (pecking) or dorsally from the tomial edges (biting). The digging motions of the Bank Swallow exert lateral, dorso-lateral, and postero-lateral pressures on the frontonasal hinge (Figs. 2, 3). For all practical purposes, the applied force may be considered the same as those applied to the tomium in biting, that is, at an angle to the axis of the bill—with three critical exceptions. First, the lateral orientation of the applied force exerts a tearing or shearing action along the axis of the hinge. Second, both the bill and hinge are relatively inflexible in a lateral direction. Third, often in the process of digging, the bill is subjected to forces tending to rotate it around its longitudinal axis as well as around the hinge or any point in the hinge.

In digging, the bill forms a portion of a lever system. The "Force" of Fig. 2 is actually the resistance of the substrate to the motion of the bird's head. For the sake of simplicity, the force is considered to be applied at the tip of the bill and at a right angle to the axis of the bill. Torque at any point along the bill is equal to the product of the applied force times the distance along the axis from the point of application to the point in question. It is important to note that, in digging, torque is applied not in the plane of rotation of the frontonasal hinge, but around a point in the center of the hinge (technically, around any point in the hinge) in a plane in which it is inflexible. Thus, the shorter the bill, the less torque around this point.

Increased relative width of the hinge enables it to withstand increased torque around its center. The hinge can be considered the base of an equilateral triangle with its apex at the tip of the bill (Fig. 2). If the triangle is to remain stable, each half of the base must be able to compensate for at least half of the impinging force. The situation may be expressed mathematically by the formula:

$$(F)\ (BL) = T = (f)\ (\tfrac{1}{2}\ FNW) + (f')\ (\tfrac{1}{2}\ FNW)$$

where F is the applied force, T the torque, f and f′ the resistance to compression or tension, BL the Bill Length, and FNW the Frontonasal Width. Given no differences in structural strength, a relatively wide base will withstand more torque than a relatively narrow one. Table 4 shows that the width of the Bank Swallow's frontonasal hinge falls into the middle of the hirundinine range when compared with other non-bill characters. Thus, it is about as wide as would be predicted for a swallow the size of *Riparia*, or perhaps slightly larger, as the cranium is slightly larger than might be expected (Table 6). The hinge becomes functionally wider than in other swallows by virtue of the fact that the bill is shorter, and the height of the triangle is, therefore, relatively small.

The situation in regard to the shearing strain, that is, strain along the axis of the hinge, is somewhat different. In this case, the applied force is direct and independent of the length of the bill. Therefore, it is not subject to increase by lever action. Resistance to shearing can come only from an increase in the actual, not relative, area of supporting bone in the frontonasal hinge. There is little evidence for such an increase in my data, unless one considers that the slight enlargement of the cranium as indicated in Table 6 is sufficient to warrant considering the hinge a little wider than expected. It is perhaps best to adopt a conservative attitude and consider such an increase insignificant. On the other hand, if the Frontonasal Width were found to be reduced in accordance with measurements of the bill, resistance to shear would be lost in proportion to the lost area. Such a loss might well be critical in view of the fact that bone is adapted to withstand the stresses of compression and tension, but not shear.

By slashing primarily in a lateral direction, the Bank Swallow also reduces the possibility of having the bill forced open. The frontonasal hinge is an avian adaptation that permits the upper mandible to be raised. The ramphotheca of the upper mandible of *Riparia*, as in all swallows, slightly overlaps that of the lower mandible and extends slightly beyond it at the tip. Therefore, if slashing were oriented mainly in a vertical direction, the bill might occasionally be forced open, and the mouth filled with sand. The relatively great width of the hirundinine frontonasal hinge resists lateral bending. This resistance, combined with the overlap of the lower rhamphotheca by the upper, insures that the bill will not be forced open in lateral, or even dorso-lateral, slashing.

The situation concerning Interquadratic Width is similar, but not quite the same. Table 5 shows Interquadratic Width in *Riparia* is small, but not the smallest among the swallows. The narrow width reflects the small bill, but is more in line with characters of the cranium. It, too, can be considered the base of a triangle. This is especially important because the quadrates form the sole arthrological junction between the cranium and the lower mandible. As shown by Bowman (1961), the wider the Interquadratic Width, the greater its ability to withstand lateral pressure.

The problem of fractural strain across the bill is similar to that of lateral pressure on the frontonasal hinge. In digging, force is applied to the bill at an angle to its long axis, thereby inducing a risk of fracture. Such risk conceivably could be reduced by a broad bill with flat edges, forming a double wedge, much like the head of a double-bitted axe or the blade of a broad sword. As will be shown, considerable disadvantage would accrue from such a structure. An alternate structure would be one with a short distance between the point at which pressure is applied to the point at which it can be absorbed or dispersed. Such a structure also would reduce risk of fracture owing to excessive torque at any point along the bill.

In shape, the Bank Swallow's bill does not differ greatly from the distal portion of the bills of several species of swallows. In many respects, it re-

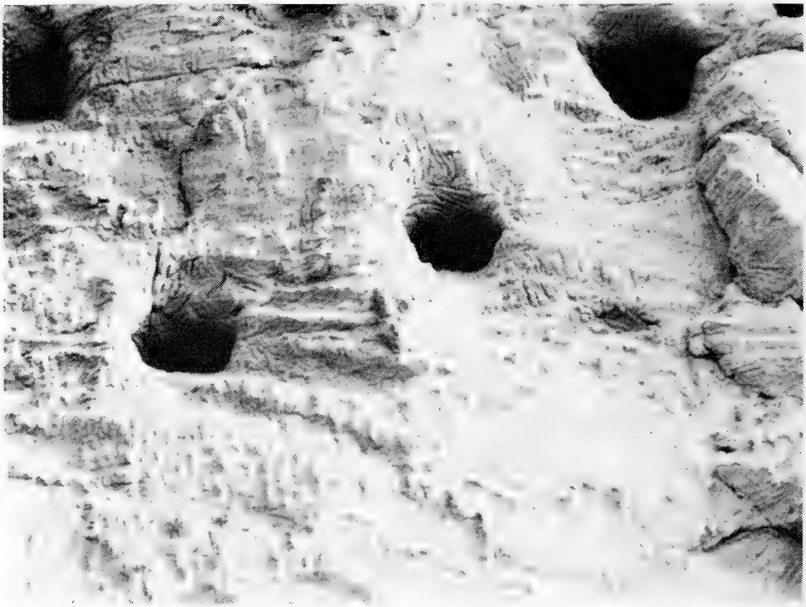

FIG. 8. Entrances to burrows of *Riparia,* south bank Kansas River, Douglas County, Kansas, June, 1962. Note, in roof of cavity, scalloped-pattern resulting from slashing action of bill.

sembles the usual hirundinine bill from which the broad, proximal portion has been removed. It is narrowness of the proximal portion that confers upon the bill its rounded cross-sectional appearance.

The rounded bill permits the Bank Swallow to slash into the substrate in any direction. While the primary motion may be lateral, the birds in fact slash in a variety of directions, including, albeit rarely, directly vertical. Such action is amply evidenced by slash marks left in the substrate (Figs. 8, 9). These slash marks also indicate that the head is frequently moved through vertical as well as horizontal arcs. Thus, pressures may impinge upon the tip of the bill from several directions in the course of a single stroke. During some strokes, the bill could be subjected to severe torque around its axis as well as around the center of the frontonasal hinge. Were the bill shaped as a double wedge, the torque around the axis would be increased by added resistance to the substrate, and the thin margins would be liable to fracture and/or tearing. Such is not true for a rounded edge in which streamlining is topologically uniform. Moreover, torque around the axis is a product of the applied force times the radius of the bill. In slashing, pressure is applied not only to the tip of the bill, but along varying portions of its length. It is, therefore, of considerable advantage to the Bank Swallow to possess a bill that remains relatively narrow for most of its length. This advantage is lost

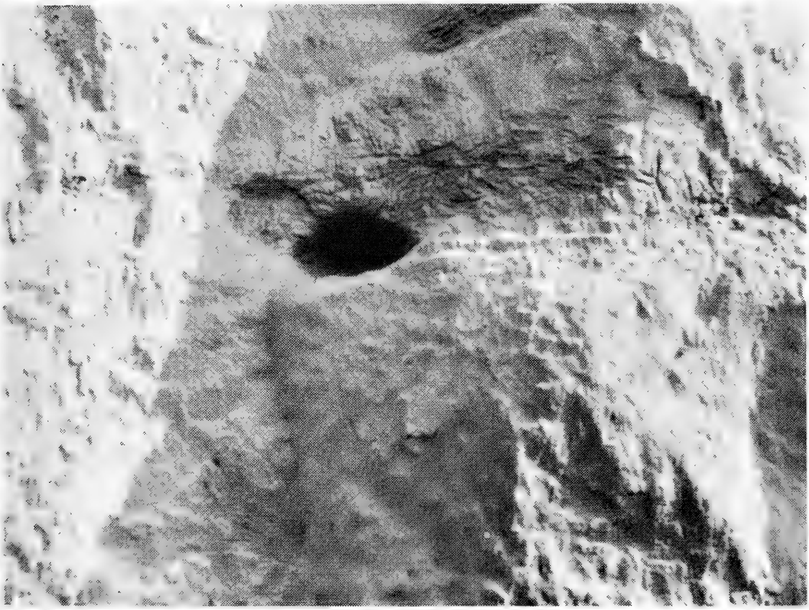

FIG. 9. Fresh marks made by slashing action of bill of *Riparia* near old burrow. Note that some of these form arcs. South bank of Kansas River, Douglas County, Kansas, June, 1962.

at the level of the cranium, thereby permitting a broadening of Maxillary and Interquadratic Width.

The shortening of the bill also increases its mechanical advantage to some extent. The skull can be considered as a lever with the fulcrum at the occipital condyle, the moment arm being posterior and the resistance arm anterior to the condyle. As such, the mechanical advantage (M.A.=length moment arm/length resistance arm) is less than one. The lever is adapted for increasing speed rather than force. Any decrease in length of the resistance arm relative to the moment arm will increase the mechanical advantage. In the case at hand, the increase is exceedingly small—possibly too small to be of selective advantage. Selection for a short bill is to be attributed more to a reduction of stress than to a gain in leverage.

An idealized perfect tool for excavating with the techniques of the Bank Swallow would be a short awl or cone suspended by a relatively large, sturdy base. The Bank Swallow's bill is by no means this perfect. It is hooked rather than pointed at the tip, although not so much as in some other swallows, and is not perfectly round in cross-section. However, it approaches the ideal more closely than the bill of any other swallow, especially in its small dimensions. There is nothing in the Bank Swallow's ecology that suggests any advantage for a relatively small bill other than those accruing during excavation. As has been shown, these advantages are several. Thus, the excavatory techniques of the Bank Swallow have engendered selective pressures for the evolution of a relatively small bill. Such could be attained either by a direct reduction of the bill or by an increase in the size of the cranium. The figures in Table 6 indicate that the cranium of *Riparia* is large relative to the Sternal Plate Length. This, however, does not fully account for the differences between the bill of *Riparia* and those of other swallows. It appears that both processes have taken place. Thus, the Bank Swallow's bill has probably been reduced in size from the ancestral condition.

Although reduced, the bill maintains its intrinsic proportions. This is, of course, necessary if it is to remain functional as part of a feeding apparatus. It does not seem necessary to postulate a series of mutations that individually and independently reduced length, width, and depth. It is more likely that the bill has been reduced as a unit through the action of one or more mutations affecting the bill "field" (Davis, 1949; Rensch, 1960).

In reduction of the bill we find a single modification that confers several adaptive advantages. This happy solution cannot be fortuitous. It is a basic tenet of evolutionary theory that mutations are random and that there can be no *a priori* direction of evolutionary change. The genesis of the raw material of any adaptive solution to a problem is strictly accidental. The probability of an organism adopting any given solution is a function of the probability of given mutations arising and being selected for in the population prior to the occurrence of genetic changes (mutations and/or recombinations) leading to any other solution. Thus, there appear in nature adaptive patterns that seem unduly complicated and/or inefficient from the standpoint of what we judge might have been developed from the structure of the supposed ancestral organism. In the Bank Swallow, however, any modification must have been one that fitted within the rigid specifications delimited by the bird's major specialization, aerial feeding. It is theoretically possible that the genetic constitution of *Riparia* could provide mutations leading toward development of a massive skull and chisel-like bill, such as is found in woodpeckers. It seems likely, however, that such development would be disadvantageous for aerial foraging. Maintenance of delicately-balanced genetic co-adaptations is such that the probability of the organism acquiring a given adaptation is increased. It is important to realize that, in the case of a highly specialized organism, modifications of specialized structures for the advantage of exploiting a new niche must be efficient at the outset. The greater the initial degree of specialization, the less opportunity the organism will have to evolve modifications that, initially, are relatively inefficient, and the greater the probability that a successful modification will be one that simultaneously confers several advantages. If the restrictions set by the specialization are sufficiently rigid, then any exploitation of a new niche will require a relatively efficient modification. The one alternative possibility is that the organism can exploit the new niche with no modification of its structure; that is, it is morphologically preadapted to the niche.

The situation can be viewed diagrammatically (Fig. 10). Assume (1) that it is advantageous for an organism to exploit a niche (burrowing nest cavities) but that its structure permits little or no use of that niche; (2) that the organism can become adapted to fuller exploitation of the niche through any of several possible modifications of its structure (A-E); (3) that any increased exploitation of the niche requires an increased output of energy. In such a situation, the advantage gained by use of the niche is balanced by the increased output of energy. Selection will favor continued modification along any line of adaptation that increases efficiency, thereby reducing the energy required. Full exploitation (self-excavation of an entire burrow) is justified only when the line of adaptation reaches a sufficient degree of efficiency. It is plain that some lines of modification will require less change to reach this degree of efficiency than others. In other words, some modifications confer a greater degree of efficiency per unit change than others. Thus, modification along line "A" would require twice as much change as along line "B" to reach the same level of efficiency. If there are no restrictions on the amount of change, then any number of solutions to the same problem can be reached from the same basic structure (Simpson, 1949). If, however, the original structure of the organism is already specialized for the exploitation of another niche (aerial feeding), there will be resistance to any change and a limit to the amount of change in any line. In Figure 10, this limitation has been set, arbitrarily, at three units of change. Only modification along line "E" will confer sufficient increase in efficiency per unit change to permit full exploitation of the niche. Thus, it is to be expected that any burrowing swallow will show modification along a relatively efficient line of adaptation. The conferring of several advantages in one change is one way that the efficiency of an adaptation is increased relative to other possible changes.

In reality, the situation is not as simple as presented. The extant characters of an organism may already permit varying degrees of exploitation along the various lines of modification (preadaptation). Also, resistance to change will vary in the different lines. The effects of these complications are

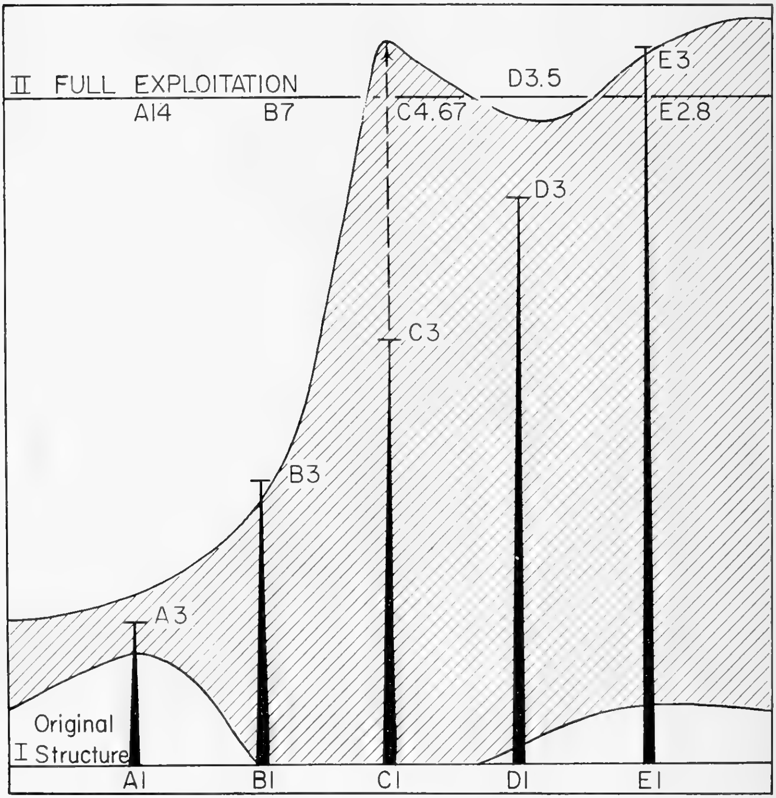

FIG. 10. Model of comparative efficiencies of various lines of evolution and effects of preadaptation and restriction by specialization. Line I represents original condition. Line II represents level at which efficiency of modification is sufficient to justify full exploitation. Numbers at Line II indicate units of change necessary for full exploitation. Lower border of hatched area indicates degree of preadaptation; upper border indicates tolerance for change.

exemplified by the hatched area in Figure 10. Thus, line "A" shows a relatively great amount of preadaptation, and line "C," though less efficient than modifications along lines "D" or "E," shows a relatively greater tolerance for change than these latter lines.

The idea of "unit of change" is an abstraction involving the nature and number of structures modified, the nature of the modifications, the number of pertinent mutations, etc. Obviously, this concept is not subject to rigorous definition. I judge, however, that this does not reduce its validity for purposes of theoretical discussion.

The structure and excavatory techniques of the Bank Swallow have attained a level of efficiency that justifies full exploitation of a cavity-burrowing niche. The imprecision of the term "unit of change" and the absence of a complete fossil record make it difficult to draw a line that precisely represents *Riparia* in Figure 10. The data presented indicate that, as expected, line "E" fairly represents *Riparia* insofar as modification of the bill is concerned. The cranium of the Bank Swallow is slightly larger, the bill slightly smaller, than one would expect to find in a swallow of its size. In only three instances, Beak Length/Cranial Length, Beak Length/Interquadratic Width, and Frontonasal Width/Maxillary Width (Table 8) do any of the mean proportions of the Bank Swallow's bill fall completely beyond the range found in other swallows. There are no rearrangements of structures and no additional mass or supporting structures. Yet, the slight change in mean proportions of the bill relative to the cranium confer several distinct advantages.

It is probable that the osteology of the skull in all swallows and, therefore, the ancestral form of *Riparia*, is preadapted to a slashing mode of excavation. The hirundinine bill is short, flat, and broad. It has been mentioned that a short, flat, broad blade could be used as a slashing tool, but that such a tool is limited to slashing in one plane. The hirundinine bill would be most effectively used in a lateral plane, which is the plane of the majority of strokes made by the Bank Swallow. Also, the frontonasal hinge of all swallows is relatively wide. Seemingly, any swallow would have the basic physical equipment necessary for excavation of the type performed by *Riparia*. The reduction of the Bank Swallow's bill is a postadaptation increasing the versatility of the structure and decreasing the risk of fracture and the effect of torque on the frontonasal hinge.

The term "preadaptation" has had a varied and sometimes confusing usage during its brief history. Throughout this paper, it is used in reference to structures that have been evolved to fulfill one function but are capable of performing another should the need arise (Bock, 1959). This use of the term is distinct from the mutational approach criticized by Simpson (1953a: 134-135) and closer to his later use of the term (*ibid*:191-193). It seems clear that the structure of the skulls of most swallows would permit some exploitation of a burrowing niche. However, full exploitation is evidently impossible, or at least impractical, without some modification (postadaptation).

MYOLOGY

The lack of distinct pattern of modification in the muscles studied has already been mentioned. However, Table 7 presents data indicating that the cucullaris-lateral rectus complex (hereafter referred to as the CLR-complex) is relatively large in *Riparia*. A large CLR-complex is well-suited to the needs of the Bank Swallow. As mentioned above, the two members of the complex can turn the head up and toward the side. While carving the arched roof of the tunnel and dome of the nest chamber, the birds must perform a considerable amount of slashing at a level above the plane in which the head is normally held. Strong musculature for tilting the head dorsally and laterally is, therefore, of advantage. It is interesting to note in this regard that the tunnel of the burrow frequently slopes slightly upward from the mouth (Stoner, 1936). The slope aids in drainage of the nesting cavity. By balancing a tendency toward strong dorsal slashes with an attempt to keep the body horizontal, or with strong scratching by the feet, the bird would achieve a slanted rather than a level or upward curving tunnel. Therefore, it is possible, even probable, that there has been selection for greater emphasis on dorsal strokes, a selection that would favor increase of the CLR-complex.

Besides drawing the head dorsally and laterally, contraction of the CLR-complex on one side only will cause the head to rotate on its axis. Rotary movement may be augmented in the swallows by medial extension of the insertion of the lateral rectus. Thus, there is in all swallows a well-developed ability to move the tip of the bill through both lateral and vertical arcs. To this ability—a function of "swallowness"—can be attributed both the shape of the tunnel and the arc-shaped grooves mentioned above.

The small size of the biventer may be related, in part, to the increase of the CLR-complex. Simultaneous contraction of both pairs of the CLR-complex effects the same movement as contraction of the biventers. It is reasonable on grounds of conservation of energy that, given no increased necessity to tilt the head straight up, a genetic increase in the mass of one set of effectors will permit a proportional decrease of the other set.

The seemingly unmodified condition of the ventral rectus and of the splenius capitis (Table 7) is rather startling. On an *a priori* basis, one would expect these muscles, and especially the latter, to be enlarged.

The figures in Table 7 indicate that the ventral rectus in *Riparia* is among the largest in the swallows, relative to the length of the skull. In fact, proportions for this muscle closely agree with proportions obtained for total muscle mass. Although *Riparia* does little directly vertical slashing, contraction of one side of the ventral rectus probably aids the CLR-complex in swinging the head through a dorso-ventral arc. The splenius capitis is almost exactly the size one would expect relative to length of skull. In view of the lateral digging motion of *Riparia*, the lack of a distinctly large splenius capitis, accompanied by no noticeable change in origin, insertion, or structure, is puzzling. This observation, combined with the fact that the Bank Swallow's musculature is generally not large relative to the size of the skull, indicates that there is no selective advantage to an increase of the effects of the muscles beyond what is already present in swallows as a group. Again, the Bank Swallow is seen to be preadapted, by virtue of adaptations found throughout the hirundinids, to its mode of excavation.

The motor patterns of foraging of swallows have not, to my knowledge, been studied in detail. Certain facts, however, are evident, and others can be inferred. It is obvious that swallows cannot be filter feeders that strain insects from a continuous airstream. Nor is it at all probable that swallows trap insects in pockets formed by the wing and tail in the manner of some bats (McCue, 1961). Although I have not observed them do so, it is possible that some feeding is done by a form of aerial skimming in which the bill is gaped until one or more insects has struck it and/or become lodged in the buccal cavity. This manner of feeding would be most effective when the birds are preying upon small, swarming insects such as gnats or mosquitoes. Such food is not always available, and the birds must, most of the time, prey upon insects that have to be captured individually. These insects are plucked from the air with a snapping motion. If it were necessary for the birds to center each insect directly in front of the bill before snapping, their flight would be slower and more capricious than it is. The birds can, and do, snap at angles to the line of flight. I have seen foraging Bank Swallows "strike" laterally with great vigor. Significantly, the Bank Swallow, with small bill, glides less and follows a more irregular course than other swallows (Blake, 1948).

It has already been mentioned that the head of a bird can be considered as a lever with a mechanical advantage less than one, specifically, a Class I lever. This type of lever is useful whenever it is desirous to have the resistance arm move rapidly through an arc, and circumstances prevent use of a Class III lever (Brown and Schwachtgen, 1949). Obviously, for any given lever, the greater the force applied to the moment arm, the faster will the arc be traversed by the resistance arm. It is evident that there is selective advantage to a swallow in being able to swing its head rapidly.

Another factor that may lend selective advantage to heavy neck musculature is collision shock at the moment of capture. With small insects, this shock is probably insignificant, but with larger insects, such as bees, it may be considerable, especially if the capture is head-on rather than overtaking. If the insect is in a direct line with the body of the bird, the shock can be passed through the skull and neck to be absorbed by the body, or can be mitigated by recoiling of the neck. If the insect is not directly in line with the body, increased musculature may be necessary either to absorb the shock directly or to permit the bird an elastic follow-through of the head and neck.

The slight magnitude of the differences between the Bank Swallow's musculature and that of other swallows indicates that the excavatory habits of *Riparia* require little myological change from the usual hirundinid condition. In this sense, the swallows are better preadapted myologically than osteologically to the task of slashing into a substrate.

No matter how perfectly the extant physical characters of the swallows may lend themselves to any technique of excavation, the behavioral patterns requisite to that technique must be developed if the bird is to be an effective miner. The adoption of suitable behavioral patterns is, therefore, a key modification. There are no data relevant to the evolution of the digging movements of the Bank Swallow. Conceivably, such movements arose from nest-building movements, possibly in connection with the enlargement or modification of pre-existing holes. A careful study of the nest-building movements of the entire genus *Riparia* might provide useful information in this regard.

Although slashing behavior may be the key to effective use of hirundinine adaptations, it is not necessary to assume that appropriate behavior was developed prior to or even simultaneously with the physical modifications. Many of the arguments pertaining to reduction of the bill can be applied to a pecking mode of excavation. As I have shown, physical modifications are severely limited by the general specialization of the swallows for aerial foraging. The only limits imposed on behavior are those placed upon it by the structure of the organism. Behavior is easily modified by the process of learning. In fact, there is no indication that excavation behavior of the Bank Swallow is presently genetically controlled. Even supposing that the general behavior pattern of slashing rather than pecking is now genetically controlled, it could have been a learned process at one point in the evolution of digging techniques. Learned behavior can be assimilated into the genotype, if it is selectively advantageous to do so, possibly via the Baldwin effect (Simpson, 1953b; Waddington, 1953).

At this point, it is necessary to insert a word of caution concerning many of the major points of this study. Even given a substantial increase in sizes of samples, certain reservations would be wise. Virtually nothing is known of the selective forces operating on the skulls of swallows, either generally or specifically. As previously mentioned, I know of no detailed analysis of the feeding motions of the various swallows. The differences found in their flight patterns (Blake, 1948) suggest that their styles of feeding differ. Differences, particularly if large, would be the results of slightly different selective forces in the past, and would modify those now operating. Again, selective forces on the skull must differ between birds with such a wide range of nest types and nesting sites. There are undoubtedly selective forces that have not been mentioned, and some that might not be readily anticipated.

The action of varying selective pressures, mostly unexplained, can be seen in even the limited number of specimens and species at my disposal. Certain variations in myology have been mentioned. The skulls of *Tachycineta thalassina*, *Iridoprocne bicolor*, and *Stelgidopteryx ruficollis* are all much alike and may be taken to represent a hypothetical "basic pattern." *Riparia riparia* differs from this pattern only in the relative dimensions of the bill. *Hirundo rustica* seems to represent a slightly narrowed and elongate version of the pattern, and *Petrochelidon pyrrhonota* is the opposite, being short and broad. *Progne subis* is quite different from the pattern in many features, especially in mass.

The Rough-winged Swallow

The paucity of detailed information on whatever excavation techniques the rough-wing may employ in modifying Bank Swallow burrows invalidates any attempt at a thorough analysis of its skull. In view of what has been said about the Bank Swallow, however, there are enough data present for certain speculations. They indicate (Tables 2, 7) that the rough-wing has an extremely flat bill, a small CLR-complex, and relatively large splenius capitis and biventer muscles. I have noted that the burrows of Bank Swallows that appeared to have been modified by rough-wings were frequently modified more extensively in a lateral than a vertical direction. The flattening of the bill and large size of the splenius capitis strongly suggest that, when and if the rough-wing does use its bill for excavation, it does so by slashing in a horizontal plane. Its adaptations, then, would follow the pattern of a sword blade. Since this induces severe risk of fracture at the margins of the bill in the event of any rotary motion, it is of advantage to reduce the possibilities of such movement. It has been mentioned that the CLR-complex can impart rotary motion to the skull, and this is the group of muscles that appears smallest in the rough-wing relative to both the total muscle mass and the length of the skull. The smallness of the CLR-complex would reduce somewhat the ability of the bird to tilt its head upward. Possibly in compensation for this, the biventer appears to be relatively large. It would seem that *Stelgidopteryx* has evolved one of the possible, but seemingly inefficient, modifications for digging. If so, this may explain why the rough-wing does not excavate its own burrow but only modifies existing holes to its own needs. In terms of Figure 10, the rough-wing may be represented by line "A" or "B." It has begun to modify, but has been prevented by prior specialization from achieving an effective solution.

Evolution of Burrowing in Swallows

It is perhaps not beyond the scope of this study to offer some comments on the evolution of burrowing in the swallows. The major question is, "What advantages accrue to those swallows nesting in burrows, either preexisting or self-excavated?" The answer is actually rather obvious. The evidence clearly suggests an advantage of differential productivity gained through increasing the number of available nesting sites.

The swallows as a group seem to be severely restricted in the types of nesting sites that they may choose. All swallow nesting sites have one factor in common. They are all so situated that, immediately upon leaving the nest, the birds are in open airspace. Thus, we find swallows nesting in cavities in trees and in the ground, in artificial nest-boxes (but usually not if the box is close under leafy branches), in mud-cup nests on real or artificial ledges, and in closed mud nests that are plastered to vertical walls.

A paucity of nesting sites seems to be a major limiting factor on populations of North American swallows. Local populations can be increased dramatically if appropriate nesting sites are provided (Buss, 1942; Goodsell, 1919; McCanne, 1936). Austin and Low (1932) comment, "The relative abundance of Tree Swallows on Cape Cod during its breeding season depends directly on the availability of nesting sites." Low (1933) further remarks on the success of artificial nest-boxes. Johnston and Hardy (1962) attribute the early arrival (up to two months prior to egg-laying) of the Purple Martin in the breeding area to "intraspecific 'competition' for nesting cavities in past time, prior to the relatively recent availability of man-made colony houses." Similar, though not so dramatic, patterns of early arrival have been reported for the Violet-green Swallow (Gullion, 1947), the Tree Swallow (Paynter, 1954), and the Rough-winged Swallow (Lunk, 1962). McCanne (1936) remarks that Barn and Cliff Swallows are able to delay nesting until mud is available for the construction of their nests. The delay of nesting in the Rough-winged, Barn, and Cliff Swallows can be attributed to a lack of immediately available sites or materials. For the Purple Martin, the early arrival date insures sufficient time in which to search out nesting cavities before the onset of those conditions necessary for the rearing of a brood.

I have noted that Bank Swallows that nest at the river site usually commence excavation somewhat later than those at the sand pits. In 1961, birds delayed the onset of excavation at the river until late May and early June. The reasons for these delays, especially the latter, are obscure but may be related to the flood cycle of the river or associated phenomena. I have been unable to determine any correlation between the onset of excavation and any single cause or obvious combination of phenomena.

Many swallows have evolved behavioral patterns that tend to increase the number of available sites. Some, as *Stelgidopteryx*, will nest in a wide variety of places (Lunk, 1962). Most are colonial. Emlen (1952) correctly points out that colonialism and reduced territorial behavior allow the Cliff Swallow to make maximum use of available sites. The same argument can be applied to the majority of swallows. Even those species of North American swallows that are only weakly colonial show reduced territorial behavior. Thus, if the opportunity presents itself, a colony may be formed at a suitable nesting site. The Purple Martin is a prime example. Before the advent of European man, Purple Martins nested in separate pairs or small colonies, as they still do in less settled portions of North America. Today, it is rare to find a single pair east of the Rocky Mountains. Here the birds take advantage of colonial houses and are considered colonial birds. In view of this evidence, it seems probable that any modification that would permit a swallow to exploit new or relatively unused nesting sites would confer a distinct selective advantage.

It is difficult to say if the habit of nesting in earthen cavities developed before, with, or after cavity-nesting in trees, or even if the use of cavities of any sort is primitive within the swallows. Mayr and Bond (1943) suggest that *Phedinia*, a cup-nest builder, may be the "least specialized" of the Old World swallows, but also refer to *Riparia* as "Apparently a rather primitive genus." In any case, the problem is somewhat academic. The first ground-nesting swallows undoubtedly used pre-existing burrows, as many species still do. Seemingly, there would be selective advantage in being able to perform more and more extensive modifications on less and less suitable holes. Eventually, the birds would be able to construct their own burrows.

The present center of distribution of the genus *Riparia* is in Africa, where it probably evolved, although Darlington (1957) remarks that "swallows have plainly undergone successive as well as multiple dispersal, and I hesitate to deduce any simple history from their present distribution." As there are no burrowing swallows in Europe, northern Asia, or North America other than *Riparia riparia,* it is probable that at one time a vast area awaited any of the burrowing African swallows that developed the physiological adaptations requisite to a northward extension of range. It is, of course, impossible to state just what factors are responsible for the ability of an organism to occupy an extensive range, unless detailed information concerning that organism's ecology, physiology, and history is available. While the ecology of the Bank Swallow has been well studied, its physiology is but incompletely known and there are no data available as to the history of the species. Unquestionably, however, a successful solution to the housing problems has been a major factor in the occupancy of the relatively enormous range enjoyed by this bird.

SUMMARY

Studies of fossorial modifications in the Bank Swallow *(Riparia riparia)* are described and discussed in this paper.

The members of the family Hirundinidae are all highly specialized for aerial foraging. They are characterized by generally light construction with short, flat bills, small legs and feet, and long, narrow wings. In spite of the delicacy of their structure, members of three not closely related genera dig nesting burrows, a behavior frequently associated with sturdy anatomy.

The Bank Swallow is the only North American swallow that characteristically performs extensive excavation. The burrows are dug not by pecking or drilling but by lateral or dorso-lateral slashing at the substrate with the bill.

Comparisons were made of proportions of the skull between *Riparia riparia* and six other North American swallows, *Tachycineta thalassina, Iridoprocne bicolor, Stelgidopteryx ruficollis, Hirundo rustica, Petrochelidon pyrrhonota*, and *Progne subis*. These comparisons show that the Bank Swallow's bill is small relative to cranial measurements and the Sternal Plate Length. In addition, the Bank Swallow's bill is more nearly round in cross-section than those of other swallows.

Similar comparisons were made of the weights of five pairs of muscles that control the appropriffiate slashing movements, M. cucullaris, M. biventer cervicis, M. splenius capitis, M. rectus capitis lateralis, and M. rectus capitis ventralis. *Iridoprocne albilinea* was used in these comparisons in addition to the other six species. The comparisons indicate that, with the exception of a relatively large cucullaris-lateral rectus complex, the weights of muscles of the Bank Swallow are appropriate to a swallow of its size.

The small size of the Bank Swallow's bill decreases the effects of torque upon the bill and the frontonasal hinge, reduces the risk of fracture across the bill, and slightly increases the mechanical advantage of the excavating structures. The rounding of the bill reduces its resistance to the substrate, thereby reducing torque and permitting slashing in other than a strictly lateral plane.

In a specialized organism, resistance is imposed against modification by the co-adapted system. Therefore, successful modifications are likely to be those that initially impart a high degree of efficiency with a minimum of change. The small size of the bill in the Bank Swallow can be considered to be reduced from that of its ancestors, and this represents an efficient solution by virtue of the fact that it confers several advantages.

The lack of extensive modification of the muscles studied suggests that the swallows as a group are myologically preadapted to a slashing mode of excavation. The muscular requirements for aerial foraging seem to be quite similar to those for lateral or dorso-lateral slashing.

The Rough-winged Swallow *(Stelgidopteryx ruficollis)* also nests in burrows, but it does not excavate them. In comparison with the Bank Swallow, the rough-wing seems to be but slightly modified for digging, and such modifications as it does possess appear to be quite inefficient.

The Hirundinidae as a group are pressed for available nesting sites. The use of pre-excavated cavities is an adaptation to increase the numbers of available sites. Burrowing probably evolved from attempts to modify already existing holes of various types.

The successful development of fossorial adaptations is undoubtedly a contributing factor to the wide range of the Bank Swallow.

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APPENDIX A

The tables in this appendix provide additional data concerning the proportions discussed in text. Table A-1 concerns proportions first appearing in Table 1, Table A-2 those first appearing in Table 2, etc. The data for each proportion are presented only once, in the table corresponding to the first text table in which the proportion appears. The data are presented in the following pattern:

Mean ± 2 Standard Errors of the Mean
Range; Number.

Table A-1. Bill Length, Data.

	$\frac{\text{Bill Length}}{\text{Cranial Length}}$	$\frac{\text{Bill Length}}{\text{Sternal Plate Length}}$	$\frac{\text{Bill Length}}{\text{Interquadratic Width}}$	$\frac{\text{Bill Length}}{\text{Frontonasal Width}}$	$\frac{\text{Bill Length}}{\text{Maxillary Width}}$
Riparia	.459±.020	.543±.030	.401±.008	1.707±.102	.894±.060
	.412—.503;10	.517—.612;9	.377—.430;6	1.500—1.976;9	.797—1.097;9
Tachycineta	.476±.012	.559±.012	.419±.016	1.929±.128	.965±.012
	.448—.509;5	.528—.582;5	.410—.431;5	1.738—2.102;5	.937—.987;5
Iridoprocne	.486±.022	.536±.020	.411±.012	1.914±.066	.943±.048
	.420—.531;16	.477—.596;16	.364—.446;16	1.673—2.065;16	.795—1.097;15
Stelgidopteryx	.489±.028	.557±.034	.422±.014	1.707±.142	.865±.058
	.411—.548;8	.474—.622;8	.371—.453;8	1.358—1.957;8	.734—.989;8
Hirundo	.559±.014	.639±.020	.453±.008	2.121±.064	.882±.020
	.517—.615;14	.589—.700;13	.428—.470;13	1.937—2.382;14	.823—.973;14
Petrochelidon	.475±.008	.556±.010	.406±.006	1.684±.044	.841±.028
	.437—.514;20	.506—.613;20	.376—.446;20	1.500—1.934;20	.766—.922;18
Progne	.643	.660	.468	1.920	.947
	.636—.650;2	.650—.671;2	.466—.470;2	1.907—1.933;2	.947;2

TABLE A-2. Bill Depth, Data.

	$\frac{\text{Bill Depth}}{\text{Cranial Depth}}$	$\frac{\text{Bill Depth}}{\text{Sternal Plate Length}}$	$\frac{\text{Bill Depth}}{\text{Frontonasal Width}}$	$\frac{\text{Bill Depth}}{\text{Bill Length}}$	$\frac{\text{Bill Depth}}{\text{Maxillary Width}}$
Riparia	.224±.012	.158±.010	.482±.050	.292±.014	.250±.028
	.189—.252;12	.130—.178;12	.428—.571;11	.214—.333;9	.212—.319;12
Tachycineta	.238±.008	.169±.004	.579±.020	.298±.016	.294±.022
	.216—.262;16	.145—.215;19	.534—.704;19	.268—.328;5	.256—.369;19
Iridoprocne	.242±.028	.159±.004	.560±.016	.288±.012	.279±.008
	.209—.294;23	:135—.186;24	.488—.652;24	.235—.350;14	.242—.316;24
Stelgidopteryx	.220±.012	.147±.004	.449±.028	.260±.008	.162±.008
	.198—.244;8	.132—.162;8	.377—.510;8	.235±.277;8	.148—.176;7
Hirundo	.247±.010	.163±.008	.546±.020	.257±.012	.226±.008
	.207—.300;22	.138—.194;21	.469—.652;23	.221—.303;14	.190—.275;23
Petrochelidon	.234±.006	.162±.006	.497±.012	.294±.008	.243±.006
	.203—.274;28	.140—.181;28	.442—.549;29	.266—.325;16	.215—.272;28
Progne	.343±.012	.201±.004	.579±.024	.303	.284±.004
	.322—.375;7	.183—.220;8	.532—.640;8	.296—.310;2	.270—.308;8

TABLE A-3. Maxillary Width, Data.

	$\frac{\text{Cranial Width}}{\text{Maxillary Width}}$	$\frac{\text{Sternal Plate Length}}{\text{Maxillary Width}}$
Riparia	1.576±.064	1.657±.090
	1.415—1.806;13	1.483—2.076;13
Tachycineta	1.671±.022	1.748±.038
	1.557—1.747;18	1.612—1.852;19
Iridoprocne	1.597±.026	1.760±.042
	1.469—1.726;25	1.552—1.976;25
Stelgidopteryx	1.413±.036	1.553±.048
	1.360—1.494;7	1.469—1.663;8
Hirundo	1.256±.016	1.390±.018
	1.183—1.346;22	1.292—1.491;22
Petrochelidon	1.468±.026	1.499±.034
	1.357—1.652;29	1.357—1.764;29
Progne	1.142±.036	1.418±.058
	1.061—1.189;8	1.252—1.547;8

TABLE A-4. Frontonasal Width, Data.

	Frontonasal Width	Frontonasal Width	Frontonasal Width	Frontonasal Width
	Sternal Plate Length	Cranial Width	Cranial Length	Maxillary Width
Riparia	.318±.014	.332±.032	.273±.006	.526±.024
	.262—.356;13	.311—.360;13	.253—.291;12	.477—.611;12
Tachycineta	.294±.006	.307±.004	.249±.006	.511±.012
	.268—.323;20	.282—.325;20	.234—.274;19	.469—.558;19
Iridoprocne	.282±.004	.312±.002	.256±.004	.498±.006
	.259—.304;26	.286—.335;26	.239—.276;26	.447—.541;25
Stelgidopteryx	.327±.014	.358±.018	.288±.006	.508±.060
	.300—.353;8	.330—.392;8	.262—.306;8	.480—.540;8
Hirundo	.299±.004	.332±.002	.264±.004	.416±.004
	.269—.327;22	.312—.356;22	.246—.284;24	.389—.452;24
Petrochelidon	.326±.006	.334±.004	.278±.004	.490±.010
	.304—.364;32	.315—.364;32	.262—.298;33	.450—.550;30
Progne	.346±.010	.389±.006	.337±.008	.490±.016
	.336—.372;8	.375—.402;8	.326—.345;8	.463—.527;8

TABLE A-5. Interquadratic Width, Data.

	Interquadratic Width	Interquadratic Width	Interquadratic Width	Interquadratic Width	Interquadratic Width
	Cranial Width	Sternal Plate Length	Skull Length	Cranial Length	Maxillary Width
Riparia	.785±.016	.727±.036	.438±.006	.634±.008	1.199±.056
	.755—.830;9	.664—.818;9	.409—.455;6	.619—.651;8	1.095—1.379;9
Tachycineta	.780±.018	.746±.014	.438±.008	.634±.008	1.304±.028
	.733—.883;19	.693—.826;19	.427—.464;5	.598—.691;19	1.231—1.461;19
Iridoprocne	.812±.010	.735±.014	.447±.008	.666±.002	1.298±.020
	.765—.840;26	.660—.785;26	.429—.460;16	.620—.704;26	1.200—1.393;25
Stelgidopteryx	.770±.016	.673±.018	.410±.018	.611±.006	1.070±.018
	.720—.807;6	.644—.729;7	.376—.441;7	.583—.626;7	1.029—1.112;7
Hirundo	.800±.012	.721±.014	.407±.002	.635±.008	1.003±.018
	.736—.866;21	.642—.768;21	.397—.427;14	.589—.676;23	.913—1.069;23
Petrochelidon	.845±.008	.826±.006	.479±.004	.704±.004	1.241±.024
	.810—.900;32	.786—.870;32	.461—.498;20	.681—.733;33	1.144—1.404;30
Progne	.885±.020	.788±.014	.464	.768±.010	1.115±.036
	.821—.931;8	.757—.823;8	.459—.469;2	.741—.798;8	1.030—1.184;8

TABLE A-6. Miscellaneous Measurements, Data.

	Cranial Width / Sternal Plate Length	Skull Length / Sternal Plate Length	Cranial Length / Sternal Plate Length
Riparia	.956±.040	1.704±.014	1.175±.034
	.817—1.056;14	1.470—1.871;11	1.056—1.282;13
Tachycineta	.954±.014	1.735±.054	1.181±.018
	.900—1.038;19	1.683—1.815;5	1.121—1.271;19
Iridoprocne	.904±.014	1.637±.036	1.105±.016
	.830—.973;26	1.506—1.738;16	1.029—1.185;26
Stelgidopteryx	.904±.028	1.694±.058	1.140±.010
	.840—.964;7	1.601—1.833;8	1.217—1.067;8
Hirundo	.901±.008	1.778±.032	1.137±.014
	.862—.937;20	1.706—1.863;13	1.091—1.187;22
Petrochelidon	.978±.010	1.718±.028	1.176±.008
	.906—1.032;31	1.576—1.839;20	1.120—1.242;32
Progne	.807±.048	1.688	1.027±.024
	.768—.863;8	1.650—1.727;2	.987—1.088;8

TABLE A-7. Muscle Weights (Cube Roots), Data.

	Ventral Rectus / Skull Length	CLR-Complex / Skull Length	Splenius / Skull Length	Biventer / Skull Length	Total Mass / Skull Length
Riparia	.055±.001	.074±.002	.066±.002	.054±.002	.100±.003
	.052—.057;7	.068—.078;9	.061—.069;9	.044—.059;9	.094—.104;7
Tachycineta	.054	.070	.064	.053	.097
I. albilinea	.056	.072	.066	.056	.100
	.056—.057;2	.070—.073;2	.065—.066;2	.054—.057;2	.100—.101;2
I. bicolor	.052	.067	.062	.056	.095
Stelgidopteryx	.052±.001	.068±.003	.065±.002	.053±.002	.096±.004
	0.48—.058;9	.063—.076;9	.060—.072;9	.050—.058;9	.089—.106;9
Hirundo	.052±.002	.070±.002	.066±.002	.054±.003	.098±.003
	.048—.055;6	.066—.074;6	.062—.069;6	.049—.059;6	.091—.102;6
Petrochelidon	.059±.003	.077±.001	.068±.002	.056±.002	.105±.002
	.052—.067;11	.072—.080;11	.059—.073;11	.052—.062;11	.099—.112;11
Progne	.062±.001	.080±.005	.071±.001	.059±.002	.110±.002
	.061—.064;5	.078—.081;5	.068—.074;5	.054—.062;5	.105—.112;5

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A REVISION OF *MICRONECTA* OF AUSTRALIA AND MELANESIA (HETEROPTERA: CORIXIDAE)

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VOL. XLVI PAGES 147-165 JUNE 1, 1965 No. 3

A Revision of *Micronecta* of Australia and Melanesia (Heteroptera: Corixidae)[1]

By

LING-CHU CHEN

INTRODUCTION

It has been more than 40 years since the publication of Hale's (1922) paper, "Studies in the Australian Aquatic Hemiptera." There has been no other work concerning the *Micronecta* of the Australian region except one on the Melanesian species by Wróblewski (1962), which contains redescriptions of two species and a statement on the synonymy of another.

The structural differences among species in the genus have been more fully recognized in recent decades. It is, therefore, necessary to redescribe those species which have not been reviewed since Hale's work. Besides redescriptions, eight new species and a key to the Australian and Melanesian species of *Micronecta* are included in this paper. Kirkaldy described three species from Australia, but unfortunately only one has been recognized for certain, and his type specimens cannot be located. The original descriptions of his two unrecognized species are reproduced verbatim.

I wish to express my appreciation to all who have assisted me in this study. Dr. H. B. Hungerford placed at my disposal all the *Micronecta* in the Snow Entomological Museum plus some types lent from the Hungarian National Museum and the undetermined *Micronecta* that had been sent to him from the following museums: British Museum (Natural History), California Academy of Science, Chicago Natural History Museum, Hungarian National Museum, Museum of Comparative Zoology (Harvard University), South Australian Museum, and the United States National Museum. Dr. C. D. Michener and Miss Ellen Ordway have helped in revising the manuscript.

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KEY TO THE *MICRONECTA* OF AUSTRALIA AND MELANESIA (MALES)

1. Male genitalia with sinistral asymmetry; free lobe of eighth tergite with two outer, lower and upper, setigerous angles (Fig. 14) ...... *M. sinistra*
   Male genitalia with dextral or sinistral asymmetry; free lobe of eighth tergite only with outer, lower, setigerous angle 2
2. Body less than 2.5 mm. long 3
   Body more than 2.5 mm. long 5
3. Interocular space as wide as an eye or narrower 4
   Interocular space wider than an eye; parameres as in Figs. 52-53 .... *M. australiensis*
4. Clavus with three dark stripes; interocular space narrower than an eye .... *M. ludibunda*
   Clavus with two dark stripes; interocular space about as wide as an eye; parameres as in Figs. 1-4 .... *M. micra*
5. Body 3.5 mm. to 5 mm. long 6
   Body 2.5 mm. to 3.5 mm. long 7
6. Vertex roundly produced; palar claw with one margin greatly expanded as in Fig. 44 .... *M. robusta*
   Vertex conically produced; palar claw elongate (Fig. 36) .... *M. major*
7. Hemelytra of uniform color 8
   Hemelytra with dark maculations 9
8. Hemelytra black .... *M. carbonaria*
   Hemelytra yellowish brown; parameres as Figs. 80-82 . ... *M. windi*
9. Corium with many diffuse blotches centrally; pronotum with a distinct ridge behind posterior margin of head; parameres as in Figs. 58-60 .... *M. carinata*
   Corium with four broken, dark, longitudinal stripes; pronotum without a distinct ridge behind posterior margin of head 10
10. Interocular space about 1.60 times as wide as an eye; middle femur long, about 41% of the body length .... *M. virgata*
    Interocular space less than 1.55 times as wide as an eye; middle femur less than 40% of the body length 11
11. Free lobe of eighth tergite with inner angle obsolete and outer angle distinctly prolonged, completely margined with bristle-like hairs as in Fig. 78 12
    Free lobe of eighth tergite with a well developed inner angle and an outer setigerous angle as in Fig. 28 13
12. Second hair of the posterior lower flexor margin of pala slightly enlarged, palar claw with a distinct notch distally (Fig. 79); parameres as in Figs. 73-75 .... *M. queenslandica*
    No special enlarged hair on the posterior flexor margin of pala, palar claw completely margined .... *M. quadristrigata*
13. Palar claw with one margin greatly expanded (Fig. 29); parameres as in Figs. 24-25 .... *M. gracilis*

Palar claw evenly expanded (Fig. 72) 14

14. Distal end of palar claw swollen (Fig. 72); parameres as in Figs. 65-68 .... *M. halei*

Distal end of palar claw normal (Fig. 23) 15

15. Vertex strongly produced, head as long as (macropterous form) or longer (brachypterous form) than pronotum; parameres as in Figs. 16-19 .... *M. batilla*

Vertex slightly produced, head shorter than pronotum; parameres as in Figs. 45-47 .... *M. adelaidae*

Micronecta micra Kirkaldy

Micronecta micra KIRKALDY, 1905, p. 26; HALE, 1922, p. 328.

Size. Brachypterous form, length 1.9 mm. to 2.0 mm.

Color. Yellowish brown, pattern in seven specimens studied almost completely effaced. Venter and legs grayish yellow.

Structural characteristics. Head about twice as long as pronotum, vertex roundly produced in front of eyes; interocular space about as wide as eye; length to width of pronotal disk as 1.5:5.5, lateral margins of pronotum very short, making head almost contiguous with corium, posterior margin of pronotum almost truncate. Hemelytra with numerous minute setae. Wings reduced, extending to third abdominal tergite. Prestrigilar flap (fig. 5) broad and short with round tip. Submedian process of seventh abdominal sternite (fig. 6) broad basally, abruptly pointed at tip, with four extremely elongate, enlarged bristles subbasally. Free lobe of eighth tergite (fig. 7) with large, round inner angle and rather small, pointed, setigerous outer angle, posterior margin between angles slightly concave. Parameres well chitinized and shaped as in Figs. 1-4. Foreleg similar to that of *M. australiensis.*

Remarks. Kirkaldy's types are unknown, but the Snow Entomological Museum has seven specimens, two males and five females, from the type locality, Kuranda, northern Queensland. These specimens agree well with the original description, especially considering the body size and posteriorly truncated pronotum.

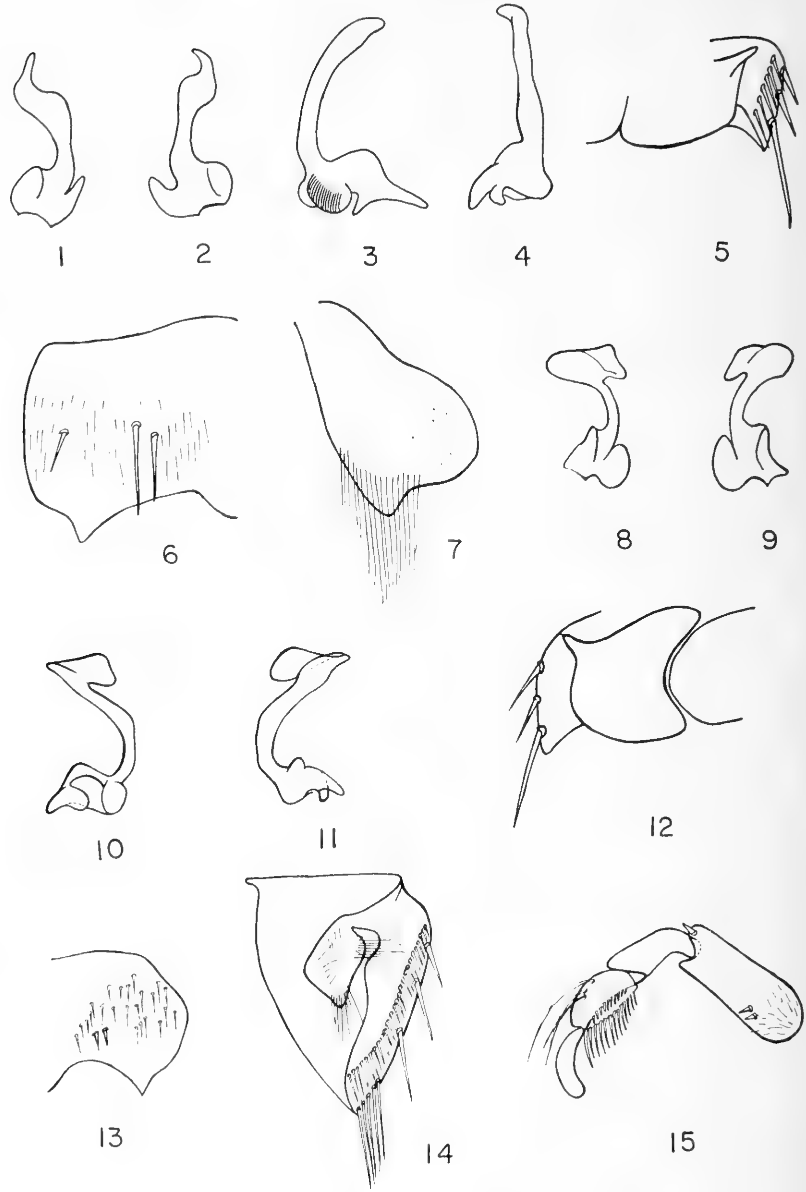
Collection data. Two males and five females, Kuranda, northern Queensland, Aug. 12, 1938 (R. G. Wind).

Micronecta batilla Hale

Micronecta batilla HALE, 1922, p. 323.

Size. Macropterous form, length 2.8 mm. to 3.3 mm. Brachypterous form, length 2.6 mm. to 3.1 mm.

Color. Grayish or yellowish to dark brown; vertex sometimes uniformly colored, usually with three parallel, reddish, longitudinal stripes. Pattern on hemelytra as in *M. robusta.* Venter and legs usually pale.



FIGS. 1 TO 7. *M. micra.* 1-2, left paramere; 3-4, right paramere; 5, prestrigilar flap; 6, submedian process of seventh abdominal sternite; 7, free lobe of eighth abdominal tergite. FIGS. 8 TO 15. *M. sinistra.* 8-9, left paramere; 10-11, right paramere; 12, prestrigilar flap; 13, submedian process of seventh abdominal sternite; 14, free lobe of eighth abdominal tergite; 15, foreleg of male.

Structural characteristics. Head about one and one half times as long as pronotum, width to length of pronotal disk as 3.1:0.9 in brachypterous form. In macropterous form, head as long as pronotum, width to length of pronotal disk as 3.3:1.2. Vertex noticeably produced beyond anterior margins of eyes, more so in brachypterous form. Interocular space as wide as eye or slightly wider; posterior margin of pronotum rounded. Hemelytra with scattered minute hairs. In brachypterous form, wings extending to seventh abdominal tergum. Prestrigilar flap (fig. 20) and submedian process of seventh abdominal sternite (fig. 21) similar to those of *M. robusta.* Free lobe of eighth tergite (fig. 22) with well developed rounded inner angle and slightly produced setigerous outer angle. Right paramere (fig. 19) slightly dilated before tip and gradually narrowed to apex; left paramere (figs. 16-18) denticulate with many small conical barbs, broad basally and constricted distally to bent apex. Foreleg (fig. 23) as in *M. robusta* but the spines on tibia uniform in size and palar claw dilated evenly.

Remarks. In the original description, the variation of body size of this species is indicated as 2.75 mm. to 5 mm. In view of the strong similarities between *M. batilla* and *M. major* n. sp., it seems that the large individuals of Hale's *M. batilla* actually were *M. major.* I have examined more than 250 specimens, including syntypes of *M. batilla,* and find no intergradation with *M. major.*

Collection data. South Australia: Adelaide (identified by H. M. Hale). *Victoria:* Bacchus Marsh, Jan., 1904. *New South Wales:* Pine Island, Federal Capital Territory (J. W. Evans); Mt. Kosciusko, 5-7000 ft., Dec. 13, 1931 (P. J. Darlington, Harvard Exp.); Dorrigo, 3000 ft., Feb., 1932; Valley Heights, near Katoamba, May 23, 1954 (E. S. Brown). *Queensland:* Brisbane, Dec., 1932 (H. Hacker); Fresh Water Creek, Redlynch, Sept. 27, 1938 (R. G. Wind). *Western Australia:* Yancheyarra, June 24, 1933 (N. B. Tindale). *Tasmania:* Lake Leake, 1937 (J. W. Evans).

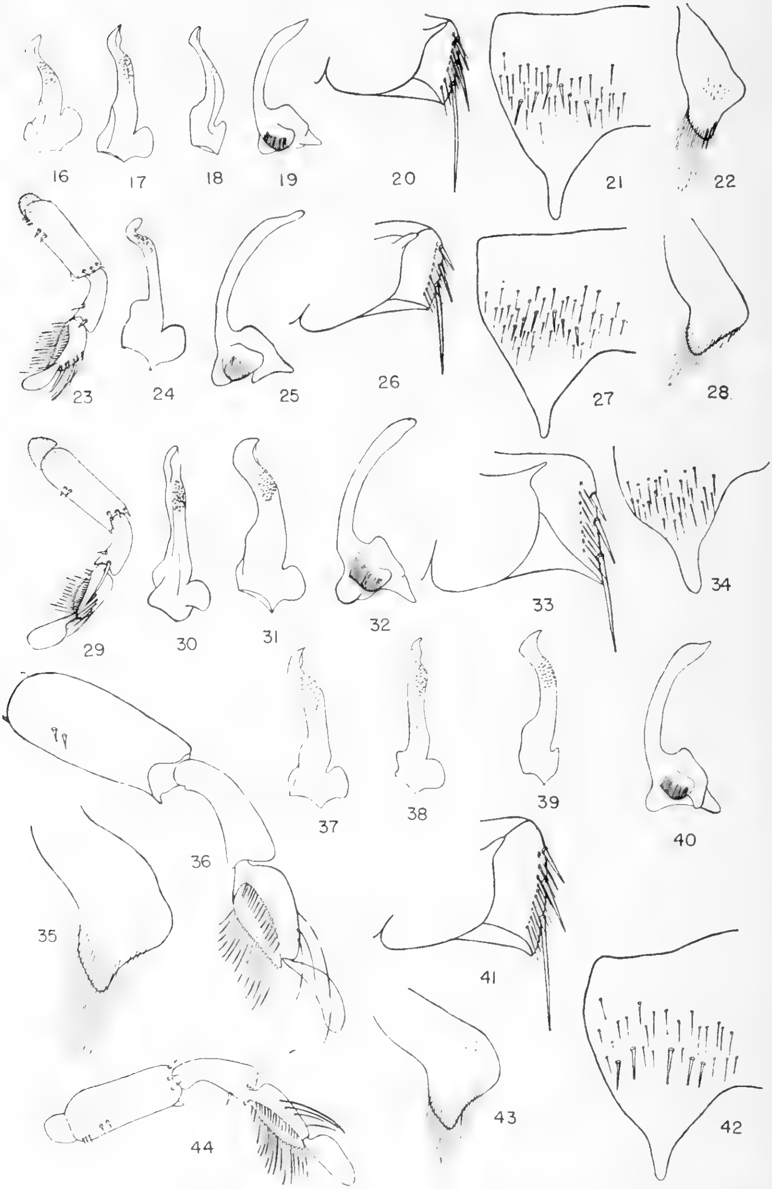
Micronecta gracilis Hale

Micronecta gracilis Hale, 1922, p. 326.

Size. Macropterous form, length, 3.26 mm. to 3.53 mm.

Color. Grayish to dull brown; vertex much lighter than rest of body, with dark central stripe; pattern of pronotum and hemelytra as in *M. robusta.* Venter and legs pale.

Structural characteristics. Body elongate, length more than twice as long as widest part (3.4:1.5). Head shorter than pronotum (1.2:1.4), vertex slightly produced beyond anterior margins of eyes; interocular space wider than eye (1.5:1.3); width to length of pronotal disk as 3.4:1.4; pronotum spindle shaped. Hemelytra with relatively long, fine hairs. Prestrigilar flap



FIGS. 16 TO 23. *M. batilla.* 16-18, left paramere; 19, right paramere; 20, prestrigilar flap; 21, submedian process of seventh abdominal sternite; 22, free lobe of eighth tergite; 23, foreleg of male. FIGS. 24 TO 29. *M. gracilis.* 24, left paramere; 25, right paramere; 26, prestrigilar flap; 27, submedian process of seventh abdominal sternite; 28, free lobe of eighth tergite; 29, foreleg of male. FIGS. 30 TO 36. *M. major.* 30-31, left paramere; 32, right paramere; 33, prestrigilar flap; 34, submedian process of seventh abdominal sternite; 35, free lobe of eighth tergite; 36, foreleg of male. FIGS. 37 TO 44. *M. robusta.* 37-39, left paramere; 40, right paramere; 41, prestrigilar flap; 42, submedian process of seventh abdominal sternite; 43, free lobe of eighth tergite; 44, foreleg of male.

of fifth tergum (fig. 26) broad and short. Subequilateral, submedian process of seventh sternite with six slightly enlarged bristles subbasally (fig. 27). Free lobe of eighth tergite with well developed postero-external setigerous and antero-internal rectangular angles (fig. 28). Right paramere (fig. 25) evenly curved, narrowing distally to blunt tip; left paramere (fig. 24) with middle part of shaft almost straight, distal part sharply curved in sickle-shape, denticulate beyond two parts. Palar claw (fig. 29) as in *M. robusta* Hale.

Remarks. The redescription is based on syntypes and specimens identified by Hale. This species, in general appearance, is close to *M. quadristrigata* Breddin. However, in the denticulate left paramere, the characteristic palar claw and the submedian process of the seventh sternite, *M. gracilis* seems more closely allied to *M. robusta.*

Collection data. South Australia: Quorn (A. H. Elston) (syntype); Myponga (A. H. Elston) (syntypes); Neales River at Algebuckina, May 10, 1953 (R. A. Stirton and R. H. Tedford) Lake Callabonna, June 3, 1953 (R. A. Stirton and R. H. Tedford); White Crossing, Coopers Creek, June 18, 1953 (R. A. Stirton); Mt. Serle, N. Flinder Range (Hale and Tindale); Well 4 m. E. Oraparinna (at light), Feb. 1956 (G. F. Gross); Everard Ranges (A. Brumby). *Queensland:* Cairns district (A. M. Lea); Kings Creek, Aug. 25, 1954 (R. A. Stirton); St .George, 1923 (G. H. Wilkins). *New South Wales:* Carbamatta, Sydney, Jan. 31, 1958 (M. J. Nikitin); Bogan River (Mr. Beane); Valley Heights, near Katoomba, May 23, 1954. *Western Australia:* 20 m. South of Erlinda Station, Oct. 23, 1953 (N. B. Tindale); Yeeda Station, Aug. 25, 1953 (N. B. Tindale); Warburton Ranges (A. Brumby). *Victoria* (no detailed data on specimens).

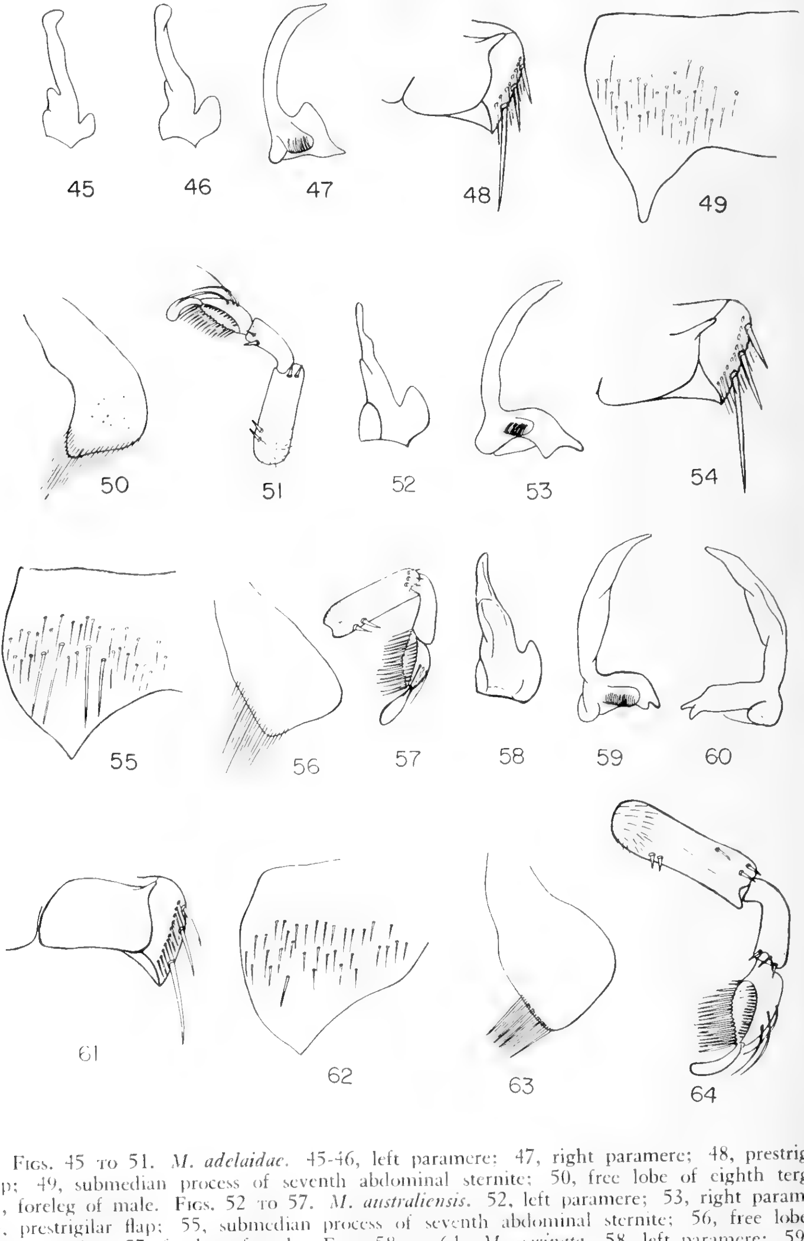
Micronecta robusta Hale

Micronecta robusta HALE, 1922, p. 325.

Size. Macropterous form, length 3.5 mm. to 4.2 mm.

Color. Head pale to dark brown either with uniform color throughout or with a central longitudinal yellowish brown stripe, sometimes with light spot between eye and central stripe. Pronotum and hemelytra usually much darker than head, pronotum crossed by a pronounced, broken, transverse band visible only in specimens with light background. Clavus margined with stripe along inner and outer edges and corium marked with four longitudinal broken stripes. Venter and legs grayish yellow to grayish fuscous.

Structural characteristics. Body stout, length less than twice as long as widest part (4.2:2.0); head noticeably shorter than pronotum; vertex not produced but rounded in front of eyes; interocular space broad, usually one and one half times as wide as an eye; width to length of pronotal disk as 4.2:1.5; many specimens with posterior margin of pronotum, in front of



FIGS. 45 TO 51. *M. adelaidae.* 45-46, left paramere; 47, right paramere; 48, prestrigilar flap; 49, submedian process of seventh abdominal sternite; 50, free lobe of eighth tergite; 51, foreleg of male. FIGS. 52 TO 57. *M. australiensis.* 52, left paramere; 53, right paramere; 54, prestrigilar flap; 55, submedian process of seventh abdominal sternite; 56, free lobe of eighth tergite; 57, foreleg of male. FIGS. 58 TO 64. *M. carinata.* 58, left paramere; 59-60, right paramere; 61, prestrigilar flap; 62, submedian process of seventh abdominal sternite; 63, free lobe of eighth tergite; 64, foreleg of male.

scutellum, somewhat straight. Hemelytra shiny and smooth, with numerous hairs. Prestrigilar flap broad and short (fig. 41). Submedian process of seventh abdominal sternite well produced, with four to six enlarged bristles subbasally (fig. 42). Free lobe of eighth tergite (fig. 43) as in *M. major*. Right paramere (fig. 40) distinctly dilated just before tip and suddenly constricted distally; left paramere (figs. 37-39) somewhat straight at middle, bent toward poined apex. Femur of foreleg (fig. 44) with two spinelike setae on lower side and three apical spinelike hairs near outer margin; tibia with large apical spine on inner margin and subapical spine on flexor margin; palar claw greatly dilated near base.

Remarks. This redescription is based on eight specimens from Murray Bridge, South Australia, which were determined by Dr. Hale, and on the syntypical specimens which I have also examined. In addition, more than 150 specimens of this species from various places were studied. The large body size and the shape of the free lobe of the eighth tergite are similar to those of *M. major* but they differ in the relative sizes of the interocular space and the eye, the shape of the palar claw, and the genitalia.

Collection data. South Australia: Adelaide (H. M. Hale); Murray Bridge. *Western Australia:* Seaforth, June, 1952 (Mrs. B. Y. Main); Rottnest Island, near Perth, Oct. (P. J. Darlington, Harvard Exp.); Mt. Sterling, Aug. 19, 1957 (J. A. L. Watson); Bickley Swamp, Sept. 29, 1954 (E. P. Hodgkin). *New South Wales:* Carbramatta, Sydney, Feb., 1958 (M. J. Nikitin); Pine Island, near Canberra, Fed. Cap. Terr. (J. W. Evans); Valley Heights, near Katoomba, May 23, 1954. *Tasmania:* Hobart, April, 1937 (J. W. Evans).

Micronecta adelaidae n. sp.

Size. Macropterous form, length 2.5 mm. to 2.7 mm.

Color. General coloration dark; head yellow with three contrasting parallel, longitudinal, brown stripes on vertex, one median, other two close to inner margin of each eye; pronotum, scutellum and hemelytra brown, with pattern of hemelytra as in *M. batilla* but broken stripes on corium more pronounced. Venter and legs yellowish gray.

Structural characteristics. Head shorter than pronotum, vertex slightly produced in front of eyes; posterior margin of eyes approximate posterior margin of head; interocular space about one and one-thirds times as wide as an eye; length to width of pronotal disk as 1.1:2.8; pronotum spindle shaped, with anterior and posterior margins rounded. Hemelytra shiny and smooth, with sparsely scattered, fine, short hairs. Prestrigilar flag as in Fig. 48. Submedian process of seventh sternite (fig. 49) moderately produced, apex blunt. Free lobe of eighth tergite as in Fig. 50. Right paramere (fig. 47) evenly curved and pointed apically; left paramere (figs. 45-46) smooth with knoblike expanded apex. Foreleg (fig. 51) as in *M. carinata.*

Comparative notes. In general appearance, this species is similar to *M. queenslandica*, but *M. adelaidae* has a narrower interocular space. The well sclerotized left paramere of *M. adelaidae* is similar to those of *M. windi* and *M. halei.*

Holotype. Male, Adelaide River 70 mi. South of Darwin, Northern Territory, Mar. 25, 1954 (B. Malkin) in the United States National Museum.

Allotype. Female, same data as for holotype.

Paratypes. One female and two males with same data as above, one male in the United States National Museum, and one male and one female in the Snow Entomological Museum of The University of Kansas.

Micronecta australiensis n. sp.

Size. Brachypterous form, length 2.03 mm. to 2.33 mm.

Color. Light to dark brown, pattern partially or completely effaced; when present, masculations as in *M. batilla.* Head, legs and thoracic venter usually pale; abdominal venter usually black.

Structural characteristics. Head longer than pronotum, vertex rounded in front of eyes; interocular space wider than eye (3.1:2.2); width to length of pronotal disk as 6.5:1.4; posterior margin of pronotum almost straight; pronotum, scutellum and hemelytra slightly rugulose, hemelytra with scattered pale hairs. Wings reaching sixth abdominal tergum. Prestrigilar flap (fig. 54) and submedian process of seventh sternite (fig. 55) both similar in outline of those of *M. micra.* Free lobe of eighth tergite (fig. 56) with rounded, setigerous inner angle, rectangular outer angle, posterior margin between angles almost straight. Right paramere (fig. 53) simply curved to blunt point; left paramere (fig. 52) styliform, unevenly narrowed toward blunt point. Foreleg as in Fig. 57.

Camparative notes. This species is similar in general appearance and structure to *M. micra*, but differs in the body size, the relative sizes of the interocular space and the eye, and the genitalia.

Holotype. Male, Federal Capital Territory (near Canberra), Australia, Mar. 25, 1931 (J. Evans) in the Snow Entomological Museum of The University of Kansas.

Allotype. Female, same data as for holotype.

Paratypes. Nineteen males and twenty-two females, same data as holotype; one male, Alexandra, Victoria, F. L. Billinghurst, all in the Snow Entomological Museum of The University of Kansas, except three males and three females in the South Australian Museum.

Micronecta carinata n. sp.

Size. Brachypterous form, length 2.5 mm. to 2.6 mm.

Color. Ground color of dorsum yellow to light brown, with dark brown maculations; head with a central longitudinal stripe on vertex; pronotum without maculations; clavus with irregular dark blotches basally and distally; corium with four longitudinal broken stripes, tending to fuse near center. Venter and legs dull gray.

Structural characteristics. Head longer than pronotum, vertex roundly produced in front of eyes; pronotum with noticeable ridge, along hind margin of head; interocular space narrow but slightly wider than eye (2.8:2.7); width to length of pronotal disk as 7.2:1.9; posterior margin of pronotum somewhat straight or hardly curved. Hemelytra with relatively long and dense hairs. Wings reaching seventh abdominal tergum. Prestrigilar flap (fig. 61) about twice as wide as long. Submedian process of seventh sternite (fig. 62) broad basally and gradually narrowing to short, acute point, without enlarged bristles subbasally. Free lobe of eighth tergite (fig. 63) with distinct, round inner angle, rectangular outer angle with numerous long bristles uniformly arranged along lower exterior margin. Right and left parameres broadly styliform and somewhat twisted (figs. 58-60). Foreleg as in Fig. 64.

Comparative notes. M. carinata differs from other Australian species in having four central, fused, broken, longitudinal stripes on the hemelytra, and in the broadly styliform parameres of the male. These distinct characteristics indicate that *M. carinata* is a specialized species.

Holotype. Male, Dorrigo, New South Wales, Australia (J. P. Darlington) in the Museum of Comparative Zoology (Harvard University).

Allotype. Female, same data as holotype.

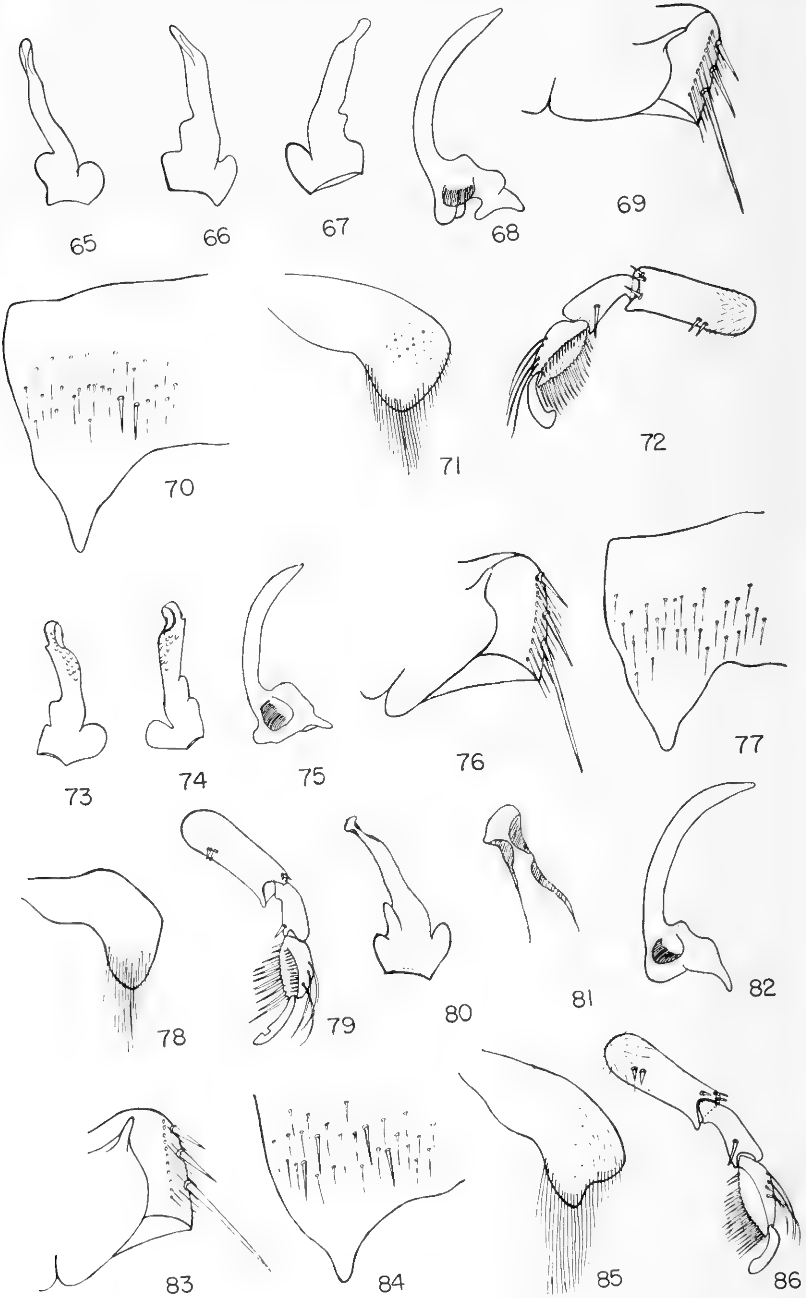
Paratype. One female, same data as holotype, in the Snow Entomological Museum of The University of Kansas.

Micronecta halei n. sp.

Size. Macropterous form, length 3.0 mm. to 3.3 mm.

Color. Dorsum generally yellowish brown, usually without color pattern, or with one transverse band on pronotum and four broken longitudinal stripes on corium. Venter and legs lighter than dorsum.

Structural characteristics. Body elongate, length more than twice greatest width (5.0:2.2); head shorter than pronotum, vertex roundly produced beyond eye margins; interocular space slightly wider than eye (3.5:3.2); width to length of pronotal disk as 8.6:3.3; pronotum spindle shaped. Hemelytra with sparsely scattered fine hairs. Prestrigilar flag as in Fig. 69. Submedian process of seventh abdominal sternite (fig. 70) moderately produced, apex



Figs. 65 to 72. *M. halei.* 65-67, left paramere; 68, right paramere; 69, prestrigilar flap; 70, submedian process of seventh abdominal sternite; 71, free lobe of eighth tergite; 72, foreleg of male. Figs. 73 to 79. *M. queenslandica.* 73-74, left paramere; 75, right paramere;

subacute, with four enlarged bristles subbasally. Free lobe of eighth tergite (fig. 71) with rounded inner angle and rather prominent setigerous outer angle. Right paramere (fig. 68) simply curved and pointed; left paramere (figs. 65-67) without denticulations, broad basally and twisted slightly toward narrow distal part. Palar claw (fig. 72) elongate and expanded apically.

Comparative notes. In general appearance, *M. halei* has no specific diagnostic feature. However, the sclerotized paramere and the shape of the submedian process of the seventh abdominal sternite indicate a close alliance to *M. windi,* from which *M. halei* differs in the twisted distal end of the left paramere and the expanded tip of the palar claw.

Holotype. Male, De Grey at Yarrie Station, Western Australia, July 10, 1953 (N. B. Tindale) in the South Australian Museum.

Allotype. Female, same data as holotype.

Paratypes. Three males and twenty females, same data as holotype. One male and twelve females in the South Australian Museum and two males and eight females in the Snow Entomological Museum of The University of Kansas.

Micronecta queenslandica n. sp.

Size. Macropterous form, length 2.6 mm. to 3.0 mm.

Color. Grayish brown above and pale yellow below. Ground color of vertex mostly grayish yellow contrasting with three parallel longitudinal reddish brown stripes arranged as in *M. batilla*; pattern on pronotum and hemelytra as in *M. robusta* but lighter. Venter of thorax and abdomen yellowish, slightly suffused with gray. Legs mostly yellow, darker on tarsi.

Structural characteristics. Head shorter than pronotum; vertex rounded beyond anterior margins of eyes; interocular space slightly wider than eye (3.5:3.2); width to length of pronotal disk as 8.7:3.0; posterior margin of pronotum somewhat straight in front of scutellum. Hemelytra shiny and smooth, with numerous fine, rather long hairs. Prestrigilar flap (fig. 76) narrow and elongate, unlike those of most other Australian species. Submedian process of seventh sternite (fig. 77) slightly prolonged, without enlarged bristles subbasally. Free lobe of eighth tergite (fig. 78) with inner angle obsolete, outer angle distinctly prolonged and completely margined with bristles. Right paramere (fig. 75) arcuate with pointed apex; left paramere (figs. 73-74) somewhat straight, denticulate with a few conical barbs, ventral margin of distal part with shallow depression, rounded apically. Palar claw with distinct notch (fig. 79).

76, prestrigilar flap; 77, submedian process of seventh abdominal sternite; 78, free lobe of eighth tergite; 79, foreleg of male. FIGS. 80 TO 86. *M. windi.* 80-81, left paramere; 82, right paramere; 83, prestrigilar flap; 84, submedian process of seventh abdominal sternite; 85, free lobe of eighth tergite; 86, foreleg of male.

Comparative notes. The unusually shaped palar claw and the prominent prestrigilar flap as well as the remarkable free lobe of the eighth tergite of the male distinguish this species. The denticulate left paramere seems to indicate a close alliance to *M. virgata*, although *M. queenslandica* has the general facies of *M. adelaidae*.

Holotype. Male, northern Queensland, Australia, Marshall Laird, June, 1954, in the Snow Entomological Museum of The University of Kansas.

Allotype. Female, same data as holotype.

Paratypes. Five males and three females, same data as holotype; one male and three females, Townsville, northern Queensland, Australia, 1920 (G. H. Hill), in the Snow Entomological Museum of The University of Kansas except one male and two females in the South Australian Museum.

Micronecta major n. sp.

Size. Macropterous form, length 4.6 mm. Brachypterous form, length 4 mm.

Color. Medium to light brown, lineations on hemelytra as in *M. robusta* but more distinct. Venter and legs uniformly yellowish.

Structural characteristics. In brachypterous form, head longer than pronotum (1.4:1.2), width to length of pronotal disk as 3.7:1.2. In macropterous form, head as long as pronotum, width to length of pronotal disk as 4.2:1.5. Vertex strongly produced beyond anterior margins of eyes; interocular space as wide as eye or slightly wider; pronotum rounded at posterior margin. Hemelytra shiny with numerous fine hairs. Wings reaching eighth abdominal tergite in brachypterous form. Prestrigilar flap (fig. 33) broad and short, with rounded apex. Submedian process of seventh sternite (fig. 34) prolonger to blunt point, without enlarged bristles subbasally. Free lobe of eighth tergite as in Fig. 35. Right paramere (fig. 32) evenly curved and rounded apically; left paramere stout, slightly curved and denticulate with many conical barbs (figs. 30-31). Femur of foreleg (fig. 36) with two spine-like setae on lower side, palar claw elongate.

Comparative notes. The general appearance of this species and, particularly, the distinctly produced vertex and the relative sizes of the interocular space and the eye, are similar to those of *M. batilla*, but *M. major* differs from *M. batilla* in the parameres, which have a stouter shaft and a rounded distal end, and in the larger body size.

Holotype. Male, Coolabah, New South Wales, Nov. 15, 1900 (W. Froggatt) in the Hungarian National Museum, Budapest.

Allotype. Female, same data as for holotype.

Paratypes. Four females, two in the Hungarian National Museum, Budapest and two in the Snow Entomological Museum of The University of Kansas.

Micronecta windi n. sp.

Size. Macropterous form, length 2.9 mm.

Color. Yellowish brown throughout, pattern completely faded.

Structural characteristics. Head about as long as pronotum, vertex triangularly produced in front of eyes; interocular space wider than eye (3.8:2.9); pronotum spindle shaped; width to length of pronotal disk as 8.0:3.0. Hemelytra shiny and smooth, with sparsely scattered hairs. Prestrigilar flap as in Fig. 83. Submedian process of seventh sternite (fig. 84) noticeably prolonged, with four enlarged bristles subbasally. Free lobe of eighth tergite(fig. 85) with well developed inner rounded angle and pointed setigerous outer angle, posterior margin between angles concave. Right paramere (fig. 82) arcuate, gradually narrowing toward distal point; left paramere (figs. 80-81) slightly curved, free portion emarginate ventrally, distal margin somewhat folded. Palar claw elongate and slightly expanded apically (fig. 86).

Comparative notes. The color pattern of the two available specimens is completely effaced. *M. windi* has the general facies of *M. gracilis* except the former is much smaller. *M. windi* is also similar to *M. halei*; the chief differences are cited under that species.

Holotype. Male, Kuranda, northern Queensland, Australia, Aug. 12, 1938 (R. G. Wind) in the Snow Entomological Museum of The University of Kansas.

Paratype. One male, same data as holotype.

Micronecta sinistra n. sp.

Size. Macropterous form, length 1.7 mm.

Color. Medium brown, head yellowish, pronotum and hemelytra darker; pattern almost completely effaced except for one dark stripe running along outer margin of corium. Venter blackish.

Structural characteristics. Head about as long as pronotum; vertex moderately produced in front; interocular space wider than eye (0.8:0.7). Hemelytra smooth and shiny, with scattered very fine hairs, almost invisible. Abdomen with usual asymmetry reversed, having strigil on the left. Submarginal bristles on left side of fifth abdominal tergite absent (as in most species of *minutissima* group), tergite and prestrigilar flap as in Fig. 12. Submedian process of seventh sternite (fig. 13) broad basally and pointed distally, with four slightly enlarged bristles subbasally. Free lobe of the right, eighth tergite (fig. 14) different from that of dextral species, having two outer, lower and upper, setigerous angles and one inner rounded angle. Right and left parameres (figs. 8-11) similar, free portions curved and well chininized with extremely expanded distal lobe. Foreleg as in Fig. 15.

Comparative notes. The single specimen has sinistral abdominal asymmetry, which deviates from other species of *Micronecta*, but has been recorded once before by Wróblewski (1962) who described a sinistral male individual of *M. quadristrigata* Breddin from Viet-Nam. *M. sinistra* might represent an independent offshoot from the original stock of *Micronecta* because the structural characteristics of the male parameres and the free lobe of the eighth tergite show many differences from other *taxa*.

Holotype. Male, Astrolabe Bay, Stephansort, New Guinea (Biró 97), in the Hungarian National Museum, Budapest.

NOTES ON ADDITIONAL SPECIES

Micronecta annae Kirkaldy

Micronecta annae Kirkaldy, 1905, p. 262.

On the basis of the original description, copied below, it is impossible to recognize this species:

"*M. annae* sp. n.—Head pallid. Pronotum dark fuscous brown, with darker transverse median line. Tegmina fuscuous brown (the margins of the areas narrowly darker), somewhat superficially punctured. Head a little longer than pronotum, rounded in front. Pronotum elongate ellipitical, lateral margins very short, much less than half the width of the posterior margin of an eye. Mesoxyphus acutely triangular. Terminal segment of antenna elongate, somewhat thickened. Intermediate femur equal in length to tibia, tarsus and claw together; tarsus one-half longer than a claw, which is equal in length to the tibia, subcostal furrow much as in *M. vanduzeei*. Length 3¼ mm.

"Australia, Victoria (my collection)."

Micronecta annae Kirkaldy var. *Pallida* Kirkaldy

Micronecta annae Kirkaldy var. *pallida* Kirkaldy, 1907, p. 788.

Recognition of a variety of any *Micronecta* species on the basis of coloration alone, without discussion of the individual variation within the species, seems unacceptable. The following is a copy of the original description:

"*M. annae* Kirkaldy var. *pallida* nov.

No transverse line on pronotum; tegmina with a pale castereous basal band.

"Hab.—Q.: Kuranda (Aug.;Perkins)."

Micronecta erato Kirkaldy

Micronecta erato Kirkaldy, 1905, p. 263.

The original description of this species is mostly based on coloration and almost agrees with all the Australian *Micronecta*. Kirkaldy did give certain structural information on *M. erato* (head, pronotum and body size) which suggests *M. batilla*, but this synonymy is still far from established. The following is a copy of the original description:

"*M. erato* sp. n.—Head and underside pale stramineous. Pronotum pale sordid yellow, with a broad blackish brown median transverse stripe which does not reach the lateral margins. Tegmina sordid stramineous; clavus with two narrow dark brown lines running parallel to interior and corial margins, uniting at the apex of clavus. Corium with two elongate suboval areas narrowly dark-brown-bordered, and the exterior lateral margins also brownish black. Pronotum, scutellum and tegmina somewhat superficially punctured. Head rounded in front, longer than the pronotum; lateral margins of pronotum obsolescent; membrane apically angulate. Length about 3 mm.

"Australia, Victoria (my collection)."

Micronecta carbonaria Horvath

Micronecta carbonaria HORVATH, 1904, p. 595; WRÓBLEWSKI, 1962b, p. 319.

Among the materials lent from the National Hungarian Museum, Budapest, is a specimen of *M. carbonaria* bearing a type label beside the collection label (Berlinhafen, Lemien, New Guinea, 1896 (Biró), although Horvath did not designate a type specimen in his original description. Since Wróblewski recently (1962b) has given a complete description of this species based on the materials from the type series, redescription is not necessary here. Because of the similarities of the parameres, free lobe of eighth tergite, and the palar claw of the foreleg, *M. carbonaria*, *M. virgata* and *M. batilla* seem to be closely related species.

Collection data. Berlinhafen, Lemien, New Guinea, 1896 (Birō) Type; Sepik River, New Guinea (K. P. Schmidt).

Micronecta ludibunda Breddin

Micronecta ludibunda BREDDIN, 1905, p. 57; CHEN, 1960b, p. 115; WRÓBLEWSKI, 1962b, p. 323.

Micronecta inconspicua LUNDBLAD, 1933, p. 96.

Micronecta striatella LUNDBLAD, 1933, p. 98.

Micronecta graphiptera HORVATH, 1918, p. 146.

One female type of *M. graphiptera* from the Hungarian National Museum, Budapest, is available for this study; it confirms Wróblewski's statements (1962b) that *M. graphiptera* is a synonym of *M. ludibunda*.

M. ludibunda is a widely spread species, known from Thailand, Sumatra, New Guinea and the Solomon Islands.

Micronecta quadristrigata Breddin

Micronecta quadristrigata BREDDIN, 1905, p. 57; LUNDBLAD, 1933, p. 87; HUTCHINSON, 1940, p. 376; WRÓBLEWSKI, 1960, p. 301; WRÓBLEWSKI, 1962a, p. 176.
Micronecta minthe DISTANT, 1910, p. 347.

Two specimens, one male and one female, labelled Astrolabe Bay, Stephansort, New Guinea (Biró 97) from the Hungarian National Museum belong to this species. The male is 2.4 mm. and female 2.5 mm. long; most other features of these two specimens agree well with the previous descriptions by Lundblad, Hutchinson, and Wróblewski except for the relative widths of the interocular space and the eye. The ratio of the interocular space to an eye, in the New Guinea specimens, is 1.03, smaller than the same ratio for specimens from Hong Kong and Celebes (Wróblewski, 1960).

Micronecta quadristrigata, because of many unusual morphological structures, was considered a primitive species by Wróblewski, 1960. In 1962, he found one aberrant male from Viet-Nam that showed sinistral abdominal asymmetry. In my opinion, this is additional evidence of the primitiveness of this species. Another species from New Guinea, *M. sinistra*, also has the abdomen sinistrally asymmetrical; at the same time it has many primitive structures such as the undifferentiated, enlarged bristles on the seventh abdominal sternite (fig. 13) and parameres (figs. 8-11) as in some *Tenagobia* species (Deay, 1935). The left and right parameres of *M. sinistra* both have a narrow median shaft and a large expanded lobelike distal end which is almost as large as the basal end, while most other *Micronecta* species have a stout shaft, narrower or pointed distal end, and a broad base. It is possible that dextral and sinistral asymmetrical forms were both common in the early members of this genus. Through the long course of the evolution the most favored form, in this case the dextral, has become dominant. Since only two sinistrally asymmetrical specimens are known (the type of *M. sinistra* and the aberrant *M. quadristrigata*), they may be phylogenetic relics.

In 1962, Wróblewski placed *M. quadristrigata* in a new monotypic subgenus *Sigmonecta*, based on the sigmoid shape of the free lobe of eighth tergite. However, *M. queenslandica* of Australia and *M. eupompe* Hutchinson (1930) of Abyssinia also have such a characteristically shaped free lobe. Yet there is no other structure which shows their affinity. The left parameres of the three species (often used for indicating phyletic relationships among species of *Micronecta*) are strongly different. It seems doubtful that the sigmoid free lobe of eighth tergite alone can have much value for establishing a subgenus.

Micronecta virgata Hale

Micronecta virgata HALE, 1922, p. 327; WRÓBLEWSKI, 1962b, p. 320.

This species is very easy to distinguish from other Australian taxa since it has the largest ratio of the interocular space to the eye width and the longest middle femur of all the known Australian species. After comparing the female syntype from the South Australian Museum with other specimens listed in the following paragraph, I found no special difference between them. In 1962, Wróblewski redescribed this species from specimens from the Solomon Islands; therefore, a redescription is omitted here.

Collection data. Queensland: Carins district (A. M. Lea) (syntype); Townsville, 1920 (G. F. Hill); Townsville, March, 1932 (P. J. Darlington, Harvard Expedition). *Solomon Islands:* Russell Island, Ufa, Sept. 1955 (E. S. Brown); San Cristobal, Ugi, April, 1955 (E. S. Brown).

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MICROGEOGRAPHIC VARIATION AND COVARIATION IN *PEMPHIGUS POPULI-TRANSVERSUS*

By

Richard C. Rinkel

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Microgeographic Variation and Covariation in *Pemphigus populi-transversus*[1, 2]

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ABSTRACT

This study is a quantitative analysis of the microgeographic variation and covariation of 24 characters of two forms of the gall forming aphid, *Pemphigus populi-transversus.* The variation and covariation are separately studied at three levels: within galls, among galls within localities, and among localities. Covariation is studied by means of correlations among the characters and restated in terms of fewer dimensions (factors) by means of factor analysis. The analysis is based on 15 localities of 15 galls each, from Douglas and Leavenworth counties, Kansas.

The two central problems considered are (1) the comparison of the amounts of variation present in this study with corresponding amounts present in previous studies, and (2) a consideration of character covariation within a limited geographic area compared with character covariation over a much larger area.

To determine the amounts of variation present in this study for the characters involved, 24 separate hierarchic analyses of variance were calculated for each of the three levels of variation. It was found that variation among localities forms a much smaller portion of the total variance than in the previous studies, which

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[1] Contribution No. 1202 from the Department of Entomology, The University of Kansas, Lawrence. This paper is part of a thesis presented in partial fulfilment of the requirements for the M.A. degree in Entomology.

[2] Part 4 of a study of variation in the aphid genus *Pemphigus.* Parts 1 to 3, respectively, are the following publications: Sokal (1952), Sokal (1962), Sokal and Rinkel (1963); part 5 is Sokal and Thomas (1965).

[3] The author wishes to express his gratitude to Dr. Robert R. Sokal, Professor of Statistical Biology, without whose assistance this study would have been impossible. Thanks are also due Drs. Charles D. Michener and George W. Byers for their appropriate and helpful comments on the manuscript. Mrs. Betty Lou Deffley and Mrs. Maxine L. Howe assisted in the preparation of the material for study and in the preparation of the data for analysis. The University of Kansas Computation Center furnished computer time to carry out the numerous computations of this study.

involved a much larger geographic area. Variation among galls within localities and variation within galls were found to be of the same general magnitude in the present study as before.

In order to study character covariation, matrices of correlation coefficients among the 24 characters for each level of variation were computed. These were compared with the corresponding matrices from the previous studies, and factor analyses were performed in an attempt to reduce the complexity of the covariation patterns.

At the within-gall-level of variation, the wing, head, and thorax variables seem to be influenced by the same factor as in the previous studies. The remaining variables appear to be influenced by somewhat different factors in the present study. At the intergall level of variation, the patterns of covariation consist of general size factors for each of the two forms studied. At the inter-locality level of variation the factors extracted bear little resemblance to the factors at this level in the previous studies. This would seem to indicate that covariational patterns at the interlocality level in the present study are almost entirely determined by local influences.

In an attempt to describe geographic variation over the area studied, maps of locality means for each of the characters were plotted. A multiple range test was employed on these means to find groups of significantly different locality means. These tests, as expected from the above results, reveal less differentiation among localities in the present study than in the study for eastern North America.

INTRODUCTION

This study is a quantitative analysis of microgeographic variation and covariation of 24 characters of two forms of the gall-forming aphid, *Pemphigus populi-transversus* Riley. It will form part four of a general study of the geographic variation and covariation of morphological characters of this organism.

Part one of this general study (Sokal, 1952) dealt with variation and covariation within a local population at Ripley, Ohio. The 21 characters in this initial study were analyzed with a view to selecting those most useful for a study of intraspecific variation. The characters so analyzed were studied singly by means of the analysis of variance and in combination by means of the analysis of covariance and partitioning of the correlation coefficients.

The second part of the general study (Sokal, 1962) dealt principally with a quantitative assessment of the variation and covariation of 18 of the above characters of the alate forms over eastern North America. The analysis of covariance was abandoned in favor of factor analysis as a means of summarizing patterns of covariation among the characters.

The third part of the general study (Sokal and Rinkel, 1963) was primarily concerned with the description of the geographic variation of the characters studied. Meaningful patterns of variation of the 18 alate characters studied over eastern North America were sought, and various techniques were used in an attempt to clarify the variational trends. The use of multiple range tests (such as the Student-Newman-Keuls test) on locality means of the various characters was introduced.

This study is based on 15 localities from northeastern Douglas County and western Leavenworth County, Kansas. Two main problems are investigated. The first is a comparison of the amounts of variation present at the various levels of this study with those of previous studies. Consideration of this problem should lead to a better understanding of amounts of variation in populations of the organism in areas of various sizes. Allied with a comparison of the amounts of variation present is a comparison of the locality means of the present study with those of the larger studies (Sokal and Rinkel, 1962; Sokal and Thomas, 1963). This should give added information about the patterns of geographic variation of characters in this species.

The second problem is a comparison of character covariation of a limited area with a much larger area. Patterns of covariation at various levels among the characters studied are likely to be somewhat different within a restricted geographic area, as indeed proved to be the case.

Covariation among the stem mother characters, and among stem mother and alate characters combined, are here examined at the interlocality level for the first time.

The variation and covariation of the 24 characters are separately studied at three levels of variation; within galls, among galls within localities, and among localities for the alate characters; among galls within localities and among localities for the stem mother characters. Covariation is studied by means of correlations among the characters and restated in terms of fewer dimensions (factors) by means of factor analysis. Results of the various analyses performed are compared with results from the previous studies.

MATERIALS AND METHODS

The biological material used for this study consisted of both alate fundatrigeniae and apterous fundatrices or stem mothers of *P. populi-transversus*. The fundatrigeniae are the parthenogenetic offspring of the stem mothers, and both occur in the petiole gall formed around the stem mother on the cottonwood, *Populus deltoides*, in the spring. The stem mother hatches from an overwintering egg. The terms alate and stem mother, whenever used below, refer to the fundatrigeniae and the fundatrices, respectively.

The localities from Douglas County and Leavenworth County, Kansas, were chosen because they were sources of 15 or more galls containing a stem mother and at least two alates each. Where more than 15 such galls were available at any one locality, 15 were selected at random from those collected. The localities usually consisted of two or sometimes three cottonwoods. At locality number 15, three samples of 15 galls each were taken from each of three trees within one locality.

Localities within the study were chosen to give as comprehensive coverage of the area as was possible within the ecological limitations of the host plant. A list of localities is given in Table 1.

All material for this study was collected during September, 1961. Galls were snipped from the cottonwoods and placed immediately into containers of 70 per cent ethyl alcohol.

The galls were then sorted and the stem mothers and alates contained in each were removed and placed in separate, numbered vials.

Both alates and stem mothers were prepared for measurement by clearing in successive solutions of dioxane, dioxane-xylene, and pure xylene. They were then mounted in balsam on microscope slides. If more than three alates per gall were available, three were chosen at random from among these and mounted. During measurement, two out of these three were chosen at random for actual measurement.

The alate characters were the same as those used by Sokal (1962); the stem mother characters the same as those employed by Sokal (1952), except for total length and last rostral segment length, which had proved to be unreliable. Of the 18 alate characters measured, 12 were continuous and the last six were meristic. All six stem mother characters were continuous.

In the interest of brevity, abbreviated names, such as antenna III for length of antennal segment III, sensoria III for number of sensoria on antennal segment III, and islands V for number of sclerotic islands in the primary sensorium of antennal segment V, will be used below.

All measurements were made by means of a Reichert microprojector fitted with a vernier scale to correct the difference between real and apparent length of any structure which did not lie level on a slide. Whenever such was the case, the difference in elevation of the two ends of the structure was measured. The true length of the structure was calculated as the hypothenuse of a triangle whose sides were the apparent length of the structure and the difference in elevation of the two ends of the structure, respectively.

ANALYSES OF VARIANCE

Twenty-four separate hierarchic analyses of variance were performed, 12 for the continuous alate characters, six for the meristic alate characters in coded form, and six for the stem mother characters, which were all continuous. Coding of the meristic alate characters was accomplished by adding 0.5 to each of the original values and taking the square root of this value. The coding of the meristic variables was performed in an attempt to normalize their distribution.

For the alate characters, the three levels of variation were between alates within galls, among galls within localities, and among localities, with 225, 210, and 14 degrees of freedom, respectively. For the stem mother characters, the two levels of variation were among galls (individuals) within localities, and among localities, with 210 and 14 degrees of freedom, respectively.

These analyses are interpreted here as model II analyses of variance. The localities can be thought of as being chosen at random from those available in the general area, and the aim here is to estimate the variance components at the various levels of variation.

The results of these analyses are shown in Table 2 and 3, along with some of the results of Sokal (1962) and Sokal and Thomas (1965).

The first two columns of Table 2 show the variances of individuals within galls for the 18 alate characters of both the present study and that of Sokal (1962). These figures represent an average within-gall variance over all localities in the two studies. Since, presumably, all individuals within any one gall are genetically identical, these variances are due entirely to environmental influences. A comparison of these variances between the two columns reveals that they are of nearly equal magnitude except for the characters tibia length and sensoria V. A two-tailed *F* test of the ratios of the variances for each of these two characters showed no significant difference between them.

The next two columns of Table 2 show the sum of the variance components within galls and among galls for the present study and a comparable quantity, the variances among galls within a locality found by Sokal and Thomas (1965). Only eight alate characters and five stem mother characters were used by Sokal and Thomas. Comparison of the two columns again shows nearly equal values. The one exception is for the stem mother character, tibia length. Here the ratio of the two variances shows significant difference at the 0.01 level when tested.

The above comparisons establish that with few exceptions the variances at the two lower levels of variation of the three studies are of the same order of magnitude. Comparisons of the variances at the interlocality level should therefore give a clear picture of the contrast in the amounts of variation present at this level in the various studies.

The next four columns of Table 2 show the mean square of galls within a locality, the mean square of localities, and the significance levels for the *F* ratios calculated for the present study. All the alate continuous characters except head length and antenna V and VI show significant variation among galls and localities. Head length exhibits no added variance at all, antenna V shows significant variation among localities and antenna VI does so among galls. None of the meristic alate characters varies significantly among localities and only one, islands VI, shows added variance among galls. Only two of the stem mother characters, head width and antenna III, show significant variance among localities.

At locality 15, three trees within 50 feet of one another were selected, and 15 galls, each containing a stem mother and at least two alates, were collected from each tree. Measurements were taken of the same 18 alate characters and 18 more analyses of variances were performed.

None of the characters exhibited a significant added variance component among trees at the 1 per cent level, and only one (islands VI) showed significance at the 5 per cent level. None of the meristic variables showed an added variance component among galls within trees; however, the same continuous characters that proved significant at this level for the entire area under study are again significant.

Table 3 contains various ratios of variance components from the four studies under consideration. The first four columns of this table contain the ratios of variance among galls within localities to variance among individuals within galls. The first column is derived from Sokal's (1952) study of one locality near Ripley, Ohio. The second and third columns are from the present study and are the ratios for the main study and for the separate study of three trees, respectively. The fourth column gives the same statistic from Sokal's (1962) study of 23 localities in eastern North America. The ratios from the present study are in general much closer to those of Sokal's later study (1962) than to the earlier one (Sokal, 1952). Since it had been found that the galls of the Ripley, Ohio, locality were unusually well differentiated (Sokal, 1962), these results were to be expected and probably reflect the actual relationship between the two variance components. The fact that no variance components exist at the intergall level for several of the characters which did exhibit small components in the 1962 study, is probably due to the smaller sample sizes of the present study. The same phenomenon is exhibited in the ratios from the separate study of three trees. Since all of the ratios from both the present study and Sokal (1962) are near to or less than one, variance among galls within a locality, in general, accounts for less of the total variance than does variance among individuals within galls.

The next two columns of Table 3 show the ratios of variance among localities to variance among individuals within galls for the present study and for that of Sokal (1962), respectively. It will be noted that in every case the ratios from this study are smaller than the corresponding ratios from Sokal. These results confirm the idea that a much smaller portion of the total variance is due to variation among localities in the present study than in the previous ones. Several of the characters studied, notably the meristic ones, show no added variance component at this level (among localities), while all the characters but one did so over eastern North America. These results are not surprising in view of the minute geographic area of the present study. The lack of variance components for several of the antennal sensoria characters tends to support the hypothesis that they are in general less variable than the continuous characters at the intergall and interlocality levels.

The interlocality ratios just discussed could not be directly compared with the findings of Sokal and Thomas (1965), since the study of these authors was based on but one alate per gall and thus lacked intragall variance. The last three columns of Table 3 show the ratio of the variance component among localities divided by the sum of the variance components within and among galls for the present study and that of Sokal (1962), as well as a comparable ratio, the variance component of localities divided by the variance within localities, for the data of Sokal and Thomas (1965). The ratios from the present study are again in all cases smaller than those from the studies of the wider geographical area. The columns of the present study and that of Sokal and Thomas (1965) also contain ratios for several stem mother characters. For the two stem mother characters (head width and tarsus length) which exhibit significant variation among localities, the ratios of variance among localities to variance among galls within localities are smaller than the comparable ratios obtained by Sokal and Thomas (1965). This again indicates that, for the limited area under study, variance among localities contributes only a small portion of the total variance.

CORRELATIONS

The cross-products for the 24 variables studied were obtained simultaneously with the analyses of variance by matrix operations carried out by programs written for the IBM 650 digital computer. These programs are written in the FORTRAN interpretive language and hence are available for use on almost all IBM and many other computers.

The three levels of alate variation yielded three covariance matrices, intragall, intergall, and interlocality. The two levels of stem mother variation yielded two covariance matrices. In each case the covariances obtained correspond to the partitioning of the variance for that particular level. Covariances for the alate-stem mother character correlations were obtained by using gall sums of the alate characters and proceeding as above.

Product-moment correlations were obtained from all of the above matrices in the usual manner; that is, by dividing each covariance by the geometric mean of the appropriate variances. Component correlations (Sokal, 1962) were computed for the two higher levels of variation for the alate characters and for the interlocality level of the stem mother characters.

THE INTRAGALL CORRELATIONS

The intragall correlation coefficients (for alate characters only) are shown in the half matrix below the diagonal in Table 4. In general these correlations are low. On the average they are lower than the intragall correlations found by Sokal (1962), but essentially the same pattern of significant ($P < 0.01$) coefficients obtains in the present study as in the previous one. Several differences will, however, be noted. As in the previous study, correlations among the meristic characters are practically nonexistent. The continuous characters are significantly correlated, with several exceptions. Head length shows significant correlation with only three other characters. Antenna VI shows significant correlation with only half of the other continuous variables and several of the other continuous characters are significantly correlated with only one-half to two-thirds of the others. This pattern would seem to agree more closely with the results of Sokal (1952, table 4) on a local population than with his study of eastern North America in which all the continuous characters were significantly correlated. This may in part be due to the fewer degrees of freedom employed in the present study.

A cluster analysis of all correlations above 0.350 in the matrix reveals a major cluster of wing, head, thorax, and leg variables and also includes, rather strongly, antenna V. This cluster is similar to that obtained by Sokal (1962), for the corresponding matrix of his study. Antenna V was not, however, included in that cluster, nor were other antennal variables. The cluster of highly correlated variables obtained in the present study at the intragall level seems to be similar to the intergall component cluster of Sokal (1962) in that it does include an antennal variable.

THE INTERGALL CORRELATIONS

The intergall product-moment correlations for both alate and stem mother characters are shown in the half matrix below the diagonal in Table 5. For the alate characters, this matrix is in general quite similar to the corresponding matrix of Sokal (1962), both in the magnitude of the correlations and in the arrangement of the significant correlations within the matrix. Almost all the continuous alate variables are rather highly intercorrelated. Head length, however, is not as highly correlated with the other continuous characters as in Sokal's (1962) intergall matrix and in general fewer of the correlations among the continuous variables are significant than in that matrix. This again may be due to the fact that fewer degrees of freedom were available in the present study.

Almost without exception the meristic alate characters show no appreciable correlation, either among themselves or with the continuous characters. Sensoria III, however, is significantly correlated with seven of the continuous alate characters, and sensoria IV is significantly correlated with tarsus length as is islands VI with thorax width.

Most of the stem mother characters are significantly intercorrelated, with the exception of tibia length with tarsus length, and tibia length with antenna IV.

None of the correlations between alate and stem mother characters proved to be significant at the intergall level. This confirms Sokal's (1952) finding of no covariation of alate and stem mother characters within a locality.

The intergall component correlation coefficients are shown in the half matrix above the diagonal in Table 6. Intergall component correlations could not be calculated for head length, antenna V, and all of the meristic characters except islands VI, since these characters showed no added variance component at this level of variation.

The component correlations shown are, in general, higher than the corresponding product-moment correlations. All the applicable continuous characters are highly correlated and islands VI is significantly correlated with almost half the other characters in contrast to correlation with only one, in the case of the product-moment correlations. Thus by eliminating contributions from lower levels of variation by means of component correlations, we arrive at a clearer picture of the character relationships at this level.

On comparing the intergall component matrix with the intragall matrix, we find that the major differences are that the correlations are uniformly higher and that islands VI shows a much closer relationship with some of the continuous variables.

A cluster analysis of all component correlations greater than 0.600 reveals a cluster of wing, head, thorax, leg, and antennal variables similar to the cluster derived for the intragall correlations of this study. However, the antennal variable involved here is antenna VI rather than antenna V.

Cluster analysis of the corresponding matrix of Sokal (1962) reveals much the same cluster except for the antennal variables involved. Antenna IV is included in the cluster of the present study, while it and antenna V are not in the previous study. Since it was impossible to calculate component correlations for the variable antenna V in this study, it is not known whether it would have entered this cluster. Inspection of the product-moment correlations for this variable seem to indicate that it would have been included as in the cluster in Sokal (1962).

THE INTERLOCALITY CORRELATIONS

The interlocality correlation coefficients are shown in Table 6 with the product-moment correlations below and the component correlations above the diagonal of the matrix.

In comparing the alate interlocality product-moment correlations with the analogous matrices for the two lower levels of variation, a different pattern of relationships emerges. Although the significant correlations are almost without exception among the continuous variables, they are considerably fewer in number. In general the locality product-moment matrix of correlations among alate characters agrees rather closely with the corresponding matrix of Sokal (1962).

There is only one significant product-moment correlation coefficient between alate and stem mother characters. Sensoria VI and stem mother antenna IV are highly correlated. Unfortunately neither of these variables showed significant variation among localities and thus it is impossible to follow this trend in the component correlations. Several of the other alate variables show appreciable, if nonsignificant, correlations with stem mother characters and this covariational trend at the interlocality level emerges in the factor analysis of the interlocality component matrix.

Among stem mother characters, head width, femur length, and antenna III are highly correlated.

In the matrix of locality component correlations head length, antenna VI, and all of the meristic alate characters except islands V, plus all of the stem mother characters except head width and antenna III, are missing because all of these variables lacked significant variance components at the interlocality level. In this matrix the pattern evident in the product-moment correlations becomes more pronounced. Among the alate characters there is a cluster of wing, head, thorax, and leg variables and a connection between this cluster and the character antenna IV. These results differ from those of Sokal (1962) in that the antennal variables of that matrix formed a cluster that was separate from the cluster of thorax and leg variables. The antennal variables of the present study do not cluster with the head variables, but since antenna VI is missing in this study it is impossible to say if it would have been highly correlated with head length as was the case in the previous study. Wing length in this study is not independent of the leg and thorax characters; it was not included in the interlocality cluster of Sokal (1962).

There are no significant component correlations of the alate characters and the two stem mother characters present in this matrix. Among the stem mother characters, head width and antenna III are highly correlated.

Correlations within one locality were also computed among gall size, leaf size, stem mother head width, and antenna III, since it was suspected that there might be a relationship among these variables within a locality. The two stem mother characters that were chosen from the six available were those with the highest loadings on the general size factor for stem mother characters which was extracted from the gall component matrix. Rather surprisingly, none of these variables were significantly correlated at this level, although stem mother size and gall size, and leaf size and gall size, had proved to be positively correlated on an interlocality basis in an earlier study (Sokal, unpublished results).

FACTOR ANALYSES

The use of factor analysis in the interpretation of matrices of correlations among characters at several levels of variation has been developed by Sokal (1962).

The three correlation matrices (intragall, intergall component, and interlocality component) subjected to factor analysis in this study were treated in the following manner: factors were first extracted from the matrices by Thurstone's complete centroid method. The residual matrices were then tested for completeness of factor extraction by several criteria (see Sokal, 1959). The factors were then re-extracted until estimates of the communalities stabilized. The resulting centroid factor matrices were rotated to simple structure by Sokal's (1958) mass modification of Thurstone's analytical method (MTAM). All of the above computational steps were performed on an IBM 650 digital computer with floating decimal arithmetic and indexing accumulators.

The results of these analyses, the three simple structure matrices (intergall component, intragall, and interlocality component), are shown in Table 7. These matrices represent the correlations between each variable and each factor.

In the intragall matrix, four factors were necessary to account for the major portion of the covariation, while in the intergall component and the interlocality component matrices, three were sufficient.

In the intragall simple structure matrix, factor I is a wing, head width, thorax, and femur length factor, which also affects tibia length and tarsus length to a lesser degree. This factor corresponds in general to factor I of Sokal (1962), except that tibia length and tarsus length are not so strongly affected in the present case. Factor II is an antennal factor affecting antenna III and less strongly, antenna IV, sensoria III, islands V, and islands VI. This factor seems to correspond to factor II of Sokal (1962), except that the latter factor does not affect islands V and VI. Factor III is another antennal factor acting upon antenna V and antenna VI. Factor III of Sokal (1962) does affect antenna VI but other than this the two factors have little in common. Factor IV of the present study is a leg factor affecting tibia lengh and tarsus length, and, to a much lesser extent, sensoria IV and V. Tibia length and tarsus length seem to vary much more independently of the other alate variables at this level than was the case in Sokal's (1962) material. It will be noted that head length and sensoria VI have no high loadings on any of the four factors and therefore presumably represent independent dimensions of variation at this level.

The intergall component correlation matrix involves both alate and stem mother characters. In the simple structure matrix for this level, factor I appears to be a general size factor involving all of the alate characters included in the intergall component matrix. Factor II affects islands VI and, weakly, antenna VI. Factor III involves only the stem mother characters.

The three patterns of covariation present at the intergall level are very elegantly summarized by factor analysis. Covariation of the alate characters resolves into two clusters, the continuous and the meristic characters, respectively. The stem mother characters vary together as a group quite independently of the others. Of course this information is simply a summarization of that to be derived from inspection of the matrix of correlations; however, it does seem that these results provide an additional example of the validity of simple structure solutions for this type of analysis.

In comparing the intergall component simple structure matrix of the present study with the same matrix in Sokal (1962), we find that while the covariation of the alate characters is divided between a wing-leg-antenna factor and a head-thorax factor in the latter matrix, here most of the covariation of alate characters is accounted for by a general size factor. Comparison of the intergall simple structure matrix of the present study may also be made with a similar matrix from the study of alate and stem mother character variation and covariation over eastern North America by Sokal and Thomas (1965). In this work covariation of characters at the intergall level is summarized by four factors. Two of these affect alate characters, while the remaining two involve the stem mother characters. These results confirm the independence of covariational patterns of alate and stem mother characters at the intergall level.

At the interlocality level, the component correlation matrix results in three factors. Factor I is a wing-leg-antennal factor (not including antenna V). Factor II is a head width-thorax-femur length factor. Factor III involves stem mother head width and antenna III as well as alate antenna V. This factor indicates the first evidence of covariation between alate and stem mother characters. The factor analysis of the interlocality component correlation matrix from Sokal and Thomas (1965) reinforces this indication although not involving the same characters. In the latter study, four factors account for most of the covariation. Two of these factors show influence on stem mother and alate characters. Unfortunately alate antenna V is not included in the latter study and therefore direct comparison of the two analyses for this character is impossible.

Factor III of Sokal and Thomas resembles factor I of the present study in that wing length is affected along with the head, thorax, and leg variables by both factors. This was not the case in Sokal (1962) where wing length was more highly loaded on another factor. With the exceptions of the similarities noted above, the interlocality factors of the present study bear few close resemblances to the corresponding factors of the other two studies.

DESCRIPTION AND ANALYSIS OF GEOGRAPHIC VARIATION

Figure 1 is a map of the localities and their code numbers. As a first step in analyzing the geographic variation of the characters the descriptive facts are best summarized by separate maps for each of the characters which exhibited significant variation among localities. These maps, showing the means of the populations at the various localities, are based on the data in Table 8 stated as mm. for continuous characters and counts for meristic characters. The average standard error within localities is furnished at the right of each row instead of attaching a separate standard error to each mean. This average standard error suffices for any significance testing desired, since the means are all based on the same number of individuals.

To simplify comparison of distribution maps of different characters the conventions adopted by Sokal and Rinkel (1963) were again adopted. The original scale of measurement of the data was transformed by standardization. Standardization of each locality mean was carried out by dividing its difference from the grand mean of localities by the standard deviation of locality means. This procedure results in negative standard scores for approximately half of the localities. To avoid mapping of negative quantities, the standard scores are transformed by adding 5.0 to each score. Thus a locality with a mean identical to the grand mean of localities will score 5.0, a locality with a smaller mean will score below 5.0, and a locality with a larger mean will score above 5.0. As a final step in simplifying the maps, all scores were multiplied by 10 to avoid decimal points. Thus a locality with a score of 5.2 is mapped as 52.

In studies of geographic variation the analysis of variance may be considered from two different but legitimate points of view as was pointed out by Sokal and Rinkel (1963). In the earlier portion of this study it was interpreted as a model II analysis of variance when it was desired to measure the contribution of the various sources of variation to the overall variance. In the present part of this study, however, the analysis of variance is interpreted as model I since we wish to make comparisons among the locality means. The primary concerns at this point are the patterns rather than the amounts of variation present.

The model II analyses of variance yielded 12 characters that exhibited significant variation among localities. We wish now to estimate differences in means between localities and test these for significance.

The application of ordinary *t* tests to such data is not statistically legitimate (Sokal and Rinkel, 1963). Therefore tests between means at any two localities were carried out by means of a multiple range test, the Student-Newman-Keuls (SNK) test (see Steel and Torrie, 1960). Multiple range tests have been used previously in studies of this type by Cross (1955) in a study of geographic variation of bees of the subgenus *Epinomia*, by Ehrlich (1955) in a study of the butterfly, *Erebia epipsodea*, and by Sokal and Rinkel (1963) in the study of geographic variation of *Pemphigus populi-transversus* in eastern North America. All multiple range tests array the means in order of magnitude and delimit either mutually exclusive or overlapping sets of means. Those means contained in any one such set are not significantly different among themselves. The Student-Newman-Keuls (SNK) test was adopted for the present study because of previous satisfactory results (Sokal and Rinkel, 1963), and because it yielded relatively less overlap and hence more differentiation among sets than other such tests.

Results of the SNK test are shown graphically along the righ hand margins of Figures 2 through 5 in the manner of Sokal and Rinkel (1963). These diagrams show the 15 locality means for any one character arrayed in order of magnitude from lowest to highest. Lines to the right of the array define sets of means not significantly different. Any two means not connected by a single line can be considered to be significantly different from one another at $P < 0.01$.

The conventions used for differentiating levels of means on the distribution maps (Figures 2-5) were based on the SNK tests (see Sokal and Rinkel, 1963). The low group was dotted, the intermediate group hatched with diagonal lines, and the high group cross-hatched. If significance tests are desired they may be easily performed by comparing the means on the map with the SNK diagram alongside it. Several cases were found in this study where the SNK test did not differentiate subsets among the means in spite of significant variance ratios in the analysis of variance. In such cases all means were arbitrarily coded as belonging to a homogeneous low group.

To conserve space, a map for only one character, alate thorax length, is shown in Figure 2. This character shows a group of high scores in the center of the area studied (localities 3, 4 and 5). Intermediate level scores are shown at localities 7, 1 and 15. Low areas are largely in the south and east, but also at locality 6 in the west of the area. Maps for the eleven other significantly differentiated characters can be consulted in Rinkel (1963).

As a result of the factor analyses discussed previously, three patterns of character covariation were shown at the interlocality level of variation. To represent these factors, three characters for each factor were chosen. Those characters were the ones having the highest three loadings on the factor to be represented. Wing length, tibia length, and tarsus length were chosen to represent factor I. Head width, thorax length, and femur length were chosen for factor II, as were antenna V, stem mother head width, and stem mother antenna III for factor III. Averages of the standardized scores of the three characters for each factor were computed for each locality and plotted on maps (Figures 3, 4 and 5). Estimated variances of galls within these localities were computed, based on expected variances of sums of variables and allowing for the correlations between the variables composing the average score for each factor. Using these estimates of the variance, SNK tests were applied to the average scores for the localities. Diagrams for these SNK tests are furnished at the right hand margin of Figures 3 to 5. The five per cent significance level was used in these SNK tests to provide as much differentiation as possible. Factor I (see Figure 3) produces an area of high means in the center of the area studied. Locality means decrease in magnitude outward from the center of the area. The lowest mean score is at locality 14. Factor II also produces an area of high central scores surrounded by intermediate values (Figure 4). The area of lowest scores however, includes localities 9, 10 and 13. Unfortunately factor III produced no significant differences when the SNK test was applied. However it may be seen from inspection of the map (Figure 5) that the area of highest scores is here centered at locality 1. In general three patterns of geographic variation of the factors may be seen. These patterns are not so distinct as those of Sokal and Rinkel (1963). This may in part be due to the smaller area and sample sizes of the present study having not produced as great differentiation among localities as did the previous work.

In comparing the area of the present study with that analyzed by Sokal and Rinkel (1963), locality means for the various characters must be compared in millimeter units and counts since the standardized scores from the two studies are based on different standard errors and grand means of characters. Table 9 shows the grand means for all localities of the characters of the present study along with the locality means for the same characters from the four closest localities from Sokal and Rinkel (1963), and Sokal and Thomas (1965). These localities were Hutchinson, Reno Co., Kansas; Arkansas City, Cowley Co., Kansas; Kansas City, Jackson Co., Missouri; and Delawan, Morris Co., Kansas. Also shown in Table 10 are the ranges of the locality means from both the present study and Sokal and Rinkel (1963).

It is interesting to note that, while variation among localities is much greater over eastern North America than is variation among localities in the present study, the differences between the four localities closest to the area under study here are rather large. For instance the mean value for wing length of the present study is much closer to the locality mean for the same character at New Trenton, Indiana (see Sokal, 1962, table 2) than it is to any of the four locality means from Table 9 of this study.

Comparison of the ranges of locality means of the two studies shows that for most of the characters the ranges found in the present study are contained within those found in Sokal and Rinkel (1963). However, important exceptions exist. For the alate characters, wing length, head width, thorax width, tarsus length, antenna V, and sensoria IV, the extreme high value of the present study is greater than the high value from Sokal and Rinkel (1963). For only two characters, head length and islands VI is the extreme low mean value lower than in the previous study.

DISCUSSION AND CONCLUSIONS

THE ANALYSES OF VARIANCE

In general the analyses of variance performed in the present study are of most interest when compared with similar analyses of the same characters over geographic areas of both smaller and much greater size. The most important conclusion to be derived from such comparisons is, as might be suspected, that variation among localities forms a much smaller portion of the total variance for any one character in the present study than was the case in the study of eastern North America (Sokal, 1962). The fact that fewer characters exhibited significant variation among localities in the present study tends to bear out such a conclusion. The meristic characters in general tend to be less variable than continuous characters over a geographic area and also within the localities studied. That stem mother characters tend to confirm the above conclusions is evidenced by the fact that only two such characters showed significant variation among localities in the present study, while in another study of the same characters over eastern North America (Sokal and Thomas, 1965) all stem mother characters studied yielded significant variation among localities.

The amount of variation within galls is very nearly the same for the three studies. There are two exceptions to this statement. The variance within galls for the alate character sensoria V is much smaller than the comparable variance from Sokal (1962). It may indeed be the case that the variance within galls for this character is less in this area. In the case of the stem mother character, tibia length, however, the large error variance (among galls within localities, since there was only one stem mother per gall) may be due to inaccuracy in measurement, since in many cases this structure was obscured by the large, soft body of the stem mother.

The variance within galls of the alate measurements is presumably due to environmental influences only, since all of the alates within any one gall are genetically identical, barring mutations. This environmentally induced variance is very nearly equal in this study to the variance shown for eastern North America by most of the characters. Thus the factors acting to produce this variation are probably similar.

The amount of variation present among galls within localities for the three studies seems to be of the same general magnitude. As was pointed out earlier, the Ripley, Ohio, locality studied by Sokal (1952) seems to have been unusually well differentiated among galls. Hence the ratios of variance among galls to variance within galls for that study are considerably larger in magnitude than the comparable ratios in the present study and that of Sokal (1962). Ratios of the same quantities from the substudy of three trees in the present work are of the same magnitude as the ratios of Sokal (1962), and the ratios over the whole area of the present study.

Variation among galls within localities is due to both genetic and environmental influences. Thus, considering the above results, these influences must be of relatively the same magnitude over the area studied as they are on the average over the whole of eastern North America.

Variation among localities must also be due to environmental and genetic causes. As mentioned previously, this variation is much smaller in the present study than in the previous studies. Inspection of the ratios of variance among localities to variance among individuals within galls (Table 3) reveals, however, that variation among localities is not a linear function of the distance between localities. For instance the above ratio for the alate character wing length is 0.43 in the present study. In Sokal (1962) the same ratio is 2.98. Thus the latter ratio is roughly seven times the former while the average distance between localities of Sokal's study is certainly greater than seven times the average distance between localities for this study.

Unfortunately it is impossible to partition the interlocality variance into environmental and genetic components. However, is seems that if the genetic differentiation were a function purely of the distance between localities, the interlocality variances of the Sokal (1962) study are less than would be expected. Perhaps similar environmental combinations result in similar gene complexes.

The comparatively large amount of interlocality variance present in the limited area studied suggests either that the population structure of this organism consists of many small, extremely localized populations or that microgeographically differentiated ecological factors are very important in causing phenotypic differentiation. Most likely both explanations are partially true.

The separate study of three trees within one locality revealed very little significant variation among trees within a locality. These results justify the use of the sampling procedures in which several trees within a small area are sampled and counted as one locality.

THE CORRELATIONS AND THE FACTOR ANALYSES

As mentioned by Sokal in his study of eastern North America, intragall correlations are based on common factors of environmental origin which must act during the development of the organisms, since, presumably, genetic differences do not exist among individuals within galls. The intragall correlations among the alate characters of the present study are of the same general magnitude as those found by Sokal (1962). A cluster of high correlations is again found among the wing, head, thorax, and leg variables and in the present study, one antennal variable, antenna V, is included in this cluster. The patterns of covariation at this level, as reflected by a comparison of the factor analyses, are, however, somewhat different.

Factor I of both studies involves wing length, head width, thorax length, thorax width, and femur length. In the present study, tibia length and tarsus length, however, are not affected by factor I. Tibia length is not strongly influenced by any of the four factors of the present study and may represent an independent dimension of variation. Tarsus length is most strongly influenced in the present work by factor IV. In the previous study the antennal variables were most strongly affected by factor II, while in the present study they are influenced in groups of two or less by all of the last three factors.

It appears then that in the present study the wing, head, and thorax variables are influenced by the same general environmental factor as in the previous study. The remainder of the alate variables are, however, influenced by different factors which come into play within the geographic area under study. The two leg variables, tibia length and tarsus length are influenced by a factor which also has an effect upon sensoria IV and V. Tibia length is, however, influenced in the opposite direction from tarsus length and, as noted above, not too strongly. Antenna III is influenced by factor II which has very little influence on any of the other variables. However factor II is highly correlated with factor I and thus represents a very similar dimension of variation. Antenna V and VI share factor III which, again, has little effect on the other variables.

Factor I of the present study may represent a general size factor as it did in the previous study. Factor III found here may bear some relation to factor II of the previous study but this is far from clear cut. The remainder of the factors are perhaps best interpreted as being of local origin.

At the intergall level of variation, the component correlations again reflect a cluster of the wing, head, thorax, leg, and some of the antennal variables for the alate characters. Here, however, the patterns of covariation are somewhat different from those of the previous level of variation. Factor I is again a general size factor for the alate characters. All of the alate variables included at this level are highly loaded on factor I except antenna VI and islands VI which are more strongly influenced by factor II, which appears to be an antennal extremity factor. The influence of a leg character-wing length factor such as factor II of Sokal (1962), does not appear in the present study. The stem mother variables, which are present in the correlation matrix at this level, are all highly influenced by factor III. Factor III, therefore, appears to be a general size factor for the stem mother characters of the present study. In summary, the patterns of covariation at this level of variation seem to consist of characters influenced by the general size factors for both the alates and the stem mothers. The exception to this is the appearance of an antennal extremity factor for the alate antennal characters.

The fact that no group of covarying stem mother and alate characters appears is, of course, not surprising since no high correlations involving these characters were found. In general, the patterns of covariation at this level are different from the Sokal (1962) study.

At the interlocality component level of variation, the correlation matrix gives rise to three factors. The first two of these factors represent covariational patterns among the alate characters. The third factor is of special interest since it reveals a group of both alate and stem mother characters. This is supported by the findings of Sokal and Thomas (1965) and may represent a common genetic influence at the interlocality level of variation.

In summary, it may be said that while the amounts of variation present at the respective levels in this study reflect what might be expected from a consideration of and a comparison with, previous studies, the patterns of covariation present in the material studied here differ considerably from previous results. These differences are most striking at the interlocality level where the influence of different local factors within the area studied come into play. It should also be added that the data on interlocality covariation are based on only 15 localities, hence are not too reliable. Differences in covariational patterns are, however, present at the lower levels of variation and might reflect the influence of factors present in the area studied and absent in most areas that were included in the study of eastern North America. One might expect the influence of factors of local importance in one area to be obscured by the presence of other factors in other areas in such a study as that of Sokal (1962). Investigation of the factors influencing covariation in such a study as the present one may at least give insight into the types of patterns which may be present within a microgeographic area.

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Table 1. List of localities employed in this study.

Locality Code Number	Locality	Date of Collection
1.	Douglas Co. Kan. U.S.G.S. Lawrence East map, quadrat 25, on boating ground, west bank of Kansas River.	15-IX-61
2.	Douglas Co. Kan. U.S.G.S. Midland Section map, quadrat 18, ¼ mile west of junction of U.S. Highways 40 and 24, 1 mile north of Lawrence, Kan.	27-IX-61
3.	Douglas Co. Kan. U.S.G.S. Lawrence East map, quadrat 20, east of Bismarck Grove.	8-IX-61
4.	Douglas Co. Kan. U.S.G.S. Midland Section map, quadrat 7, ½ mile east and ¼ mile north of U.S. Highway 24-59.	1-IX-61
5.	Douglas Co. Kan. U.S.G.S. Midland Section map, quadrat 17, ¼ mile north of U.S. Highway 40, east of Lawrence, Kan. airport.	1-IX-61
6.	Douglas Co. Kan. U.S.G.S. Williamstown Section map, quadrat 15, along creek north of east-west county road due south of Lakeview recreation area.	2-IX-61
7.	Douglas Co. Kan. U.S.G.S. Williamstown Section map, quadrat 15, due east of Lakeview Lake and ¼ mile southeast of Lakeview School.	2-IX-61
8.	Douglas Co. Kan. U.S.G.S. Lawrence East map, quadrat 36, along south bank of Kansas River.	6-IX-61
9.	Douglas Co. Kan. U.S.G.S. Lawrence East map, quadrat 36, between Kansas River and county road intersection No. 811.	6-IX-61
10.	Douglas Co. Kan. U.S.G.S. Lawrence East map, quadrat 33, ¼ mile north of county road intersection No. 817.	6-IX-61
11.	Douglas Co. Kan. U.S.G.S. Lawrence East map, quadrat 32, ½ mile east of county bridge No. 818.	6-IX-61
12.	Douglas Co. Kan. U.S.G.S. Lawrence East map, quadrat 33, ½ mile east of county road intersection No. 822.	8-IX-61
13.	Leavenworth Co. Kan. U.S.G.S. Lawrence East map, quadrat 27, at county road intersection No. 811.	8-IX-61
14.	Leavenworth Co. Kan. U.S.G.S. Midland Section map, quadrat 15, north of Kansas Highway 32 at county road intersection No. 879.	11-IX-61
15.	Douglas Co. Kansas. U.S.G.S. Lawrence East map, quadrat 32, ⅛ mile east of county road intersection No. 822.	15-IX-61

TABLE 2. Results of analyses of variance.

	Mean Squares						F ratios (Present study)	
Characters	Individuals within galls (present study)	Individuals within galls (Sokal, 1962)	σ^2 Gall + σ^2 within (present study)	Galls within a locality (Sokal & Thomas, 1965)	Galls within a locality (present study)	Localities (present study)	$\frac{\text{Var. among galls}}{\text{Var. within galls}}$	$\frac{\text{Var. among localities}}{\text{Var. among galls}}$
Alates:								
Wing Length	.01567	.01090	.0418	.0247	.06786	.28711	+ +	+ +
Head Length	.00022	.00025	X	X	.00024	.00035	— —	— —
Head Width	.00034	.00040	.00655	.00061	.00076	.00267	+ +	+ +
Thorax Length	.00148	.00182	.00307	.00269	.00465	.02556	+ +	+ +
Thorax Width	.00274	.00259	X	X	.00827	.05210	+ +	+ +
Femur Length	.00170	.00103	X	X	.00380	.00983	+ +	+ +
Tibia Length	.00323	.00199	.00382	.00283	.00541	.01320	+ +	+ +
Tarsus Length	.00014	.00007	X	X	.00024	.00085	+ +	+ +
Antenna III	.00019	.00015	.00030	.00026	.00042	.00099	+ +	+ +
Antenna IV	.000035	.000030	X	X	.000080	.000385	+ +	+ +
Antenna V	.000083	.000040	X	X	.000102	.000214	— —	+ +
Antenna VI	.000108	.000120	.00016	.00019	.000214	.000374	+ +	— —
Sensoria III	.9658	.7797	.9658	1.1356	.07960	.12131	— —	— —
Sensoria IV	.1137	.1015	.1137	.1600	.02340	.03352	— —	— —
Sensoria V	.0311	.0739	X	X	.00371	.00343	— —	— —
Sensoria VI	.0156	.0188	X	X	.00201	.00110	— —	— —
Islands V	.4667	.6261	X	X	.05152	.00713	— —	— —
Islands VI	.6422	.8421	X	X	.07852	.12014	+ +	— —
Stem Mothers:								
Head Width	X	X	.00094	.00120	.00094	.00330	X	+ +
Femur Length	X	X	.00112	.00110	.00112	.00159	X	— —
Tibia Length	X	X	.00495	.00079	.00495	.00344	X	— —
Tarsus Length	X	X	X	X	.000096	.000080	X	— —
Antenna III	X	X	.000275	.000270	.000275	.000531	X	+
Antenna IV	X	X	.000084	.000090	.000084	.000060	X	— —

Explanation:	
X	signs denote either variables not used or not applicable in the corresponding category.
+ +	denotes significance at the $P \leqq 0.01$ level.
+	denotes significance at the $P \leqq 0.05$ level.
— —	denotes no significance ($P > 0.05$)

TABLE 3. Comparison of ratios of variance components.

Characters	$\frac{\sigma^2 \text{ galls}}{\sigma^2 \text{ within galls}}$ (Sokal, 1952)	$\frac{\sigma^2 \text{ galls}}{\sigma^2 \text{ within galls}}$ (present study)	$\frac{\sigma^2 \text{ galls}}{\sigma^2 \text{ within galls}}$ (separate study of 3 trees)	$\frac{\sigma^2 \text{ galls}}{\sigma^2 \text{ within galls}}$ (Sokal, 1962)	$\frac{\sigma^2 \text{ localities}}{\sigma^2 \text{ within galls}}$ (present study)	$\frac{\sigma^2 \text{ localities}}{\sigma^2 \text{ within galls}}$ (Sokal, 1962)	$\frac{\sigma^2 \text{ localities}}{\sigma^2 \text{ galls} + \sigma^2 \text{ within}}$ (present study)	$\frac{\sigma^2 \text{ localities}}{\sigma^2 \text{ galls} + \sigma^2 \text{ within}}$ (Sokal, 1962)	$\frac{\sigma^2 \text{ localities}}{\sigma^2 \text{ within localities}}$ (Sokal & Thomas, 1965)
Alates:									
Wing Length	1.86	1.66	1.58	1.54	0.43	2.98	0.14	1.17	1.39
Head Length	0.64	0	0	0.21	0	0.19	X	X	X
Head Width	1.64	0.62	1.14	0.50	0.15	0.40	0.09	0.27	0.47
Thorax Length	4.81	1.07	0.71	0.86	0.44	0.97	0.21	0.52	0.67
Thorax Width	3.13	1.01	0.56	0.63	0.50	0.55	X	X	X
Femur Length	2.21	0.62	0.60	0.75	0.08	0.83	X	X	X
Tibia Length	1.82	0.71	0.70	0.65	0.08	0.83	0.05	0.48	0.59
Tarsus Length	0.92	0.36	0.98	0.58	0.11	0.82	X	X	X
Antenna III	1.07	0.61	1.50	0.76	0.07	1.21	0.04	0.69	0.84
Antenna IV	0.95	0.63	1.35	0.72	0.26	0.85	X	X	X
Antenna V	0.52	0	0	0.51	0.04	0.35	X	X	X
Antenna VI	0.88	0.49	0.96	0.39	0	0.31	0	0.22	0.12
Sensoria III	0	0	0	0.37	0	0.28	0	0.20	0.17
Sensoria IV	0	0	0	0	0	0.32	0	0.32	0.17
Sensoria V	0	0	0	0	0	0.05	X	X	X
Sensoria VI	0	0	0	0.14	0	0	X	X	X
Islands V	0	0	0	0	0	0.08	X	X	X
Islands VI	0.03	0.23	0	0	0	0.06	X	X	X
Stem Mothers:									
Head Width	X	X	X	X	X	X	0.17	X	0.29
Femur Length	X	X	X	X	X	X	0	X	0.41
Tibia Length	X	X	X	X	X	X	0	X	0.25
Tarsus Length	X	X	X	X	X	X	0	X	X
Antenna III	X	X	X	X	X	X	0.06	X	0.26
Antenna IV	X	X	X	X	X	X	0	X	0.19

Explanation: X signs denote either variables not used or inapplicable in the corresponding category.

TABLE 4. Intragall correlations.

	Wing Length	Head Length	Head Width	Thorax Length	Thorax Width	Femur Length	Tibia Length	Tarsus Length	Antenna III	Antenna IV	Antenna V	Antenna VI	Sensoria III	Sensoria IV	Sensoria V	Sensoria VI	Islands V	Islands VI
Wing Length	X	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....
Head Length	*–15*	X	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....
Head Width	33	*07*	X	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....
Thorax Length	63	–17	51	X	....	....	....	....	....	....	....	....	....	....	....	....	....	....
Thorax Width	58	*–03*	56	70	X	....	....	....	....	....	.	....	....	....	....	....	....	....
Femur Length	35	–18	23	40	40	X	....	....	....	....	....	....	....	....	....	....	....	....
Tibia Length	49	*15*	23	23	32	28	X	....	....	...	....	....	....	....	....	....	....	....
Tarsus Length	*–05*	*–08*	34	37	44	20	*–12*	X	....	....	....	....	....	....	....	....	....	....
Antenna III	25	*–12*	30	31	32	*12*	*14*	34	X	....	....	....	....	....	....	....	....	....
Antenna IV	18	20	*09*	*09*	20	*10*	31	–02	22	X	....	....	....	....	....	....	....	....
Antenna V	47	–18	*12*	41	35	25	35	*12*	30	31	X	....	....	....	....	....	....	....
Antenna VI	28	*00*	*10*	18	*14*	*09*	30	*01*	21	24	46	X	....	....	....	....	....	....
Sensoria III	*07*	*–03*	18	*15*	*15*	*06*	*14*	*15*	35	*01*	*03*	*03*	X	....	....	....	....	....
Sensoria IV	19	*–06*	*15*	*14*	18	*10*	–21	44	*13*	*–00*	*–08*	*–12*	*07*	X	....	....	....	....
Sensoria V	*14*	*–05*	*00*	*09*	*11*	*05*	*–14*	22	*08*	*–10*	*–01*	*–10*	*04*	*06*	X	....	....	....
Sensoria VI	*00*	*–02*	*–00*	*–11*	*–05*	*–02*	*–12*	*01*	*05*	*–03*	*–04*	*06*	*–14*	*–07*	*00*	X	....	....
Islands V	24	*07*	26	*16*	24	*04*	*12*	*04*	23	*14*	*14*	*09*	*17*	*–03*	*–06*	*07*	X	....
Islands VI	*05*	*01*	*–02*	*–07*	*–07*	*02*	*03*	*–01*	*07*	*06*	*03*	*01*	*11*	*–07*	*01*	*–00*	*11*	X

Explanation: All coefficients are product-moment correlation coefficients; those significant at P≦.01 (r≧0.17) are in roman type. Decimal points have been omitted.

	Wing Length	Head Length	Head Width	Thorax Length	Thorax Width	Femur Length	Tibia Length	Tarsus Length	Antenna III	Antenna IV	Antenna V	Antenna VI	Sensoria III	Sensoria IV	Sensoria V	Sensoria VI	Islands V	Islands VI	SM Head Width	SM Femur Lengt	SM Tibia Length	SM Tarsus Lengt	SM Antenna III	SM Antenna IV
Wing Length	X	*	89	89	86	91	81	88	97	91	*	63	*	*	*	*	*	26	*	*	*	*	*	*
Head Length	21	X	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Head Width	68	27	X	84	92	86	76	72	84	85	*	82	*	*	*	*	*	40	*	*	*	*	*	*
Thorax Length	82	*16*	71	X	85	83	81	67	88	86	*	73	*	*	*	*	*	39	*	*	*	*	*	*
Thorax Width	78	20	78	80	X	88	77	66	79	72	*	61	*	*	*	*	*	52	*	*	*	*	*	*
Femur Length	71	*14*	58	66	68	X	92	76	93	76	*	57	*	*	*	*	*	20	*	*	*	*	*	*
Tibia Length	70	30	53	60	60	64	X	93	88	65	*	62	*	*	*	*	*	*16*	*	*	*	*	*	*
Tarsus Length	48	18	52	51	54	47	40	X	88	87	*	50	*	*	*	*	*	*–01*	*	*	*	*	*	*
Antenna III	71	26	59	65	60	56	56	59	X	89	*	67	*	*	*	*	*	*–16*	*	*	*	*	*	*
Antenna IV	66	18	51	57	51	47	50	41	59	X	*	65	*	*	*	*	*	*12*	*	*	*	*	*	*
Antenna V	54	37	42	46	43	35	52	34	59	61	X	*	*	*	*	*	*	X	*	*	*	*	*	*
Antenna VI	48	*18*	47	50	41	34	47	23	45	46	*54*	X	*	*	*	*	*	45	*	*	*	*	*	*
Sensoria III	34	*06*	*15*	28	*18*	23	25	*12*	40	*23*	*23*	*10*	X	*	*	*	*	*	*	*	*	*	*	*
Sensoria IV	*–07*	*–06*	*13*	*10*	*12*	*06*	*–04*	27	*12*	*07*	*–04*	*–02*	*02*	X	*	*	*	*	*	*	*	*	*	*
Sensoria V	*–01*	*01*	*13*	*11*	*12*	*06*	*–03*	*18*	*15*	*06*	*–07*	*09*	*09*	*16*	X	*	*	*	*	*	*	*	*	*
Sensoria VI	*–07*	*01*	*–07*	*–06*	*00*	*02*	*02*	*04*	*–07*	*–02*	*–04*	*–05*	*06*	*01*	*–02*	X	*	*	*	*	*	*	*	*
Islands V	*04*	*02*	*02*	*01*	*01*	*15*	*15*	*08*	*09*	*10*	*10*	*06*	*06*	*00*	*–03*	*12*	X	*	*	*	*	*	*	*
Islands VI	*15*	*01*	*16*	*15*	20	*10*	*08*	*–01*	*–03*	*08*	*06*	19	*–08*	*–02*	*04*	*13*	*14*	X	*	*	*	*	*	*
SM Head Width	*16*	*03*	*10*	*10*	*09*	*12*	*05*	*06*	*17*	*14*	*09*	*02*	*09*	*–04*	*–06*	*–00*	*–05*	*–06*	X	*	*	*	*	*
SM Femur Length	*13*	*03*	*12*	*04*	*07*	*07*	*07*	*06*	*14*	*12*	*03*	*–03*	*07*	*–13*	*–03*	*–01*	*–08*	*–06*	45	X	*	*	*	*
SM Tibia Length	*11*	*03*	*10*	*10*	*09*	*05*	*03*	*06*	*03*	*04*	*05*	*04*	*03*	*–05*	*–03*	*–02*	*06*	*04*	21	23	X	*	*	*
SM Tarsus Length	*14*	*08*	*09*	*08*	*08*	*10*	*08*	*02*	*11*	21	*07*	*03*	*12*	*–03*	*–04*	*03*	*–05*	*03*	38	40	*17*	X	*	*
SM Antenna III	*17*	*07*	*10*	*07*	*11*	*13*	*12*	*18*	*17*	23	*13*	*05*	*17*	*–03*	*–01*	*–02*	*07*	*–04*	41	58	33	42	X	*
SM Antenna IV	*–01*	*02*	*–03*	*–03*	*–02*	*–04*	*07*	*–08*	*05*	*05*	*08*	*07*	*12*	*–04*	*–07*	*–01*	*11*	*–01*	30	33	*17*	21	41	X

Explanation: Coefficients below diagonal are product-moment correlations; above diagonal component correlations. All product-moment coefficients significant at $P \leqq .01$ ($r \geqq .19$) are in roman type. Since significance levels for component correlations are unknown, the same significance level has been chosen arbitrarily. Decimal points have been omitted. Asterisks represent component correlations impossible to compute since no significant variance components were present. Characters preceded by SM are stem mother characters.

TABLE 6. Interlocality correlations.

	Wing Length	Head Length	Head Width	Thorax Length	Thorax Width	Femur Length	Tibia Length	Tarsus Length	Antenna III	Antenna IV	Antenna V	Antenna VI	Sensoria III	Sensoria IV	Sensoria V	Sensoria VI	Islands V	Islands VI	SM Head Width	SM Femur Length	SM Tibia Length	SM Tarsus Length	SM Antenna III	SM Antenna IV
Wing Length	X	*	72	74	73	61	60	67	65	65	33	*	*	*	*	*	*	*	19	*	*	*	–19	*
Head Length	46	X	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Head Width	83	63	X	78	72	69	36	42	37	56	30	*	*	*	*	*	*	*	08	*	*	*	–04	*
Thorax Length	85	55	88	X	76	70	61	61	43	63	42	*	*	*	*	*	*	*	17	*	*	*	–04	*
Thorax Width	82	48	84	85	X	84	66	59	46	69	24	*	*	*	*	*	*	*	–13	*	*	*	–40	*
Femur Length	76	46	82	82	94	X	58	56	40	69	38	*	*	*	*	*	*	*	05	*	*	*	–15	*
Tibia Length	75	16	51	72	75	77	X	69	50	72	22	*	*	*	*	*	*	*	53	*	*	*	–04	*
Tarsus Length	75	29	52	69	67	67	77	X	34	64	37	*	*	*	*	*	*	*	24	*	*	*	–32	*
Antenna III	81	29	54	57	58	58	68	52	X	60	46	*	*	*	*	*	*	*	40	*	*	*	26	*
Antenna IV	75	06	64	70	74	76	80	70	72	X	44	*	*	*	*	*	*	*	30	*	*	*	03	*
Antenna V	49	34	44	53	35	50	44	48	70	61	X	*	*	*	*	*	*	*	44	*	*	*	52	*
Antenna VI	46	34	55	66	58	72	56	52	32	45	56	X	*	*	*	*	*	*	*	*	*	*	*	*
Sensoria III	–15	21	–26	–15	–33	–28	–11	06	–06	–35	08	–06	X	*	*	*	*	*	*	*	*	*	*	*
Sensoria IV	51	38	60	50	61	64	40	61	36	57	38	24	08	X	*	*	*	*	*	*	*	*	*	*
Sensoria V	30	–11	18	22	06	10	03	22	40	30	49	16	–03	03	X	*	*	*	*	*	*	*	*	*
Sensoria VI	–15	33	02	01	07	12	09	–35	–01	–13	–11	06	–05	–11	–51	X	*	*	*	*	*	*	*	*
Islands V	–44	–20	–31	–42	–10	–09	–23	–20	–26	–10	–20	–18	20	17	–19	02	X	*	*	*	*	*	*	*
Islands VI	–26	–34	–12	–24	01	–04	–04	–01	–48	05	–53	–25	–43	13	–60	–00	29	X	*	*	*	*	*	*
SM Head Width	18	–12	09	15	–08	08	32	18	31	26	30	10	23	25	12	24	–28	–31	X	*	*	*	95	*
SM Femur Length	22	08	13	24	08	18	37	15	42	25	39	23	24	09	14	05	–09	–59	80	X	*	*	*	*
SM Tibia Length	12	19	08	09	14	–01	08	–07	24	18	–06	–12	–23	–10	–09	12	–05	–03	–27	–26	X	*	*	*
SM Tarsus Length	03	04	10	–10	–21	–30	–33	–14	–05	–21	–17	–34	34	04	17	–02	18	–16	26	32	–15	X	*	*
SM Antenna III	–05	–13	02	–00	–21	–02	04	–11	22	10	32	14	27	–03	35	28	12	–44	72	82	–04	44	X	*
SM Antenna IV	–00	32	22	31	–17	05	–04	09	–11	–19	33	47	49	–05	34	62	–23	–24	18	09	14	–02	28	X

Explanation: Coefficients below diagonal are product-moment correlations; above diagonal are component correlations. All product-moment coefficients significant at P $\leqq$ .01 ($r \geqq$ .62) are in roman type. Since significance levels are unknown for component correlations, the same significance level has been chosen arbitrarily. Decimal points have been omitted. Asterisks represent component correlations impossible to compute since no significant variance components were present. Characters preceded by SM are stem mother characters.

TABLE 7. Factor loadings for the intragall product-moment, intergall component and interlocality component correlation matrices.

	Intragall				Intergall Component			Interlocality Component		
Factors	I	II	III	IV	I	II	III	I	II	III
Characters:										
Alates:										
Wing Length	++			—	+++			+		
Head Length					X	X	X	X	X	X
Head Width	+				++				+++	
Thorax Length	+++				+++				++	
Thorax Width	+++				++				+++	
Femur Length	+				+++				++	
Tibia Length				—	+++			+++		
Tarsus Length				++	+++			++		
Antenna III		++	+		+++					
Antenna IV					+++					
Antenna V			++		X	X	X			+
Antenna VI			++					X	X	X
Sensoria III					X	X	X	X	X	X
Sensoria IV				+	X	X	X	X	X	X
Sensoria V					X	X	X	X	X	X
Sensoria VI					X	X	X	X	X	X
Islands V					X	X	X	X	X	X
Islands VI						++		X	X	X
Stem Mothers:										
Head Width	X	X	X	X			+			+++
Femur Length	X	X	X	X			++	X	X	X
Tibia Length	X	X	X	X				X	X	X
Tarsus Length	X	X	X	X				X	X	X
Antenna III	X	X	X	X			+++			+++
Antenna IV	X	X	X	X				X	X	X

Explanation: This table represents simple structure factor loadings which are correlations of reference vectors with the variables. They are proportional to the primary patterns (standard partial regression coefficients on primary factors) which are not shown here to conserve space, but together with the correlations between these factors are available from the author upon request. Plus or minus signs represent the following magnitudes of factor loadings (positive or negative, respectively): Intragall, 3 signs $\geqq|0.65|$, 2 signs $\geqq|0.50|$, 1 signs $\geqq|0.35|$; intergall component, 3 signs $\geqq|0.75|$, 2 signs $\geqq|0.65|$, 1 sign $\geqq|0.55|$; interlocality component, 3 signs $\geqq|0.65|$, 2 signs $\geqq|0.55|$, 1 sign $\geqq|0.45)$. X-signs denote variables not used in the study indicated.

TABLE 8. Means of all characters for all localities.

	Locality Code Numbers															
Characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Average Standard Errors of the Means
Alates:																
Wing Length	2.09	2.16	2.24	2.33	2.15	2.04	2.22	2.09	1.99	2.04	2.09	2.18	2.06	1.98	2.18	.184
Head Length	.18	.18	.18	.19	.18	.18	.19	.18	.18	.19	.18	.19	.18	.18	.19	.010
Head Width	.38	.38	.38	.40	.33	.37	.39	.37	.36	.37	.38	.39	.37	.38	.38	.019
Thorax Length	.56	.55	.59	.61	.58	.53	.57	.54	.52	.53	.53	.59	.52	.55	.56	.048
Thorax Width	.60	.59	.67	.70	.62	.62	.67	.60	.57	.55	.62	.67	.60	.61	.65	.064
Femur Length	.46	.45	.49	.50	.47	.47	.48	.45	.43	.45	.47	.49	.46	.47	.48	.044
Tibia Length	.65	.66	.69	.69	.69	.66	.66	.63	.63	.63	.66	.66	.67	.64	.67	.052
Tarsus Length	.17	.18	.19	.19	.18	.18	.18	.17	.17	.18	.17	.18	.18	.17	.18	.011
Antenna III	.17	.16	.17	.18	.16	.16	.17	.16	.16	.17	.16	.16	.16	.15	.16	.014
Antenna IV	.08	.07	.08	.08	.07	.07	.08	.07	.07	.07	.07	.08	.08	.07	.07	.006
Antenna V	.11	.10	.11	.11	.10	.10	.10	.10	.10	.11	.10	.10	.10	.10	.10	.007
Antenna VI	.17	.17	.17	.18	.17	.17	.17	.17	.16	.17	.16	.17	.16	.17	.17	.010
Sensoria III	3.50	3.70	3.87	3.50	3.87	3.57	3.43	3.37	3.97	4.07	3.97	3.53	3.30	3.50	3.50	.179
Sensoria IV	0.00	.03	.10	1.33	.07	.07	1.00	.03	0.00	.03	.17	.28	.03	0.00	0.00	.098
Sensora V	1.07	1.03	1.10	1.03	1.00	1.00	1.03	1.07	1.00	1.07	1.00	1.03	1.03	1.00	1.00	.045
Sensoria VI	1.03	1.00	1.00	1.00	1.03	1.03	1.03	1.00	1.00	1.00	1.03	1.00	1.00	1.03	1.03	.032
Islands V	2.37	2.23	2.53	2.33	2.07	2.60	2.43	2.17	2.77	2.40	2.77	2.47	2.53	2.63	2.23	.143
Islands VI	2.17	2.53	2.10	2.37	2.47	2.63	2.60	2.33	2.63	2.27	2.47	2.83	3.03	2.70	2.50	.164
Stem Mothers:																
Head Width	.47	.47	.46	.44	.47	.46	.43	.44	.43	.53	.46	.45	.44	.43	.44	.031
Femur Length	.43	.42	.42	.41	.41	.42	.40	.40	.40	.40	.41	.41	.40	.40	.41	.034
Tibia Length	.35	.34	.34	.34	.35	.34	.39	.34	.34	.33	.34	.32	.34	.34	.33	.070
Tarsus Length	.14	.14	.14	.13	.13	.14	.14	.13	.14	.16	.14	.14	.13	.13	.14	.010
Antenna III	.17	.16	.16	.15	.15	.16	.15	.15	.15	.18	.16	.16	.15	.15	.15	.017
Antenna IV	.11	.11	.11	.11	.11	.11	.11	.11	.11	.13	.11	.11	.10	.11	.11	.009

All continuous variables are given in millimeters; all meristic ones as counts.

TABLE 9. Comparison of locality means with related studies.

Characters	Grand mean of all localities (present study)	Hutchinson, Kansas (Sokal & Rinkel, 1963)	Arkansas City, Kansas (Sokal & Rinkel, 1963)	Delawan, Morris Co., Kansas (Sokal & Thomas, 1965)	Kansas City, Missouri (Sokal & Rinkel, 1963)	Range (Present study)	Range (Sokal & Rinkel. 1963)
Alates:							
Wing Length	2.12	1.55	1.52	1.50	1.52	1.98-2.33	1.52-2.10
Head Length	.18	.21	.21	X	.10	.18- .19	.19- .21
Head Width	.38	.37	.36	.30	.34	.36- .40	.34- .39
Thorax Length	.56	.52	.52	.45	.44	.52- .61	.44- .63
Thorox Width	.62	.54	.52	X	.46	.55- .70	.46- .65
Femur Length	.47	.42	.41	X	.40	.43- .50	.40- .52
Tibia Length	.66	.55	.56	.56	.57	.63- .69	.55- .71
Tarsus Length	.18	.13	.13	X	.13	.17- .19	.13- .16
Antenna III	.16	.14	.14	.14	.14	.15- .18	.14- .18
Antenna IV	.07	.06	.06	X	.06	.07- .08	.06- .08
Antenna V	.10	.09	.09	X	.10	.10- .11	.09- .10
Antenna VI	.17	.17	.17	.17	.17	.16- .18	.16- .18
Sensoria III	3.63	2.27	3.33	3.00	3.47	3.30-4.07	2.27-4.17
Sensoria IV	.25	.00	.00	.00	.00	.00-1.33	.00- .83
Sensoria V	1.03	1.03	1.00	X	1.03	1.00-1.07	1.00-1.27
Sensoria VI	1.01	1.03	1.03	X	1.00	1.00-1.03	1.00-1.07
Islands V	2.44	2.13	1.77	X	2.13	2.07-2.77	1.73-2.80
Islands VI	2.51	3.20	2.77	X	3.00	2.10-3.03	2.20-3.30
Stem Mothers:							
Head Width	.45	X	X	.41	X	.43- .53	X
Femur Length	.41	X	X	.37	X	.40- .43	X
Tibia Length	.34	X	X	.33	X	.32- .39	X
Tarsus Length	.14	X	X	X	X	.13- .14	X
Antenna III	.16	X	X	.15	X	.15- .18	X
Antenna IV	.11	X	X	.12	X	.10- .13	X

Explanation: X-signs denote variables not used in the study indicated.
All continuous variables are given in millimeters; all meristic ones as counts.

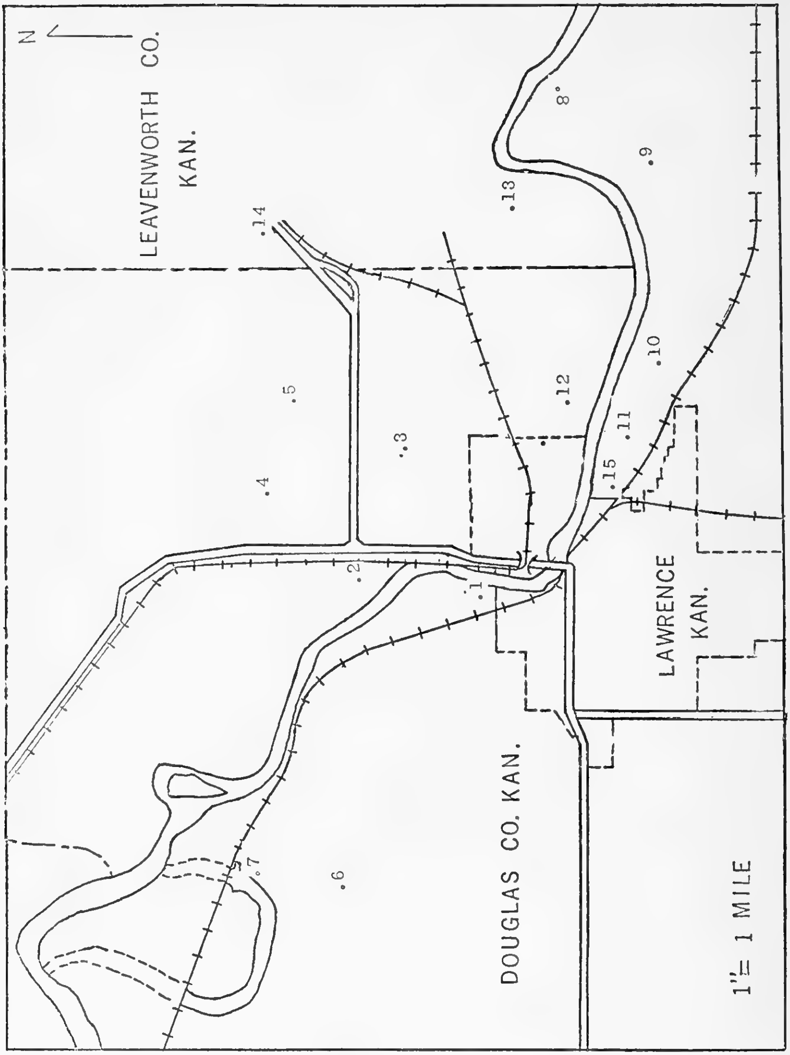

FIG. 1. Map of localities and locality numbers.

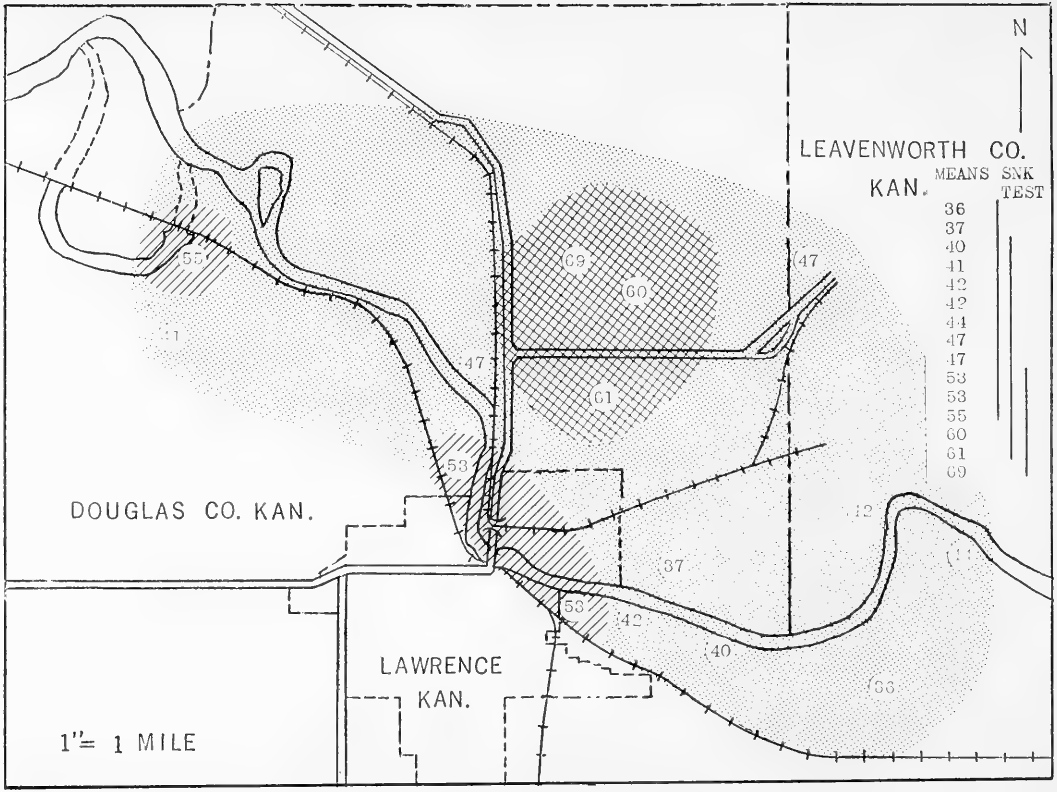

Fig. 2. Map of locality means for the character *tho ax length.*

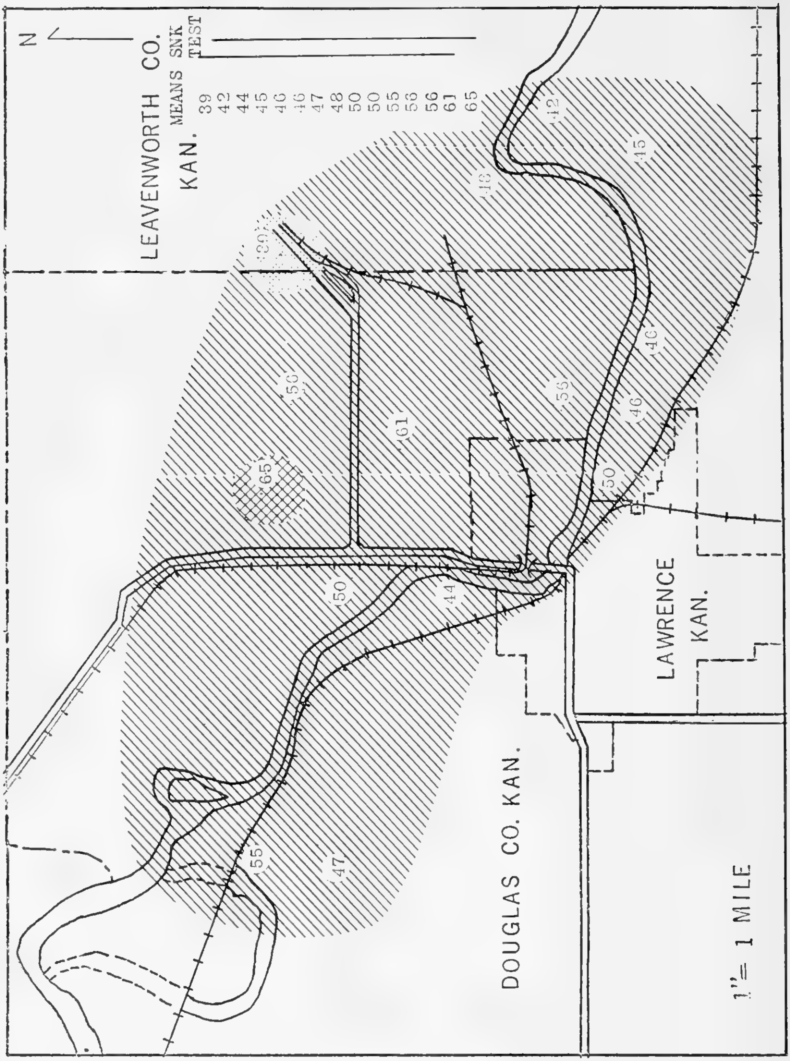

FIG. 3. Map of average locality means representing factor I (see text for explanation).

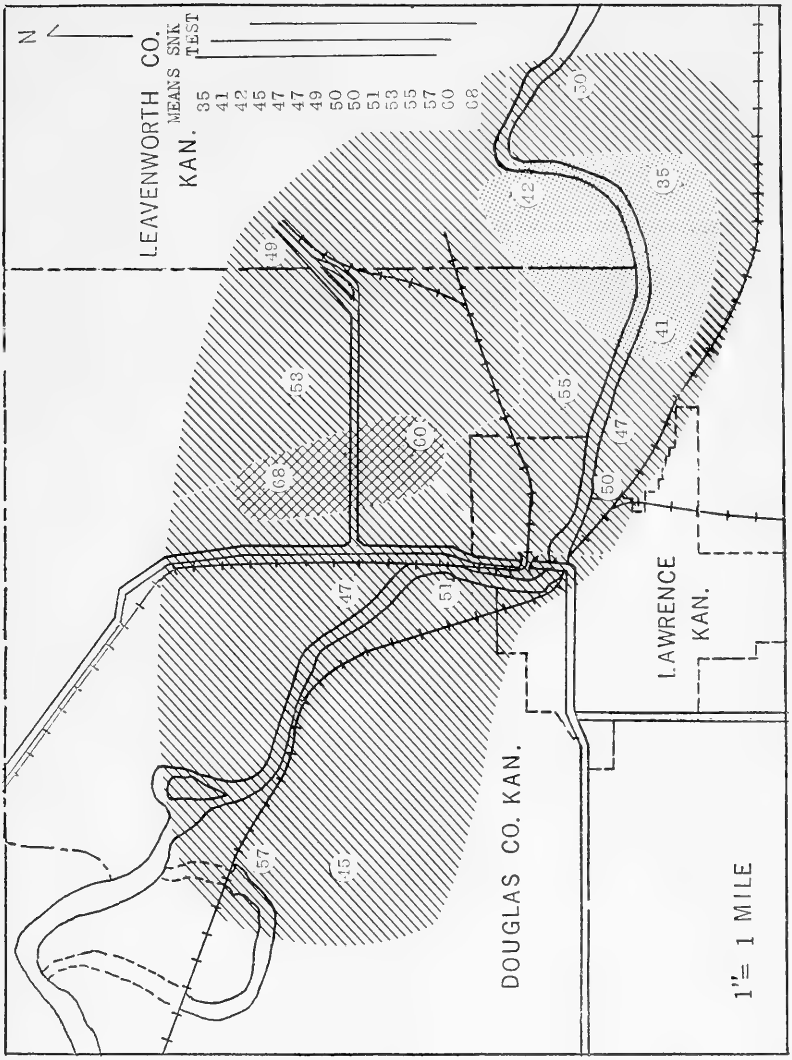

FIG. 4. Map of average locality means representing factor II (see text for explanation).

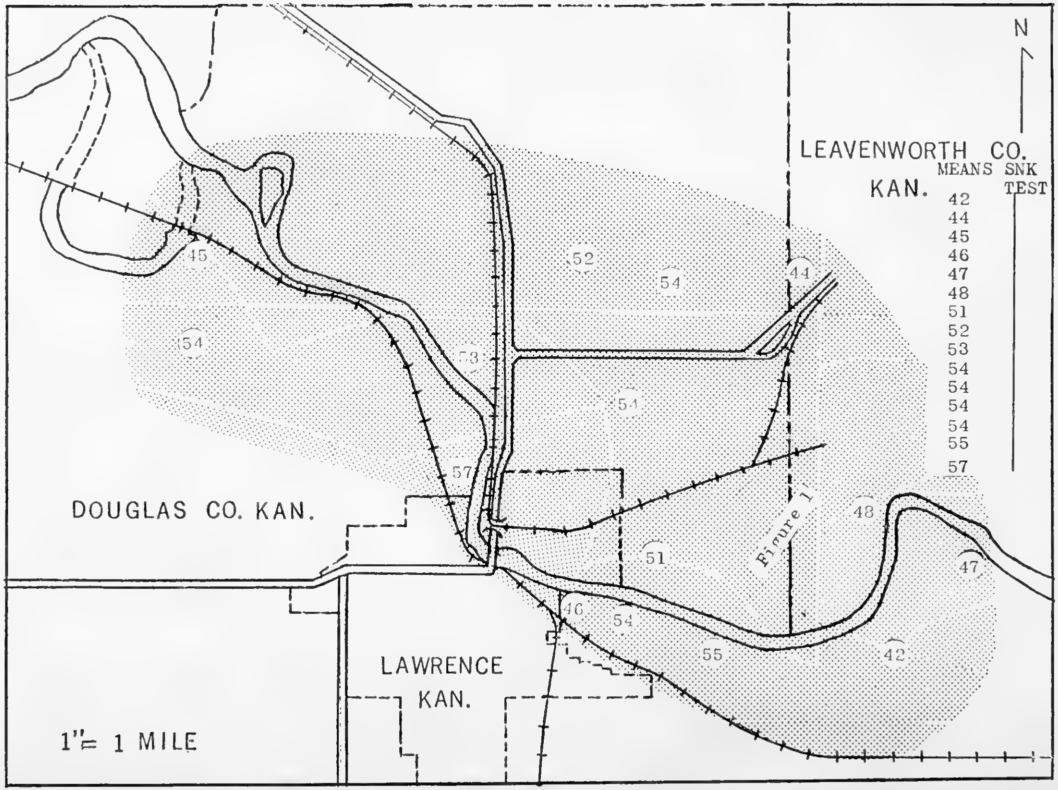

Fig. 5. Map of average locality means representing factor III (see text for explanation).

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GEOGRAPHIC VARIATION OF *PEMPHIGUS POPULI-TRANSVERSUS* IN EASTERN NORTH AMERICA:

STEM MOTHERS AND NEW DATA ON ALATES

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Geographic Variation of *Pemphigus populi-transversus* in Eastern North America: Stem mothers and new data on alates[1, 2]

By

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ABSTRACT

This paper continues earlier studies of the geographic variation and covariation of morphological characters of the gall-making aphid *Pemphigus populi-transversus* in eastern North America (see footnote 1). Samples of galls from 74 localities ranging from Massachusetts to Kansas and Wisconsin to Florida were employed in the study. Alate aphids were found in 57 of these localities. Eight alate characters, chosen to represent the three interlocality factors obtained by Sokal (1962), were measured together with six stem mother characters. Analyses of variance yielded significant interlocality variance components for all characters. The proportions of interlocality and intergall variance agree with previous results. As expected there is considerably more interlocality variance than in a study of microgeographic variation by Rinkel (1965).

Separate correlation matrices were computed at the intergall and interlocality levels of covariation. The intergall correlations of alate characters agree with previous findings. There are no significant intergall correlations between alates and stem mothers, a remarkable finding in view of their genetical identity. High

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[1] Part 5 of a study of variation in the aphid genus *Pemphigus*. Parts 1 to 4 are, respectively, the following publications: Sokal (1952), Sokal (1962), Sokal and Rinkel (1963), and Rinkel (1965).

[2] Contribution No. 1218 from the Department of Entomology of The University of Kansas, Lawrence, Kansas.

[3] This paper is based on aphid material collected and measured between 1949 and 1951 when the senior author was a graduate student in the Department of Zoology at the University of Chicago. Computations for the various analyses were carried out by the junior author.

The authors acknowledge the assistance of Dr. F. James Rohlf and Mr. Richard C. Rinkel with computer programs employed in this work. Mrs. Julie C. Sokal drew the maps. The computations were carried out at The University of Kansas Computation Center.

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interlocality correlations are found among stem mother and alate characters, and there are some important cross correlations between the two morphotypes. Multiple factor analysis with rotation to simple structure was carried out on both correlation matrices. Partial results are shown in Table 4. Four common factors account for most of the observed correlations at both levels of covariation. It is possible to homologize all but one of the factors affecting alates in the present study with those found in earlier work. New factors affecting stem mother characters emerge from this study. Maps of the geographic variation of the 14 characters investigated are shown in Figures 2-15. Locality means have been transformed to probits for ease of comparison. The differences among localities are tested by means of a multiple comparisons test (SNK test), the results of which are shown in tables at the right hand margin of the figures. The method of representation of the present data is modified from the technique of Sokal and Rinkel (1963). The multiple factor analyses of interlocality correlations permitted the geographic variation to be summarized in four geographic variation pattern maps, each showing one interlocality factor (Figures 17-20). Techniques for categorization of infraspecific taxa are examined and illustrated in Figure 21. The implications of this study are discussed with reference to (1) consistency of geographic variation patterns based on earlier, more restricted samples, and (2) the correlation and absence thereof between stem mother and alate characters and possible genetic and ecological reasons to account for the observed phenomena.

INTRODUCTION

This paper continues the study of variation and covariation of morphological characters of the aphid, *Pemphigus populi-transversus* Riley, published in earlier papers of this series. The present study extends the analysis of geographic variation to 57 localities in eastern North America for eight morphological characters of the alates. These were selected by factor analysis from the 18 characters studied by Sokal (1962) and Sokal and Rinkel (1963)[1] in a smaller sample of localities. The study also introduces for the first time an analysis of the geographic variation of stem mother characters, six of which were measured. The number of localities with stem mothers is 74, which includes all those localities from which alates were also obtained, plus others in which only stem mothers were found. The method of representation of geographic variation has been altered somewhat from that of Sokal and Rinkel (1963), a step taken for several reasons discussed below. Studies of variation and covariation of characters were again undertaken. In view of the extensive previous analyses of variation and covariation within galls, it did not seem necessary to repeat such work here; thus the basic unit of sampling and measurement was a gall, represented by one stem mother and one alate individual.

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[1] See erratum following Literature Cited.

The general significance and implications of this work have been sufficiently discussed in the previous papers of this series (cf. Sokal, 1962; Sokal and Rinkel, 1963), and can be referred to there. The special points of interest and emphasis in the present paper follow.

1. The study affords us an opportunity to compare variances in the earlier sampled 23 localities with the more extensive results presented below. We shall investigate whether the components of variance established in earlier work are similar in magnitude to those found here.

2. A second point relates to comparison of the covariation pattern previously established with that found below. This is done by comparing the previous and present results of factor analysis of correlations among alate characters. From the point of view of biological application of factor analysis, it is important to know whether the results of factor analytic work are replicable from study to study. This problem of factorial invariance is also of considerable importance in the field of factor analysis itself.

3. We wish to examine the effect of increasing the number of locality samples on the stability of geographic variation patterns established earlier by Sokal and Rinkel (1963).

4. An entirely new aspect of this study is the analysis of geographic variation of the stem mothers. In addition to the intrinsic interest of such an analysis, its major importance is that it will permit the comparison of geographic variation in stem mothers and alates. It will be remembered that these two forms are isogenic (the alate is a diploid parthenogenetic offspring of the stem mother in each case). *A priori* it might be thought that character correlations between the two forms should be as high as those within each form and that their geographic variation patterns should be concordant. It will be shown that this is not so, raising interesting problems of evolutionary adaptation as well as delineation of subspecific populations. We believe this to be the first study of concurrent geographic variation and covariation of characters of two distinct morphotypes in any species.

MATERIAL

A brief description of the complex life history of these aphids has been given in Sokal (1952). They form galls on petioles of the cottonwood, *Populus deltoides,* as the primary host and migrate to the roots of herbaceous plants in the summer. In the present study we employ both the fundatrix or stem mother and the alate fundatrigeniae found in the same gall with her. The term alate, whenever employed, refers to such forms only.

The present study extends over 74 localities, based on a minimum of two and a maximum of 25 galls each. Each gall contains at least a stem mother and many of them contain alates as well. Since the number of galls per locality was unequal, some complications, to be discussed below, arose in the analysis of the data. A further complication was caused by the fact that some localities contained only stem mothers and no alates, while others contained both morphotypes. In order to obtain maximum information on stem mothers, all localities and all galls containing them were employed in the computation of means and variances of stem mother characters. These "complete" data were also employed in calculating the correlations among stem mother characters. However, for the computation of correlations among stem mother and alate characters all galls containing only stem mothers had to be eliminated from the study. Therefore such correlations could be computed only over the 57 localities which contained both stem mothers and alates.

Figure 1 is a map of the eastern United States on which are plotted all studied localities. The localities and the dates of collection are listed in Table 1. The code numbers of the first 23 localities correspond with those of the earlier study (Sokal and Rinkel, 1963). In that study, however, localities 18, 19 and 20 each contained several small samples from the Southeast, which had been combined to obtain localities of 15 galls each. Since other localities in the present study have unequal sample sizes, it was not necessary here to combine these localities and they are listed separately. In order to retain a consistent numbering system they have been numbered by adding a letter to the locality number, e.g. 18a, 18b, etc. The number of galls containing alates and stem mothers, respectively, are in Tables 5 and 6 of this paper. The number of alates measured per locality is generally less or at most equal to the number of stem mothers measured. Galls containing alates, but no stem mothers were excluded from the study. Locality 9 of the previous study was excluded since data on stem mothers were not available. The means of alate characters in the present study will not agree exactly for any given locality with those given by Sokal and Rinkel (1963). This is due to the discrepancy in the number of galls employed in both studies and to the fact that only one alate was measured per gall in the present study as compared with two alates in the previous one.

The single alate measured per gall was chosen at random from among those found in the gall. In the 23 localities of the previous study, one of the two alates was recorded at random from the data.

Eight alate characters were chosen to represent the three interlocality factors obtained by Sokal (1962). Their names and those of the stem mother characters are listed in the section on Description and Analysis of Geographic Variation and Covariation. Their definition has been given in the previous papers (Sokal, 1952, 1962). For brevity we shall use abbreviated names such as antenna III for antennal segment III length, and sensoria III for number of sensoria on antennal segment III. Two of the stem mother characters described in Sokal (1952), tarsus length and last rostral segment length, were not employed in the present analysis. Of the eight alate characters, two are meristic and the others are continuous. All stem mother characters are continuous. The entire study involved 10,780 measurements of characters.

ANALYSES OF VARIANCE

The data were subjected to 14 analyses of variance, one for each character. The structure of the sample permitted computation of variance among localities and variance within localities (=variance among galls), with 73 and 1036 degrees of freedom, respectively, for stem mother characters (56 and 458 d.f. for the alate characters). At this stage of the study the analyses were considered as model II analyses of variance, and variance components were estimated for them. For the two meristic alate characters, sensoria III and sensoria IV, square root transformations were attempted to see whether these would affect the outcome of the analyses. No important differences in proportions of mean squares or F values were found; the data presented here are based on untransformed values.

The results of the analyses of variance are in Table 2. Mean squares among localities are significant ($P < 0.01$) for all characters, indicating the presence of a significant variance component among localities for every character measured. The first two columns in Table 2 show the percentages of the total variation attributable to the two levels of variation. The characters grade from forewing length, which has as much as 58% of its variance among localities, to antenna VI with only 11% interlocality variance. In general, alate characters, other than antenna VI and the meristic ones, have a high proportion of interlocality variance, while the stem mother characters are not as differentiated among the localities of the study, 13.5% for total length to 28.9% for femur length.

In order to compare the present findings with earlier ones, it is necessary to study ratios of the variance components because in the earlier study three hierarchic levels had been investigated and the total percentage was thus divided three ways. Column 3 of Table 2 shows the ratio of the locality variance component over the within localities variance component of the present study. Since in the present study only one alate was measured per gall, an estimate comparable to the present within localities variance can be constructed from the components obtained by Sokal (1962) by adding the component of galls to that of within galls. The comparable ratio is given in column 4 of Table 2. The two sets of ratios are quite similar as might have been expected since the present study is based in part upon the data of Sokal (1962). However, it is reassuring to find that the sample of the smaller study was quite representative of the larger domain. The only noticeable discrepancy is in alate head width, which has a ratio twice that of the previous study. The comparison cannot be made for stem mothers since these had not been studied previously. In the final column of Table 2 are shown similar estimated ratios based on the study of Rinkel (1965), in which variance components were calculated based on samples from a local area where the greatest distance between any two localities was eight miles. We note that the ratio in this study of microgeographic variation is much lower and that some of the interlocality variance components were not significant, as might have been expected in samples so close to each other.

CORRELATIONS

Correlations among the 14 variables of this study were computed on an IBM 650 digital computer. The structuring of the sample permitted the computation of correlations among galls within localities (intergall correlations) as well as among localities. Since the lowest sampling unit was galls within localities, the intergall correlations are product-moment coefficients. The interlocality correlations were computed both as product-moment and as component correlations (Sokal, 1962). Only the component correlations are shown here to conserve space. Subsequent analyses at the interlocality level are all based on the component correlations.

The computations of the correlation coefficients for the stem mothers are based only on those galls which also had alates. Correlations among all the stem mothers were also computed but were not appreciably different from those of the more limited sample, hence are not given here.

The present data permitted for the first time a correlation of stem mother characters with alate characters, both on an intergall and an interlocality basis. The only earlier attempt at such correlations was based on a single locality (Sokal, 1952) and was therefore not very representative.

Table 3 shows the correlation coefficients with the intergall product-moment correlations below the principal diagonal and the interlocality component correlations above the principal diagonal of the matrix.

INTERGALL CORRELATIONS

The intergall correlations are not very high in absolute magnitude. Most high ones involve continuous alate variables, but not including antenna VI. Correlations among stem mother characters are only moderately high, except femur against tibia length. There are no high correlations between stem mother and alate characters.

In comparing these correlations with the intergall product moment correlations found by Sokal (1962), we find a considerable amount of agreement. An average difference of –0.05 is found between the corresponding correlations of the earlier and the present study, indicating that the earlier correlations were slightly higher. However, this difference is only slightly greater than one standard error of the correlation coefficients. It should be pointed out that the intergall product-moment correlations of the earlier study were based on galls containing two alates each, while galls in the present study contain only one alate each. Thus the intragall variance component in the earlier study was only half of that in the present one. The thorax-head width cluster of intergall correlations illustrated in Sokal (1962) is again shown in these data, although in a more limited manner since fewer variables are employed.

INTERLOCALITY CORRELATIONS

The interlocality component correlations are shown above the diagonal in Table 3. They are generally much higher than the intergall correlations and comprise the continuous variables of the alates, excluding antenna VI which has high correlations only with tibia length and antenna III. High correlations are also found among most stem mother characters, although stem mother total length is correlated with the other characters only in a limited way, and antenna IV (which is homologous to antenna VI in the alates) is quite independent from the rest of the measurements and negatively correlated with most (except with antenna VI with which it has a correlation of 0.60). There are some interesting high cross correlations between stem mother and alate characters in addition to those involving stem mother antenna IV, which is also highly negatively correlated with forewing length ($r = -0.71$). Most important cross correlations involve stem mother head width which is highly and positively correlated with the continuous variables of the alates.

Comparing the interlocality component correlations with those computed by Sokal (1962), we find only minor differences, the average being only 0.08 which in view of the lower number of degrees of freedom is not a significant difference.

A clustering of the correlation coefficients similar to that carried out by Sokal (1962) yielded a wing-thorax-antenna III cluster, more or less corresponding to the pattern found by Sokal except that these patterns were not too distinct since there were fewer characters employed. A marked change was noted in the correlation between sensoria III and IV which has a value of 0.97 in the present study.

The relations among the variables will be put into clearer focus and also simplified as a result of the factor analyses.

FACTOR ANALYSES

The intergall product-moment and interlocality component correlation matrices were next subjected to multiple factor analysis with rotation to simple structure. A brief explanation of factor analysis, an account of its application to biology, and a description of the computational steps carried out are given in Sokal (1962), where identical techniques were employed. The results are expressed in the form of primary pattern matrices of pattern coefficients (Harman, 1960), representing the standard partial regression coefficients of each variable (character) on each factor. The two primary pattern matrices are not shown here to conserve space. They have been reproduced in mimeographed form, together with the correlation matrices among primary factors, and can be obtained by writing to the senior author. Table 4 gives the primary pattern matrices as a scheme of + and − signs representing only the important pattern coefficients. This permits a relatively simple and instructive picture of the nature of the factors. We note that four common factors account for covariation in both of the correlation matrices. In Table 4 the factors are first of all numbered in sequence, but underneath these numbers are given other numbers homologizing the factors with those of the earlier study (Sokal, 1962) or a new symbol if they have not been encountered before.

The intergall product moment correlations yielded a satisfactory simple structure. Factors I and II affect only alates and do not seem to affect stem mother characters at all. In trying to homologize factor I, we note that its loadings are an amalgam of factors I and II of the intergall component and the intergall product-moment primary pattern matrices obtained by Sokal (1962). These two factors of the earlier study appear to have collapsed here into a single factor. This should not occasion surprise since the earlier factors I and II were extremely highly correlated ($r=0.93$ in the intergall product moment matrix and $r=0.71$ in the intergall component matrix). Factor I therefore represents a size factor affecting the continuous, but not the meristic, variables of the alates. The second factor affecting alates cannot be easily identified. It is clearly an antennal factor, strongly influencing antenna III and sensoria III, a combination which did not occur before; it also weakly affects sensoria IV (not shown in Table 4). We shall call it intergall factor IV.

The other two intergall factors exclusively influence stem mother characters. Factor III (henceforth called F-1, meaning intergall fundatrix factor 1) moderately affects stem mother total length and head width. Factor IV (henceforth called F-2) affects the appendages and antennae of stem mothers. There are no important correlations involving the primary factors.

The interlocality component factors can be more easily homologized than the intergall factors with the results of the previous analysis by Sokal (1962). Factor I affects sensoria III and sensoria IV strongly and antenna III mildly. This is a similar pattern to that of interlocality factor I of the previous study. Interlocality factor II affects antenna VI strongly and mildly affects head width, thorax length and tibia length (not shown in Table 4). This resembles interlocality factor II in the previous study, except that in that study head width loaded higher on the factor than did antenna VI. A new feature in this factor is its strong loading on stem mother antenna IV. This character is homologous to antenna VI in the alates (being in each case the terminal segment of the antenna), and it is interesting that geographic variation patterns for these two characters would coincide when no similar intergall correlations between homologous body structures in stem mothers and alates are found. Interlocality factor III strongly affects forewing length, head width, thorax length, tibia length and also antenna VI. Except for the latter loading this factor represents factor III of the 1962 study. Factor III also affects total length of stem mother weakly (not shown in Table 4). There is appreciable negative correlation between interlocality factors II and III ($r = -0.68$), which was not the case in the previous study. Interlocality factor IV (henceforth called interlocality factor F-1) is limited to stem mothers and controls stem mother femur, tibia and antenna III length and mildly also stem mother total length and head width (not shown in Table 4). This factor is quite uncorrelated with the other factors.

Thus interlocality component correlations can be accounted for to a large degree on the basis of four factors, three of which are mainly alate factors (but two of these affecting stem mother characters also), with the fourth being exclusively a stem mother factor.

The interlocality communalities of all variables save stem mother total length are very high so that these factors account well for the geographic variation at hand. This means also that four independent trends will adequately describe the geographic variation of all alate and stem mother characters of this study.

DESCRIPTION AND ANALYSIS OF GEOGRAPHIC VARIATION AND COVARIATION

The means of the alate and stem mother characters for all the localities studied are given in Tables 5 and 6, respectively. Means are stated in millimeters for continuous variables and as counts for meristic characters. Sample sizes for the stem mother means are generally greater than those for alates because some galls contained stem mothers but no alates. Furthermore there are more localities given in Table 6 than in Table 5 since 17 localities in the study had no alates at all. The standard deviation at the foot of each character column is the average standard deviation within localities. It is *not* the standard error of the means. An average standard error of the means is difficult to compute because of the variation in sample size. For a working average standard error for any character one might divide the standard deviation given in the table by the square root of the average number of galls per locality, calculated as shown in the explanations to Tables 5 and 6.

In addition to tabulating the means, graphic descriptions of geographic variation on distribution maps are necessary. Maps depicting geographic variation patterns should furnish information on two issues. They should communicate the magnitude of the changes of character means over a given area, and this is achieved by different symbols for different levels of the means or by the drawing of isophenes based on a more or less exhaustive sampling of the area. The second consideration is some measure of the reliability of the means and concomitantly some measure of testing significance of differences between means. These two statistical demands on a map, description and hypothesis testing, are to some degree in conflict, making the presentation of a suitable map something of a compromise. In their earlier study of *Pemphigus,* Sokal and Rinkel (1963) used probit scores to indicate the magnitude of the means and used shading as well as a diagrammatic representation of a multiple comparisons test to give some idea of the statistical differentiation among the means.

The probit scores for the means are obtained by dividing the difference of each mean from the grand mean of localities by the standard deviation of locality means and adding 5.0. Localities whose means are less than the grand mean will have scores of less than 5.0; those with a mean larger than the average will score above 5.0. Decimal points have been omitted for simplicity. Since the standard deviations differ, depending on the number and kinds of means included in the study, the probit scores of the previous 23 localities in the present study are not identical to those calculated by Sokal and Rinkel (1963). However, their relative magnitudes remain the same.

In the present study some changes in the representation of geographic variation were instituted for several reasons. We are in a period of experimentation in this type of work, and it is desirable to attempt a number of different approaches in order to arouse the interest of students of geographic variation in these problems. We abandoned the shading system employed earlier for two reasons. We had some qualms from the very beginning about the reality of the areas defined by the relatively few points of that study, although these were more numerous than in many studies of geographic variation in which the drawing of isophenes is therefore likely to be even more open to doubt. Some of the boundaries for areas of supposedly uniform character means are thus likely to be quite arbitrary. Secondly, since the shading of the maps by Sokal and Rinkel was based on the results of multiple comparisons tests, i.e. test of significance, the division into separate shades often made for quite unequal classes either in frequency or in range of the variable. On the present maps we decided to represent the magnitude of the mean by a probit score, as before, and to reinforce this measure of the magnitude of the character by a circle covering the geographic locality from which the sample was taken, shading this circle in one of four shades representing four groups of probit scores. These groups do not have equal class intervals, being set up so that scores greater than 63 are colored black, those between 51 and 63 are dark gray, between 37 and 50 are light gray and those less than 37 are white. These classes are based on an expected normal distribution of the probit scores in which the extreme classes represent 10% of the distribution at each tail and the two central classes make up 40% each. Since the means are not always normally distributed, the proportions in these classes are sometimes not as expected. By drawing a circle with a radius of 27 miles over the collection site but refraining from drawing any isophenes, we feel that we are presenting a less biased picture of the geographic variation than before. The large number of localities on the map form a pattern as the entire map is inspected and areas of high and low means become apparent to the viewer.

The following are brief accounts of the geographic variation patterns of each character as illustrated by Figures 2-15. Alate characters are discussed first, followed by stem mother characters.

Forewing length (Figure 2). In general an area of low means occurs in the western half of the area studied, with some low means also in New England, New York and Pennsylvania. High means are most prominent in southern Ohio, and in the Southeast but some high means occur west of the Mississippi also.

Head width (Figure 3). The lowest means are found in a triangle bounded by east-central Kansas, northern Missouri, and eastern Arkansas. High values cluster in Ohio, Indiana, northern Illinois, and extend southeast through Kentucky and Tennessee into Georgia. More high values seem to occur in the northern part of the distribution.

Thorax length (Figure 4). The highest means cluster in Ohio, Indiana, Kentucky, and Tennessee. In general all localities east of the Lower Mississippi and the Wabash valleys are high, while those west of this line are low. A single high locality is found on the border between Iowa and Missouri.

Tibia length (Figure 5). This resembles the pattern in Figure 4 with high means to the east of the Wabash-Lower Mississippi line and low means to the west of this line. Locality 13 in Decatur County, Iowa, high for the last character, is even higher for tibia length.

Antennal segment III length (Figure 6). This pattern is related to the previous ones but less clear in that some high localities extend into Illinois and Missouri, while some lower ones occur in the South, northern Pennsylvania, and Ohio.

Antennal segment VI length (Figure 7). This character shows a general north-south trend with high means in the North reaching south as far as Kentucky and Tennessee, and low means generally in the South and Southwest although some low means reach as far north as central Indiana.

Number of sensoria on antennal segment III (Figure 8). This variable shows a peculiar distribution with high values in Ohio, some extending into Illinois, Indiana and Iowa, and low values concentrated in the South and Southeast and extreme North. There is an isolated very high mean in southeast Missouri.

Number of sensoria on antennal segment IV (Figure 9). The pattern here resembles that of the previous character, but because of a strong skew to the right there are fewer high localities. The New England means are higher than before, and the locality in Wayne County, Missouri, high for the previous character, is quite low for this one.

The stem mother characters are described in Figures 10-15.

Stem mother total length (Figure 10). This character has a difficult-to-interpret pattern of variation. The highest means are found along a north-south axis from central Indiana to Mississippi with an extension into Florida, but the low means are scattered through various regions without any meaningful pattern. The distribution pattern resembles somewhat that of stem mother tibia length reported below.

Stem mother head width (Figure 11). This character features low means in the West, high means in the Mississippi Valley and generally east of the Mississippi, although low means are again found in New England.

Stem mother femur length (Figure 12). This resembles the previous character with some low means in New England, some in western Kansas, but on the whole a fairly confusing pattern in which the highs and lows are distributed almost in crazy quilt fashion over the area of study.

Stem mother tibia length (Figure 13). This pattern resembles closely the one just studied and is rather confusing. The highest means are found along a north-south axis through the middle of the map with an extension into the Great Lakes and northern Pennsylvania area. New England is generally low, as is Kansas and northern Missouri.

Stem mother antennal segment III length (Figure 14). The pattern resembles that of the two previous characters.

Stem mother antennal segment IV length (Figure 15). This character is distributed quite differently from the stem mother characters discussed so far. There is an area of high means in the North with the highest ones in the northwest of the area. With very few exceptions, means south of the level of central Illinois are low. There is a single high locality in Georgia.

Sokal and Rinkel (1963) employed the Student-Newman-Keuls (SNK) test to compare the means of the localities after the analysis of variance had been carried out. Because the present data are based on unequal sample sizes and also because of the large number of means involved, systematic testing of differences between means proved to be a very tedious procedure. For this reason we developed a computer program for the IBM 1620 computer (written in FORTRAN and available upon request from the authors) which makes multiple comparisons among means according to the SNK test as well as by Duncan's multiple range test, for both equal and unequal sample sizes. The formulae for these tests are in Steel and Torrie (1960). To gain an understanding of the workings of the SNK tests and to compare the effects of using unequal sample sizes with employing an average sample size for all localities, we processed all data by both methods. Performing the tests with unequal sample sizes proved unsatisfactory because it broke the continuity of ranges enclosing nonsignificant sets. With equal sample sizes, once a higher mean B has been shown significantly different from a lower mean A, a mean C (where $C > B$) will be significantly different from the lower mean A. There are exceptions to this rule, but they are rarely encountered in practice. With unequal sample sizes, however, it is quite possible that mean B ($B > A$) can be significantly different from A and yet mean C ($C > B$, but based on a smaller sample) would not be significantly different from mean A. Such relations are, of course, warranted by statistical theory; a mean based on a small sample is not easily proven significantly different from another mean. Yet the arraying of means and the creation of overlapping ordered groups is made impossible by such relations. For this reason we investigated the amount of error which would arise if we were to base the SNK test on an average sample size and employ the formula for equal sample sizes. Stem mother total length was analyzed by SNK tests for equal size employing the formula for n_0 in the explanation of Table 5. Parallel tests were carried out using the actual sample sizes n_i for each locality. Figure 16 illustrates the results of this comparison. It is a half matrix which shows the probit scores of the means for stem mother total length along the principal diagonal and the left hand margin. The sample sizes of each locality are given at the bottom of the matrix. In order to find out whether any given mean is significantly different from the other we look up the lower of the means along the principal diagonal and run down the column until we reach the level of the higher mean along the left hand margin of the matrix. In case of several probit means of equal score employ the mean with the appropriate sample size. If both ends are marked by an X the two means are not significantly different (based on an SNK test with unequal sample sizes); if the higher mean (the lower end of the column) lacks an X the two means are significantly different (at $P < 0.01$). The black line which cuts across the graph in zig-zag fashion is the boundary of not significantly different sets of means based on equal sample sizes and average sample size n_0; if the higher mean is within this boundary it is not significantly different, if beyond it is different from the mean at the head of the column ($P < 0.01$). In general the boundary line assuming equal sample sizes is similar to decisions based on unequal ones. If the per cent error of using equal sample sizes is computed as the percentage of comparisons wrongly included and wrongly excluded by the boundary (analogous to combining type I plus type II error) we find that 6.96% of all possible comparisons between means would be in error. This is clearly higher than the 1% type I error assumed in the tests, but is not prohibitively large in view of the heavy cost in extra work and complexity which would be exacted by using unequal sample sizes.

The standard error used in the SNK tests was the square root of the error mean square obtained in the analysis of variance. Since the q tables in Pearson and Hartley (1958) do not go beyond a n value of 20, we had to extrapolate values for the higher degrees of freedom necessary in this analysis.[1]

Since our computer program calculated Duncan's multiple range test along with the SNK, we were able to compare the results of the two tests for a number of variables. We confirmed the findings of Sokal and Rinkel (1963), that the Duncan test provides a greater amount of differentiation among means than is desirable from the point of view of our analysis.

The significance of differences between pairs of means is not evident from the maps proper, but can be learned from their right hand margin. In the previous paper Sokal and Rinkel (1963) used the common convention of overlapping lines to depict the results of the multiple comparison tests. When we attempted these on the present data, we found that the number of lines necessary for such a large sample was so great that it became almost impossible for the eye to follow any one line along the measurement scale. The convention adopted here seems more useful. The ranges provided indicate sets of not significantly different means at a probability level of 0.01. Thus if we wish to know in Figure 2 whether two localities, one with a mean score of 33, the other with a mean score of 57, are significantly different from each other, we find in the margin that no such inclusive range exists, hence the two means are significantly different at $P < 0.01$.

In order to summarize the information on geographic variation presented in the 14 maps for separate characters, we obtained factor scores for the four interlocality factors described above by averaging the scores of the two characters best representing each factor. The rationale behind this technique and details of computation are given in Sokal and Rinkel (1963). To represent factor I we used sensoria III and sensoria IV; to represent factor II we used antenna VI and stem mother antenna IV; factor III was represented by head width and thorax length, while the stem mother factor F-1 is represented by stem mother femur length and stem mother tibia length. Averages of the standardized scores of the two characters for each factor were computed for each locality and plotted on maps (Figures 17-20).

Examination of the geographic distribution of the average scores reveals four distinct patterns of variation.

Interlocality factor I (Figure 17). The distribution of this factor is

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[1] Subsequently we discovered the table by Harter (1960) which furnishes n values up to 100.

peculiar in having high means in Ohio, Indiana, and Illinois and also three high localities in New England. The low localities are found in the far north and generally in the south, southeast, and southwest of the area studied.

Interlocality factor II (Figure 18). This shows a general north-south gradient with high values in the North reaching as far south as Kentucky and Tennessee, and low values in the south, southwest, and southeast of the area with low means extending northward along the Mississippi, Wabash, and Ohio River valleys.

Interlocality factor III (Figure 19). The low means are generally found west of the Lower Mississippi and Wabash with lowest values in Kansas, Missouri, and Arkansas. High values are generally in the East with highest means found in Indiana, Ohio, Kentucky, Tennessee, and Georgia. The northern and eastern portions of the area seem to have the higher means in general.

Interlocality stem mother factor F-1 (Figure 20). This factor provides a very confusing picture, as do the stem mother characters on which it is based. No clear trends over the entire geographic area can be seen but there are patches of reasonably homogeneous means. In general, means are low west of the Mississippi. High means cluster in the Mississippi River Valley, but there are also high means in southern Ohio, Alabama, and North Carolina. A second low group is found in the Northeast.

DISCUSSION

TECHNIQUES

This study provides a further illustration of the application of analysis of variance and multiple comparisons tests to the study of geographic variation. New problems introduced by the data at hand include the great number of localities to be analyzed and compared as well as unequal sample sizes. The numerous localities make multiple comparisons among means rather laborious although not nearly so tedious as separate comparisons by t tests between all possible pairs of means would have been. Representation of the results required abandonment of the earlier scheme of representing nonsignificant sets by a line (Sokal and Rinkel, 1963), however, the system adopted in this paper has proved quite useful in checking the significances of differences between means as was done during the preparation of this paper.

The analysis of variance of numerous localities does require heavy computation but not more so than the separate computation of means and variances for each locality would involve. If, as in this study, many characters are to be measured and analyzed, the use of a digital computer is recommended to insure speed, accuracy, and economy in computation.

The unequal sample sizes do not present difficulties during the computation of the analysis of variance; simple changes in the computational formulae allow for such differences. However, the computation of multiple comparisons tests is, as we have seen, considerably slowed down and furthermore becomes difficult to interpret. Our experience in the present case has shown that substituting average sample size n_0 for n in the SNK technique for equal sample sizes does not result in conclusions so wide of the mark as to be useless. The present data are a rather severe test in this regard because several localities in the study were based on only two galls (see, for instance, Figure 16 where the locality with the score of 71 based on two galls cannot be shown to be significantly different from any other one). In data such as the present ones, where sample sizes differ drastically, certain critical comparisons between means may have to be tested by separate comparisons tests based on the formula for unequal sample sizes.

The employment of factor analysis to summarize covariation of characters among localities has again proved to be an adequate way of representing the variation patterns. The four interlocality factors are quite different in nature, although I and III, and II and III showed substantial correlations. They presumably represent different adaptational trends.

There is little evidence of specific geographic variation trends shown only by a single character. Even stem mother total length, the variable with the lowest interlocality communality, shows no distinct geographic variation pattern.

CONSISTENCY OF ALATE CHARACTERISTICS

In describing patterns of geographic variation, the degree to which the sample studied represents the area covered is always of interest. Comparison of geographic variation of alate characters in the present and previous studies affords an opportunity to gauge the consistency of pattern. The new patterns for six of the alate characters are quite consistent with their previous description. The addition of further localities has brought more intergradations to the new maps, yet, as a rule, localities with high means have not been placed in areas of low means, or vice versa. Even some peculiarities of pattern such as the tongue of low means for forewing length protruding into western Ohio has been maintained and reinforced in the present study (cf. Figure 3 in Sokal and Rinkel, 1963, with Figure 2 in this paper). Such differences as exist between the patterns of the previous and present studies largely refer to the so-called area samples of Sokal and Rinkel (1963) which were composite localities based on several small subsamples. These have been separated in the present study, and in at least one case, the Kentucky and Tennessee area sample, the separate localities show quite different means. Additional localities have also demonstrated that hypothetical narrow "land bridges" bounded by isophenes, such as the one in Sokal and Rinkel (1963, Figure 9), extending west from Ohio into northern Indiana and southern

Iowa are not correct. In Figure 5 of this paper we can see that the high mean for tibia length in Decatur County, Iowa (locality 13), represents an isolated pocket or perhaps the easternmost representation of a hypothetical area of high means extending through Nebraska and Minnesota from which samples have so far not been available.

Two of the characters, sensoria III and sensoria IV, show appreciable changes over their previous distribution patterns. The present pattern of variation of sensoria III is somewhat clearer and more meaningful than that published by Sokal and Rinkel (1963). The former narrow band of high means extending westward has expanded into a general area of highs in the Midwest with a thin belt of low means north of this area and lows to the south and southwest. An unexpected high locality in southeast Missouri is encountered. The variation pattern of sensoria IV which previously had two high mean enclaves in Illinois and northern Ohio (Figure 16 in Sokal and Rinkel, 1963) now has a more extensive high area in the Midwest with a low belt in the North and a large low area in the South. It is interesting that locality 37 in Wayne County, Missouri, with an extraordinarily high mean for the previous character has a low score for this character, although in general the two are quite highly correlated.

Comparing the geographic variation of factors in the previous and present studies, we find that interlocality factor I has changed the most, as have the two characters on which it is based (sensoria III and sensoria IV discussed above). Still this is only a relative change and the high area in Ohio extending west through Illinois into Iowa is again represented. The low area in the far West and the Southeast is also clearly shown. The variational pattern of interlocality factor II is very consistent with that of the previous study, showing a high area in the North, an intermediate area in the Southwest and Southeast, and a low area in the Mississippi River Basin. Similarly, interlocality factor III shows high values through Ohio, southern Indiana and the Southeast and an area of lows largely west of the Mississippi. Here again the two patterns are quite compatible.

We have already seen that the correlation coefficient matrices based on the alate characters show considerable resemblance to those found in the earlier study (Sokal, 1962). This supports the reliability of the findings presented here.

AGREEMENT BETWEEN ALATES AND STEM MOTHERS

Of special interest in the present study is the simultaneous analysis of two separate morphotypes, the stem mothers and their alates. This comparison is carried out at two levels of variation and covariation. The contents of one gall represent one genotype, since the stem mother and her alate offspring are isogenic. Intergall variance can be attributed to genetic differences among founding stem mothers as well as ecological differences among the galls of a given locality. One might expect that the characters of the stem mothers and of the alates should be highly correlated on an intergall basis. In fact, however, not a single appreciable intergall correlation coefficient was found between the two sets of characters, the highest r value being 0.26. We must therefore conclude that whatever factors cause the characters of stem mothers to vary from gall to gall do not affect the studied characters of alates (and vice versa).

What theoretical basis can we assume for such a phenomenon? Two explanations come to mind: (1) To the extent that intergall variance is genetic, different loci may come into play to affect the two suites of characters chosen. Thus although the two morphotypes are isogenic, the variation patterns observed would be due to different sets of active loci. (2) The ecological factors differ from the time that morphogenetic forces are at work in the stem mother to the time that such forces affect the morphogenesis of the alates. We shall now examine these hypotheses in more detail.

Evidence is mounting from a study of several organisms that gene action is selective both in site as well as in time of action. The phenomenon of puffing of chromosome bands (e.g., Clever, 1961), indicates that different loci come into play during various stages of an organism's development. It would therefore not be too surprising to find a similar phenomenon operating in this instance. Supposedly homologous characters in the stem mother and alates might respond to quite different gene products.

The environments to which these two morphotypes are subjected will also be considerably different. The stem mother is formed much earlier in the year than the alates, resulting in grossly different climatic experiences. Derived from a fertilized egg which hatches early in the spring, the stem mother makes her way to the young leaf bud on a cottonwood twig. Her early history is thus quite different from the alate born parthenogenetically within the considerably more homeostatic confines of a gall. In the very early history of the stem mother (first and possibly second instars) the term intergall environmental factor has no real meaning because the gall has not yet been established and such a level of variation reflects only the differences in the individual histories of the stem mother nymphs. After the stem mother nymph has settled on the petiole of an unfolding leaf and has begun to induce the gall, we can talk meaningfully of intergall variation. The early environment of the alates by contrast is within the body of the stem mother, while later development takes place in the mature galls.

In saying that the genetic or environmental factors affecting one stage do not act on the second stage, we do not mean to imply categorically that these factors have no effect on the other morphotype, but only that the characters examined by us in the second morphotype are not under control of these factors. We cannot at this time distinguish between the two hypotheses.

It is more than likely that both genetic and environmental influences come into play.

At the interlocality level we again cannot separate genetic from environmental covariation. Genetic differences among populations are likely to be adaptive and thus may be a secondary consequence of climatic environmental differences which, however, may affect the phenotype of the organisms in a direct primary way. More likely the organisms will be ecotypically different and thus be responding to a complex interaction of genetic and environmental differences presumably established at some time past by a mechanism such as genetic assimilation.

At the interlocality level a number of large and significant correlation coefficients are shown. These involve stem mother head width and stem mother antenna IV more than the other four stem mother characters measured. Rather than discuss these correlations in detail we might refer to the primary pattern matrix for interlocality components (Table 4) which shows only the most important of these cross correlations, namely the one between stem mother antenna IV and alate antenna VI. The actual pattern coefficients show other appreciable correlations as well. While antenna IV in the stem mother and antenna VI in the alate are homologous segments, it seems unlikely that these correlations occur because of morphological correspondence. We have seen that such relations do not hold at the intergall level where morphogenetic patterns of this sort should have considerably more influence. The stem mother-alate correlations must mean that the geographical differences to which these characters are responding are likely to be climatic factors, adaptation to which occurs independently in both morphotypes of these populations. Thus the sensory organs of the last segment of the antenna in the stem mother may be responding to the same selective forces affecting the last alate segment. In noting this correlation we should not lose sight of the fact that there is considerable difference between the patterns of geographic variation of stem mothers and alates for other characters.

CATEGORIZATION OF INFRASPECIFIC TAXA

At the conclusion of their study Sokal and Rinkel (1963) endeavored to characterize infraspecific populations by combinations of factor scores for the three interlocality factors which they found in their study. Their method has been simplified here. In lieu of plotting all localities with appropriate shading representing the characterization, we have simply drawn a relatively arbitrary boundary between the high and low means of an area. In drawing this boundary we were primarily guided by the solid black and the white circles in the factor variation maps (Figures 17-20), but we also considered the general clustering of localities with intermediate shades. Thus the lines drawn in Figure 21 represent approximate boundaries between high and low areas. While undoubtedly the great majority of localities on the two sides of the boundary are not statistically significant, the highest and lowest localities are so in each case, as can be seen from an inspection of the SNK test results in the right hand margins of Figures 17-20. The boundaries shown in Figure 21 are for interlocality factors I, II, and III. The crazy quilt distribution of interlocality factor F-1 makes it impossible to draw a single line dividing high from low localities. We have therefore copied the extreme means (black and white circles) from Figure 20 onto this map. Ignoring the areas for factor F-1 we arrive at six distinguishable areas identified by lower case or capital Roman letters to indicate the low or high states of the factors, respectively. Each of these populations is significantly different by at least one factor score from every other one and some are different by as many as three factor scores (as for example the population in northern Ohio from the population in southeastern Missouri and Arkansas).

The implications of such a categorization for the so-called subspecies controversy are discussed elsewhere (Sokal, 1965). It is obvious that further study of the organism involving more characters would result in a greater number of factors and yet more drastic subdivision of the area. Also since *Pemphigus populi-transversus* is supposedly distributed over much of the North American continent (an extensive study of this is in the planning stage) the amount of diversification and possibilities for defining distinguishable subpopulations are likely to be great.

ERRATUM

A regrettable systematic error has been discovered in Table 2 of the earlier paper in this series (Sokal and Rinkel, 1963). A corrected version of the table is reproduced after Table 6 of the present paper.

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TABLE 1. List of the Localities Employed in This Study.

Locality Code Number	Locality	Date
1	U.S. Hy. 1, 3 m. SE of Walpole, Norfolk Co., Mass.	12-VIII-50
2	U.S. Hy. 6, 2 m. W of Goshen, Orange Co., N.Y.	11-VIII-50
3	U.S. Hy. 6, 5 m. N of Wyalusing, Bradford Co., Pa.	10-VIII-50
4	North Tonawanda, Niagara Co., N.Y.	15-VIII-50
5	1½ m. SW of Laporte, Lorain Co., Ohio	10-VIII-50
6	Perrysburg, Wood Co., Ohio	16-VIII-50
7	Mishawaka, St. Joseph Co., Ind.	16-VIII-50
8	Wis. Hy. 50, 5 m. E of New Munster, Kenosha Co., Wis.	15-VII-49
10	Ohio Hy. 364 along Lake St. Marys, 3 m. SW of St. Marys, Auglaize Co., Ohio	29-VIII-50
11	U.S. Hy. 24, 2 m. E of East Peoria, Tazewell Co., Ill.	11-VII-49
12	1 m. E of Grandmound, Clinton Co., Ia.	23-VII-50
13	Leon, Decatur Co., Ia.	24-VII-50
14	U.S. Hy. 36, 5 m. W of Hull, Pike Co., Ill.	25-VII-50
15	U.S. Hy. 24, 6 m. E of Kansas City, Jackson Co., Mo.	23-VII-50
16	5 m. SE of Hutchinson, Reno Co., Kans.	2-IX-51
17	U.S. Hy. 166, 11 m. E of Arkansas City, Cowley Co., Kans.	6-IX-51
18a	U.S. Hy. 441, 2½ m. N of Ocala, Marion Co., Fla.	22-VIII-49
18b	Poulan, Worth Co., Ga.	29-VIII-49
18c	Sneads, Jackson Co., Fla.	21-VIII-49
18d	U.S. Hy. 19, 1½ m. N of Albany, Dougherty Co., Ga.	30-VIII-49
19a	U.S. Hy. 70, 10 m. SW of Brinkley, Monroe Co., Ark.	3-VIII-50
19b	Flood Plain of Arkansas River at Forth Smith, Sebastion Co., Ark.	3-VIII-50
19c	U.S. Hy. 70, 8 m. W of Lonoke, Lonoke Co., Ark.	3-VIII-50
19d	Mississippi River bed, 1 m. W of the river and 8 m. E of West Memphis, Crittenden Co., Ark.	3-VIII-50
19e	U.S. Hy. 71, 1 m. N of Texarkana, Bowie Co., Texas	3-VIII-50
20a	U.S. Hy. 41, 1 m. NW of Adams, Robertson Co., Tenn.	15-VIII-49
20b	U.S. Hy. 41, Guthrie, Todd Co., Ky.	15-VIII-49
20c	U.S. Hy. 60, 4 m. W of Kevil, Ballard Co., Ky.	31-VII-49
20d	U.S. Hy. 51, 5 m. S of Covington, Tipton Co., Tenn.	3-VIII-50
20e	U.S. Hy. 51, 1 m. S of Trimble, Dyer Co., Tenn.	3-VIII-50
21	U.S. Hy. 52, 4 m. SE of Ripley, Brown Co., Ohio	9-IX-49
22	U.S. Hy. 52, 6 m. SE of New Trenton, Franklin Co., Ind.	10-IX-49
23	Gwynneville, Shelby Co., Ind.	10-IX-49
24	U.S. Hy. 43, 6 m. S of Eutaw, Greene Co., Ala.	17-VIII-49
25	U.S. Hy. 43, 1 m. N of Fayette, Fayette Co., Ala.	16-VIII-49
26	U.S. Hy. 84, 9½ m. E. of Laurel, Jones Co., Miss.	9-VIII-49
27	U.S. Hy. 41, 3 m. N of Carlisle, Sullivan Co., Ind.	14-VIII-49
28	Beaumont, Perry Co., Miss.	19-VIII-49
29	U.S. Hy. 52, 4 m. NW of New Richmond, Clermont Co., Ohio	9-IX-49
30	U.S. Hy. 43, 4 m. N of Rockdale, Maury Co., Tenn.	15-VIII-49
31	U.S. Hy. 41, 5 m. N of Evansville, Vanderburgh Co., Ind.	14-VIII-49
32	U.S. Hy. 41, 4.7 m. S of Rockville, Parke Co., Ind.	24-VII-49
33	Ill. Hy. 34, 3 m. N of Eichorn, Hardin Co., Ill.	30-VII-49

TABLE 1. List of the Localities Employed in This Study (Continued).

Locality Code Number	Locality	Date
34	U.S. Hy. 40, 2 m. E of Putnamville, Putnam Co., Ind.	24-VII-49
35	Ill. Hy. 146, 6 m. N of U.S. Hy 45, Massac Co., Ill.	30-VII-49
36	Ill. Hy. 3, 8 m. SE of Waterloo, Monroe Co., Ill.	18-VII-50
37	Piedmont, Wayne Co., Mo.	1-VII-50
38	North Providence, Providence Co., R.I.	12-VIII-50
39	U.S. Hy. 6, 2 m. E of Walkerton, LaPorte Co., Ind.	9-VIII-50
40	U.S. Hy. 61, 4 m. SW of Davenport, Scott Co., Ia.	19-VII-50
41	Wysox, Bradford Co., Pa.	10-VIII-50
42	West end of Jefferson Barracks Bridge between Columbia, Monroe Co., Ill., and Mehlville, St. Louis Co., Mo.	18-VII-50
43	Fort Kaskaskia Mem. State Park, Randolph Co., Ill.	18-VII-50
44	U.S. Hy. 6, 2 m. W of Wawaka, Noble Co., Ind.	9-VIII-50
45	Lonedell, Franklin Co., Mo.	18-VII-50
46	U.S. Hy. 20, Esperance, Schoharie Co., N.Y.	12-VIII-50
47	⅛ m. N of Missouri R. on Mo. Hy. 19, Montgomery Co., Mo.	18-VII-50
48	½ m. E of Jefferson Barracks Bridge between Columbia, Monroe Co., Ill., and Mehlville, St. Louis Co., Mo.	18-VII-50
49	Mo. Hy. 30, Little Meramec R., E of St. Clair, Franklin Co., Mo.	18-VII-50
50	U.S. Hy. 6, 2 m. E of Vermillion-on-the-Lake, Lorain Co., Ohio	16-VIII-50
51	Mo. Hy. 34, 6 m. W of Jackson, Cape Giradeau Co., Mo.	1-VIII-50
52	Mo. Hy. 81, 8 m. N of Kahoka, Clark Co., Mo.	19-VII-50
53	Cape Fear R., Fayetteville, Cumberland Co., N.C.	1-IX-50
54	U.S. Hy. 67, 6 m. SW of Prescott, Nevada Co., Ark.	3-VIII-50
55	Palmyra, Marion Co., Mo.	19-VII-50
56	U.S. Hy. 35, 4 m. NW of Frankfort, Ross Co., Ohio	29-VIII-50
57	U.S. Hy. 20, 2½ m. E of Springfield, Hampden Co., Mass.	12-VIII-50
58	Nichols, Muscatine Co., Ia.	19-VII-50
59	U.S. Hy. 244, 5 m. E of Leroy, Medina Co., Ohio	3-IX-50
60	U.S. Hy. 20, 4½ m. SE of North Madison, Lake Co., Ohio	10-VIII-50
61	U.S. Hy. 6, 1 m. W of Woodside, Wood Co., Ohio	9-VIII-50
62	Ohio Hy. 7, 1 m. E of Tipp City, Miami Co., Ohio	29-VIII-50
63	U.S. Hy. 52, Ironton, Lawrence Co., Ohio	29-VIII-50
64	U.S. Hy. 50 N, Delavan, Morris Co., Kansas	1-IX-50

TABLE 2. Results of Analyses of Variance.

	Percentage of character variance attributed to		Ratios of variance components		
Characters	Galls within a locality	Localities	(σ^2 localities) $\div$ (σ^2 within localities) from present study	(σ^2 localities) $\div$ (σ^2 gall + σ^2 within) from Sokal (1962)	(σ^2 localities) $\div$ (σ^2 gall + σ^2 within) from Rinkel (1965)
Alates:					
Forewing length	41.8	58.2	1.39	1.17	0.14
Head width	68.0	32.0	0.47	0.27	0.09
Thorax length	59.9	40.1	0.67	0.52	0.21
Tibia length	62.8	37.2	0.59	0.48	0.05
Antenna III	54.3	45.7	0.84	0.69	0.04
Antenna VI	89.0	11.0	0.12	0.22	0
Sensoria III	85.6	14.4	0.17	0.20	0
Sensoria IV	85.2	14.8	0.17	0.32	0
Stem Mothers:					
Total length	86.5	13.5	0.16	X	X
Head width	77.5	22.5	0.29	X	0.17
Femur length	71.1	28.9	0.41	X	X
Tibia length	79.8	20.2	0.25	X	0
Antenna III	79.5	20.5	0.26	X	0.06
Antenna IV	84.3	15.7	0.19	X	0

X indicates that variables were not included in the study represented by that column.

TABLE 3. Correlation Coefficients.

	Wing Length	Head Width	Thorax Length	Tibia Length	Antenna III	Antenna VI	Sensoria III	Sensoria IV	SM Total Length	SM Head Width	SM Femur Length	SM Tibia Length	SM Antenna III	SM Antenna IV
Wing Length	X	63	84	91	89	*07*	57	37	48	76	41	45	58	–71
Head Width	51	X	81	70	57	50	*32*	*20*	40	47	14	*11*	*22*	*–13*
Thorax Length	70	61	X	92	76	49	60	36	48	69	*26*	*18*	*33*	–38
Tibia Length	63	46	56	X	89	50	72	51	49	77	38	34	49	–37
Antenna III	56	38	46	55	X	*26*	83	75	35	75	42	46	58	–55
Antenna VI	27	40	35	39	30	X	47	*16*	*–03*	*–15*	*–15*	*–30*	*–24*	60
Sensoria III	12	*10*	*01*	*03*	35	*–03*	X	97	*16*	49	50	40	56	–22
Sensoria IV	*10*	*03*	*03*	*01*	18	*–06*	*22*	X	*07*	61	*22*	41	34	–22
SM Total Length	14	*08*	*08*	*06*	*09*	*02*	*–02*	*02*	X	62	*18*	*31*	58	*–31*
SM Head Width	26	14	12	13	20	*07*	12	*00*	30	X	64	65	66	–51
SM Femur Length	26	15	17	16	20	*11*	*08*	*02*	18	38	X	85	73	*–01*
SM Tibia Length	20	*08*	*11*	14	21	*04*	12	*03*	16	35	63	X	89	*–14*
SM Antenna III	22	*08*	*10*	13	21	*09*	16	*11*	24	44	53	50	X	*–30*
SM Antenna IV	*05*	*10*	*04*	*04*	*10*	20	*02*	*04*	16	25	35	36	44	X

Explanation: Coefficients below diagonal are intergall product-moment correlations, those above the diagonal are interlocality component correlations. All intergall product-moment coefficients significant at P ≦0.01 are in roman type (*r* ≧0.12). Coefficients below this level are in italics. Since significance levels of component correlations are not known, the significance level pertaining to product-moment coefficients of 55 degrees of freedom have been chosen arbitrarily and applied to the interlocality component coefficients. The conventions of roman type for significant (P ≦0.01) coefficients (*r* ≧0.34) and of italics for not significant ones are again observed. Decimal points have been omitted. The stem mother character correlations are based only on those galls which also contained alates. SM is an abbreviation for stem mother.

TABLE 4. Primary Pattern Matrices for the Intergall and Interlocality Component Correlations.

	Intergall Factors				Interlocality Component Factors			
Factor Number in this Study	I	II	III	IV	I	II	III	IV
Permanent Factor Number	I+II	IV	F-1	F-2	I	II	III	F-1
Characters								
Wing Length	+++						++	
Head Width	+++						+++	
Thorax Length	+++						+++	
Tibia Length	+++						+++	
Antenna III	++	+						
Antenna VI	+					+++	+++	
Sensoria III		+			+++			
Sensoria IV					+++			
SM Total Length			+					
SM Head Width			+					
SM Femur Length				+++				+++
SM Tibia Length				+++				+++
SM Antenna III				++				++
SM Antenna IV				+		+++		

Explanation: Plus signs represent the following magnitudes of pattern coefficients. Intergall, +++ $\geqq$ 0.65, ++ $\geqq$ 0.55, + $\geqq$ 0.45; interlocality component, +++ $\geqq$ 0.85, ++ $\geqq$ 0.75, + $\geqq$ 0.65. The account of these data in the text is based on the complete primary pattern matrices (not shown here, but available upon request from the authors). Thus not all the results are evident from this table. SM is an abbreviation for stem mother.

TABLE 5. Means of Alate Characters for All Localities.

Locality Code Numbers	Number of Alates	Forewing Length	Head Width	Thorax Length	Tibia Length	Antenna III	Antenna VI	Sensoria III	Sensoria IV
01	13	1.70	.363	.57	.62	.161	.180	3.46	0.23
02	14	1.65	.371	.55	.62	.158	.174	3.14	0.29
03	15	1.63	.379	.55	.60	.149	.174	3.27	0.20
04	13	1.67	.361	.55	.63	.154	.180	3.31	0.08
05	15	2.00	.374	.59	.68	.189	.171	4.93	0.87
06	15	1.90	.377	.60	.64	.158	.177	3.87	0.07
07	14	1.75	.378	.56	.66	.153	.181	2.71	0.14
08	15	1.66	.378	.53	.62	.146	.177	2.93	0.00
10	15	1.71	.384	.56	.62	.156	.182	3.53	0.07
11	15	1.61	.369	.50	.60	.169	.178	4.00	0.40
12	14	1.65	.367	.54	.63	.149	.177	3.86	0.14
13	11	1.78	.375	.59	.69	.158	.185	3.91	0.27
14	14	1.53	.352	.48	.57	.133	.168	3.50	0.00
15	13	1.52	.339	.34	.58	.136	.174	3.31	0.00
16	12	1.54	.368	.51	.54	.134	.163	2.75	0.00
17	15	1.53	.359	.51	.56	.134	.170	3.20	0.00
18a	2	1.90	.361	.56	.64	.173	.160	3.00	0.00
18b	2	2.08	.356	.51	.64	.168	.156	2.00	0.00
18c	2	1.92	.361	.56	.64	.150	.162	3.50	0.00
18d	5	2.06	.388	.60	.66	.167	.166	2.60	0.00
19a	3	1.43	.336	.44	.51	.115	.153	2.33	0.00
19b	6	1.95	.376	.54	.64	.162	.168	3.33	0.00
19c	2	1.40	.328	.48	.53	.121	.164	2.51	0.00
19d	3	1.76	.358	.48	.57	.140	.158	1.33	0.00
20a	4	2.09	.384	.62	.68	.179	.177	3.76	0.00
20b	5	1.94	.381	.62	.66	.171	.180	3.80	0.20
20c	3	1.73	.345	.48	.59	.153	.158	3.33	0.00
20d	2	1.92	.365	.55	.62	.156	.148	3.50	0.00
20e	2	1.82	.375	.54	.62	.150	.168	3.00	0.00
21	25	2.04	.383	.58	.69	.175	.174	3.52	0.20
22	15	2.11	.397	.65	.71	.175	.174	3.87	0.13
23	11	1.95	.378	.61	.67	.156	.174	3.46	0.09
27	3	1.76	.364	.54	.58	.146	.155	3.00	0.00
28	2	1.74	.356	.53	.63	.152	.162	3.00	0.00
29	8	2.15	.386	.63	.71	.191	.175	3.76	0.38
32	3	1.57	.342	.52	.59	.157	.168	3.67	0.00
34	5	1.81	.344	.51	.62	.155	.159	3.40	0.20
37	2	1.78	.347	.51	.63	.168	.164	5.00	0.00
38	7	1.69	.377	.59	.63	.160	.172	3.71	0.14
39	3	1.67	.385	.57	.66	.158	.186	4.67	0.67
40	13	1.52	.347	.50	.57	.135	.172	3.15	0.00
43	11	1.49	.351	.49	.57	.143	.171	3.00	0.09
44	7	1.78	.363	.57	.64	.161	.171	3.86	0.43
50	15	1.83	.350	.54	.62	.165	.168	3.93	0.60
51	8	1.73	.345	.50	.56	.146	.157	3.12	0.12

TABLE 5. Means of Alate Characters for All Localities (Continued).

Locality Code Numbers	Number of Alates	Forewing Length	Head Width	Thorax Length	Tibia Length	Antenna III	Antenna VI	Sensoria III	Sensoria IV
52	12	1.55	.306	.49	.59	.138	.164	3.08	0.08
53	7	1.98	.365	.59	.63	.163	.167	3.86	0.00
55	5	1.60	.346	.49	.58	.146	.160	3.80	0.40
56	8	2.03	.375	.59	.68	.176	.178	4.25	0.12
57	6	1.91	.381	.58	.65	.174	.169	3.83	0.50
58	6	1.61	.367	.53	.60	.147	.173	3.50	0.17
59	13	1.95	.374	.57	.67	.186	.174	4.46	0.31
60	15	1.83	.359	.55	.66	.172	.171	4.53	0.67
61	15	1.69	.364	.56	.63	.146	.179	3.33	0.07
62	10	1.69	.347	.54	.63	.157	.173	3.90	0.10
63	8	2.11	.369	.57	.68	.184	.178	4.00	0.00
64	8	1.50	.304	.45	.56	.142	.172	3.00	0.00
Standard Deviation		.117	.024	.052	.053	.0163	.0138	1.065	.400

Explanation: The number of galls per locality is generally less than those in Table 6, because some galls had stem mothers but not alates. Furthermore, there are only 57 localities listed in the table, since 17 localities had stem mothers but no alates. All continuous variables are given in millimeters; all meristic ones as counts. The standard deviation at the foot of the table is the average standard deviation within localities. It is *not* the standard error of the means. In order to obtain an average standard error for the study, one might multiply it by 1/2.9965 which is the reciprocal of the square root of the average number of galls with alates per locality, calculated as $n_0 = \frac{1}{a-1}\left(\sum^{a} n_i - \frac{\sum^{a} n_i^2}{\sum^{a} n_i}\right)$ where a is the number of localities and n_i is the number of galls in the ith locality.

TABLE 6. Means of Stem Mother Characters for All Localities.

Locality Code Numbers	Number of Stem Mothers	Total Length	Head Width	Femur Length	Tibia Length	Antenna III	Antenna IV
01	13	2.52	.428	.352	.317	.137	.116
02	20	2.40	.432	.365	.321	.142	.115
03	20	2.30	.435	.352	.313	.138	.111
04	20	2.32	.424	.365	.307	.149	.114
05	20	2.54	.468	.390	.344	.165	.109
06	20	2.58	.454	.404	.328	.153	.110
07	18	2.93	.449	.366	.327	.154	.116
08	19	2.64	.448	.374	.317	.149	.119
10	20	2.37	.429	.381	.323	.147	.121
11	17	2.13	.409	.384	.323	.152	.114
12	20	2.49	.424	.399	.337	.156	.119
13	20	2.68	.420	.387	.327	.151	.120
14	20	2.37	.410	.348	.305	.143	.108
15	18	2.56	.405	.354	.319	.150	.109
16	20	2.33	.384	.349	.305	.140	.115
17	18	2.15	.399	.364	.313	.139	.113
18a	6	3.00	.426	.384	.319	.148	.101
18b	17	2.56	.460	.356	.334	.157	.113
18c	12	2.55	.446	.385	.318	.165	.107
18d	10	2.48	.446	.399	.322	.156	.104
19a	17	2.58	.445	.385	.323	.156	.101
19b	20	2.80	.443	.382	.333	.156	.107
19c	17	3.06	.455	.410	.350	.162	.109
19d	13	2.54	.438	.385	.351	.160	.108
19e	7	2.21	.422	.386	.322	.149	.103
20a	17	3.14	.477	.384	.328	.167	.109
20b	12	2.90	.425	.355	.307	.160	.105
20c	12	2.62	.439	.379	.323	.157	.102
20d	20	2.96	.464	.413	.357	.164	.110
20e	20	2.24	.412	.384	.333	.150	.107
21	25	2.23	.455	.411	.338	.152	.109
22	17	2.66	.460	.400	.332	.165	.106
23	20	3.03	.435	.360	.304	.140	.110
24	20	2.74	.447	.395	.351	.156	.108
25	16	3.17	.469	.384	.337	.164	.108
26	14	2.66	.460	.397	.325	.161	.105
27	9	3.09	.437	.340	.325	.154	.105
28	2	3.22	.462	.412	.370	.177	.100
29	8	2.97	.454	.353	.297	.138	.101
30	14	3.38	.446	.398	.338	.161	.102
31	5	2.58	.409	.379	.326	.148	.099
32	8	2.62	.413	.392	.336	.146	.109
33	12	2.92	.457	.412	.356	.168	.106

TABLE 6. Means of Stem Mother Characters for All Localities (Continued).

Locality Code Numbers	Number of Stem Mothers	Total Length	Head Width	Femur Length	Tibia Length	Antenna III	Antenna IV
34	17	2.75	.453	.415	.352	.157	.109
35	20	2.38	.424	.396	.341	.156	.108
36	20	2.73	.421	.358	.308	.145	.102
37	7	2.87	.443	.391	.330	.153	.106
38	7	2.04	.429	.395	.317	.140	.112
39	6	2.33	.450	.382	.308	.142	.105
40	15	2.45	.409	.389	.319	.144	.117
41	5	2.74	.442	.411	.353	.161	.114
42	18	2.90	.466	.412	.341	.161	.107
43	20	2.55	.442	.392	.323	.147	.109
44	9	2.72	.462	.411	.348	.153	.110
45	4	2.38	.460	.386	.328	.149	.104
46	4	2.33	.430	.342	.278	.116	.115
47	20	2.71	.463	.402	.351	.165	.106
48	20	2.63	.455	.398	.344	.163	.110
49	20	2.22	.446	.389	.328	.154	.106
50	20	2.28	.436	.374	.334	.146	.105
51	20	2.64	.443	.415	.352	.158	.108
52	16	2.01	.421	.375	.311	.143	.111
53	20	2.76	.458	.418	.351	.161	.108
54	15	2.79	.458	.397	.349	.166	.107
55	19	2.45	.442	.386	.328	.150	.105
56	10	2.62	.435	.412	.351	.159	.107
57	12	2.50	.432	.370	.310	.141	.103
58	7	2.49	.420	.410	.338	.159	.121
59	20	2.98	.475	.421	.346	.170	.110
60	20	2.84	.473	.405	.357	.172	.115
61	20	2.67	.440	.382	.332	.152	.118
62	10	1.87	.430	.387	.327	.143	.111
63	8	2.29	.429	.397	.342	.158	.110
64	8	2.31	.406	.371	.326	.148	.116
Standard Deviations		.379	.0341	.0338	.0283	.0165	.0098

Explanation: These means are based on all available stem mothers regardless of whether the stem mother had alates associated with her or not. All continuous variables are given in millimeters. The standard deviation at the foot of the table is the average standard deviation within localities. It is *not* the standard error of the means. In order to obtain an average standard error for the study, one might multiply it by 1/3.8693 which is the reciprocal of the square root of the average number of galls per locality, calculated as

$$n_0 = \frac{1}{a-1}\left(\sum^{a} n_i - \frac{\sum^{a} n_i^2}{\sum^{a} n_i} \right)$$

where a is the number of localities and n_i is the number of galls in the *i*th locality.

CORRECTED TABLE 2 OF SOKAL AND RINKEL (1963).—Means of All Characters for All Localities.

Locality Code Numbers	Forewing Length	Head Length	Head Width	Thorax Length	Thorax Width	Femur Length	Tibia Length	Tarsus Length	Antenna III	Antenna IV	Antenna V	Antenna VI	Sensoria III	Sensoria IV	Sensoria V	Sensoria VI	Islands V	Islands VI
1	1.68	.206	.368	.564	.552	.456	.631	.140	.159	.0634	.0942	.177	3.27	.10	1.17	1.03	1.73	2.93
2	1.70	.209	.376	.565	.563	.467	.644	.139	.158	.0658	.0932	.178	3.47	.30	1.23	1.07	2.07	2.73
3	1.65	.213	.384	.546	.580	.437	.612	.140	.152	.0609	.0899	.176	3.30	.27	1.13	1.03	1.97	3.20
4	1.66	.210	.365	.562	.563	.460	.632	.141	.152	.0640	.0927	.179	3.37	.13	1.07	1.00	2.27	3.17
5	1.99	.204	.377	.592	.593	.480	.675	.155	.185	.0753	.0952	.170	4.83	.83	1.13	1.00	2.80	3.23
6	1.92	.213	.376	.600	.611	.477	.653	.148	.160	.0680	.0965	.175	3.73	.13	1.07	1.00	2.27	2.93
7	1.75	.214	.374	.572	.584	.482	.655	.146	.153	.0637	.0935	.180	2.83	.13	1.00	1.00	2.37	2.83
8	1.65	.209	.373	.535	.562	.449	.615	.136	.145	.0582	.0893	.175	3.07	.00	1.00	1.00	2.03	3.03
9	2.09	.202	.388	.627	.651	.517	.712	.159	.184	.0760	.1049	.179	4.03	.30	1.03	1.03	2.77	2.73
10	1.71	.217	.384	.563	.591	.465	.626	.140	.153	.0646	.0945	.179	3.53	.07	1.23	1.03	2.37	3.30
11	1.60	.209	.365	.511	.549	.446	.597	.133	.166	.0718	.1010	.173	3.90	.47	1.07	1.00	2.27	2.83
12	1.64	.213	.370	.531	.548	.445	.625	.144	.149	.0617	.0948	.179	3.63	.10	1.10	1.03	2.27	3.17
13	1.72	.207	.373	.558	.559	.470	.657	.147	.154	.0638	.0930	.184	3.93	.17	1.13	1.00	2.53	3.23
14	1.54	.199	.357	.488	.509	.413	.586	.134	.140	.0559	.0890	.168	3.37	.07	1.03	1.00	2.10	3.23
15	1.52	.191	.336	.442	.462	.404	.574	.134	.136	.0570	.0951	.172	3.47	.00	1.03	1.00	2.13	3.00
16	1.55	.211	.367	.521	.543	.421	.551	.127	.136	.0552	.0873	.165	2.27	.00	1.03	1.03	2.13	3.20
17	1.52	.208	.362	.504	.516	.413	.556	.130	.136	.0598	.0921	.170	3.33	.00	1.00	1.03	1.77	2.77
18	2.00	.202	.375	.579	.583	.492	.665	.147	.169	.0700	.1003	.164	3.00	.00	1.03	1.03	2.03	2.20
19	1.72	.198	.358	.504	.519	.421	.585	.138	.141	.0635	.0921	.161	2.53	.00	1.10	1.00	2.23	2.57
20	1.90	.202	.368	.567	.540	.461	.629	.150	.164	.0670	.0990	.166	3.43	.07	1.03	1.00	2.23	2.47
21	1.98	.202	.373	.564	.593	.478	.671	.148	.170	.0714	.1018	.172	3.83	.10	1.00	1.10	2.03	2.83
22	2.10	.210	.392	.633	.597	.512	.703	.151	.176	.0701	.0997	.172	4.17	.10	1.27	1.03	1.97	2.63
23	1.90	.208	.380	.601	.611	.477	.662	.142	.156	.0660	.0956	.175	3.43	.07	1.13	1.03	2.07	2.87
Average standard errors of locality means	.039	.0034	.0051	.0128	.0140	.0093	.0122	.0022	.0036	.00166	.00173	.0026	.212	.061	.052	.028	.144	.166

All continuous variables are given in millimeters; all meristic ones as counts.

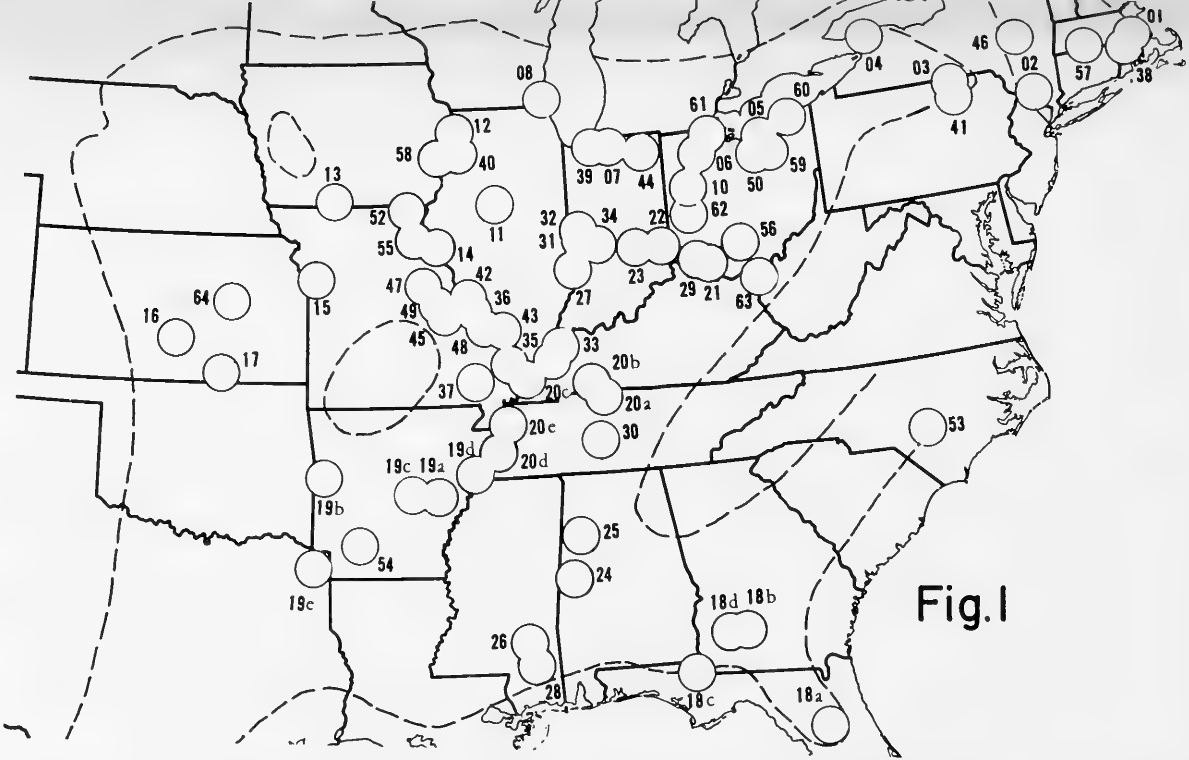

Fig.I

Fig. 1. Outline of the area studied with localities and their code numbers entered. Hollow circles represent the locality sites, numbers next to them are their locality code numbers. Localities numbers 1 to 23 are those studied by Sokal and Rinkel (1963). The "area samples" of these authors, representing composite localities based on small locality samples, are here separated and identified by lower case letters following the numbers. A detailed listing of the localities is given in Table 1. The dashed line circumscribes the distribution of the cottonwood, *Populus deltoides* Bartr., according to the map of Sudworth (1934). From collection records by the senior author this map is not entirely accurate but in lieu of a more precise map it has been accepted. The absence of cottonwoods from certain areas in Missouri and Iowa as shown on this map is questionable. The absence of cottonwoods from the Appalachian area has been verified. Exact boundaries of cottonwood distribution near the Atlantic seaboard are not indicated since no samples from there were employed.

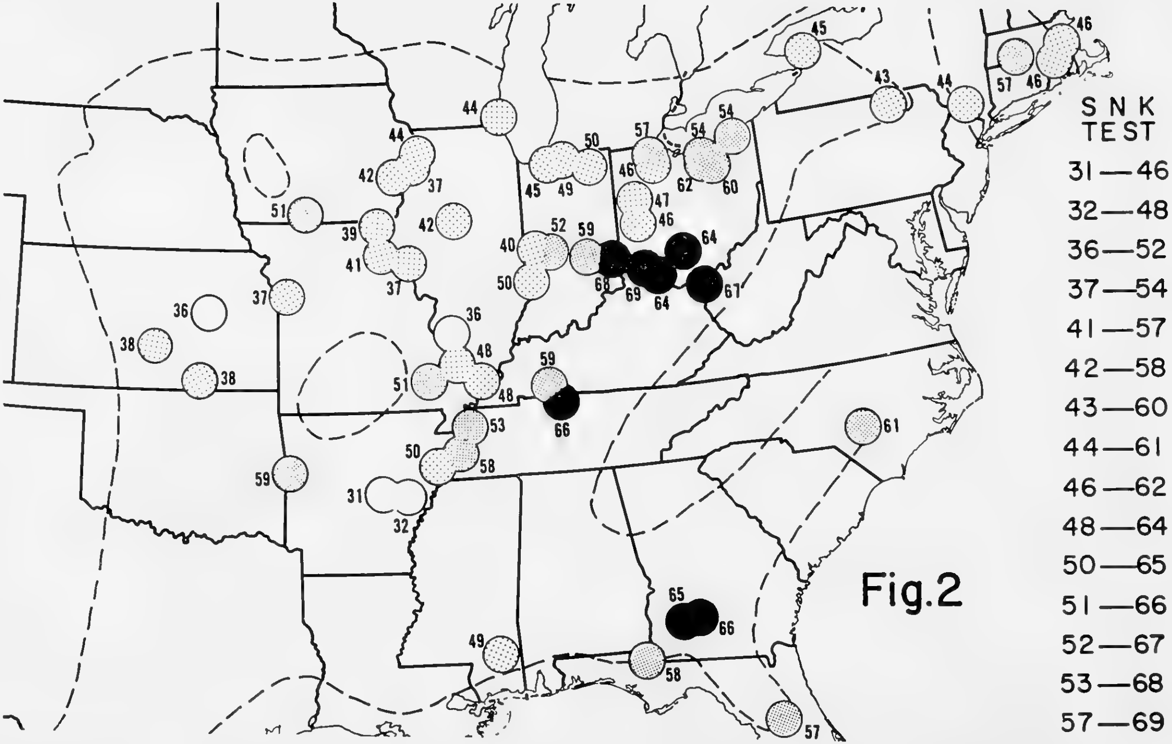

Fig.2

FIG. 2. Geographic distribution map of means of the character "forewing length" for the 57 localities containing alates. The means have been transformed into probits and multiplied by 10 for ease of comparison. Localities are represented by circles whose shading gives a general idea of the magnitude of the probit score. Means<37 are shown as white circles, means between 37 to 50 as light gray circles, between 51 to 63 as dark gray circles and >63 as black circles. The outlines have been explained in Figure 1. The results of the SNK tests are given at the right hand margin of the figure. Two means are significantly different (at P <0.01) if no line in the SNK table includes both of them within its range. Thus 61 and 66 are not significantly different; they are included in the line 57-69. However, 32 and 58 are not both included in any line of the table; hence they are significantly different from each other.

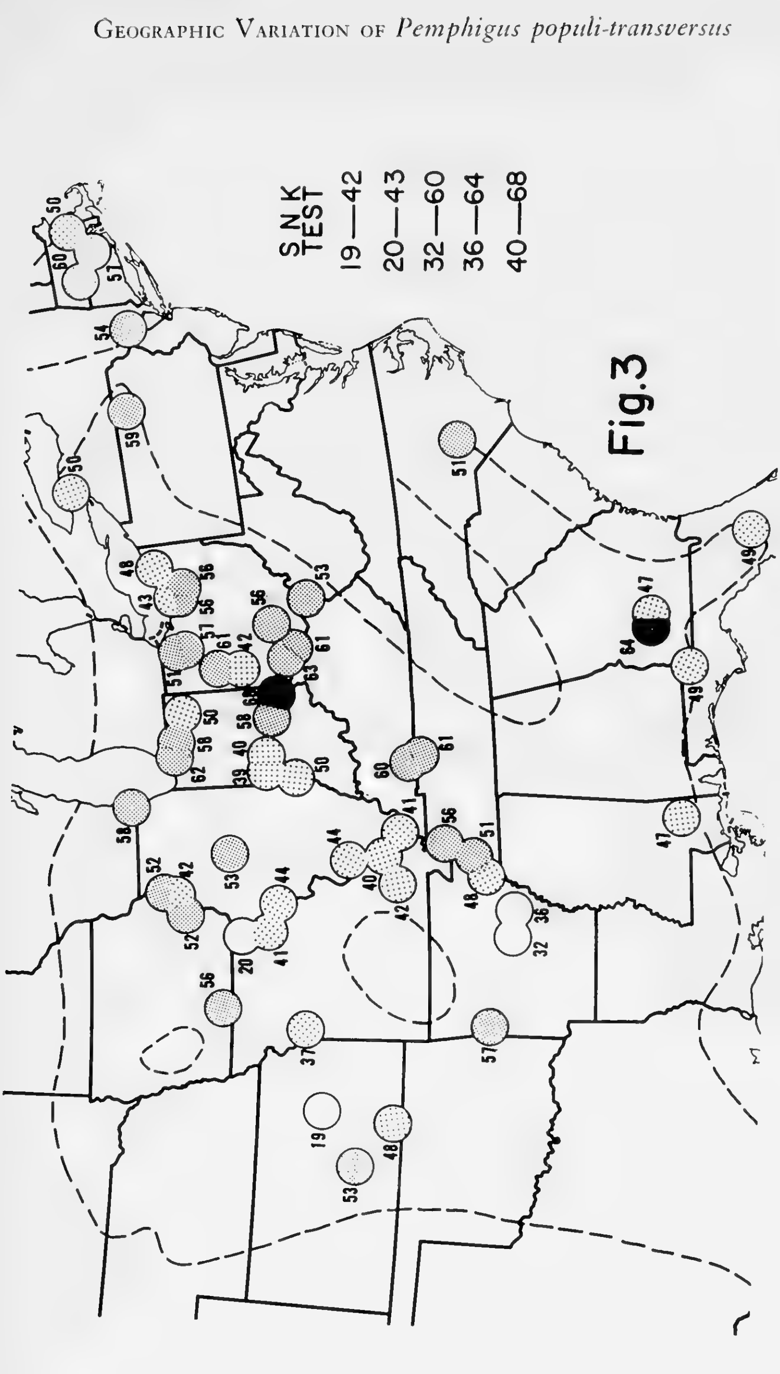

Fig.3

Fig. 3. Geographic distribution map of means of the character "head width" for the 57 localities containing alates. Explanation as in Figure 2.

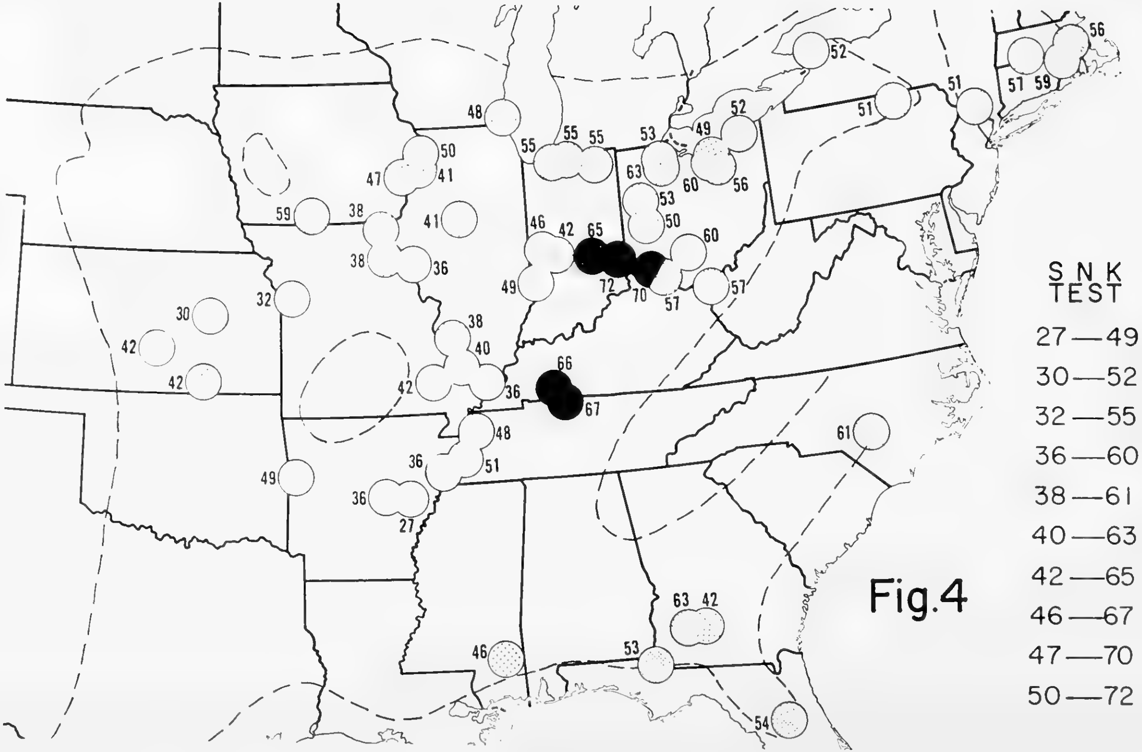

Fig. 4

FIG. 4. Geographic distribution map of means of the character "thorax length" for the 57 localities containing alates. Explanation as in Figure 2.

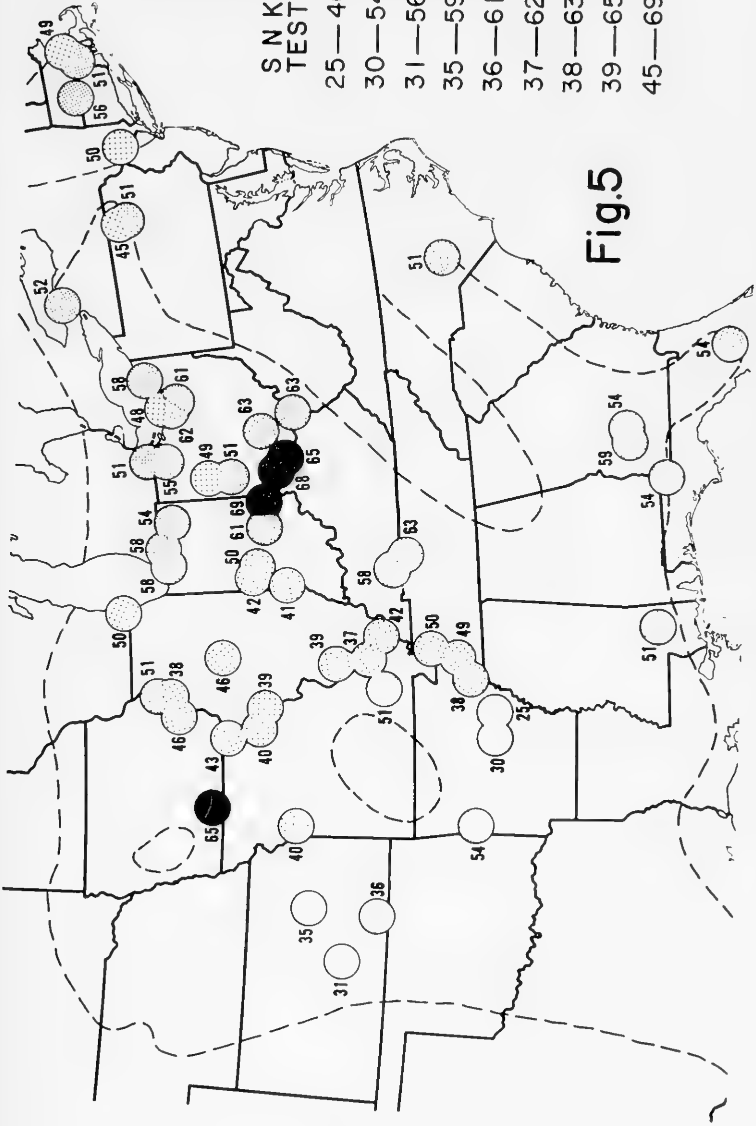

FIG. 5. Geographic distribution map of means of the character "tibia length" for the 57 localities containing alates. Explanation as in Figure 2.

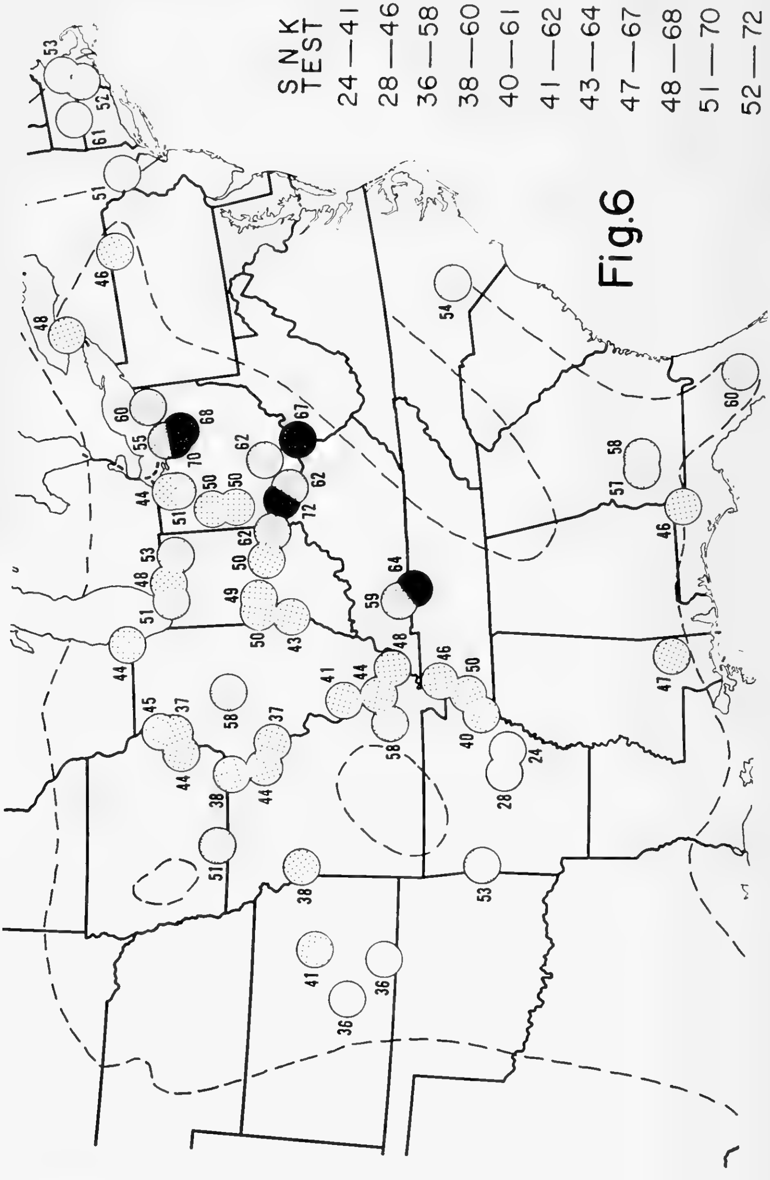

FIG. 6. Geographic distribution map of means of the character "antennal segment III length" for the 57 localities containing alates. Explanation as in Figure 2.

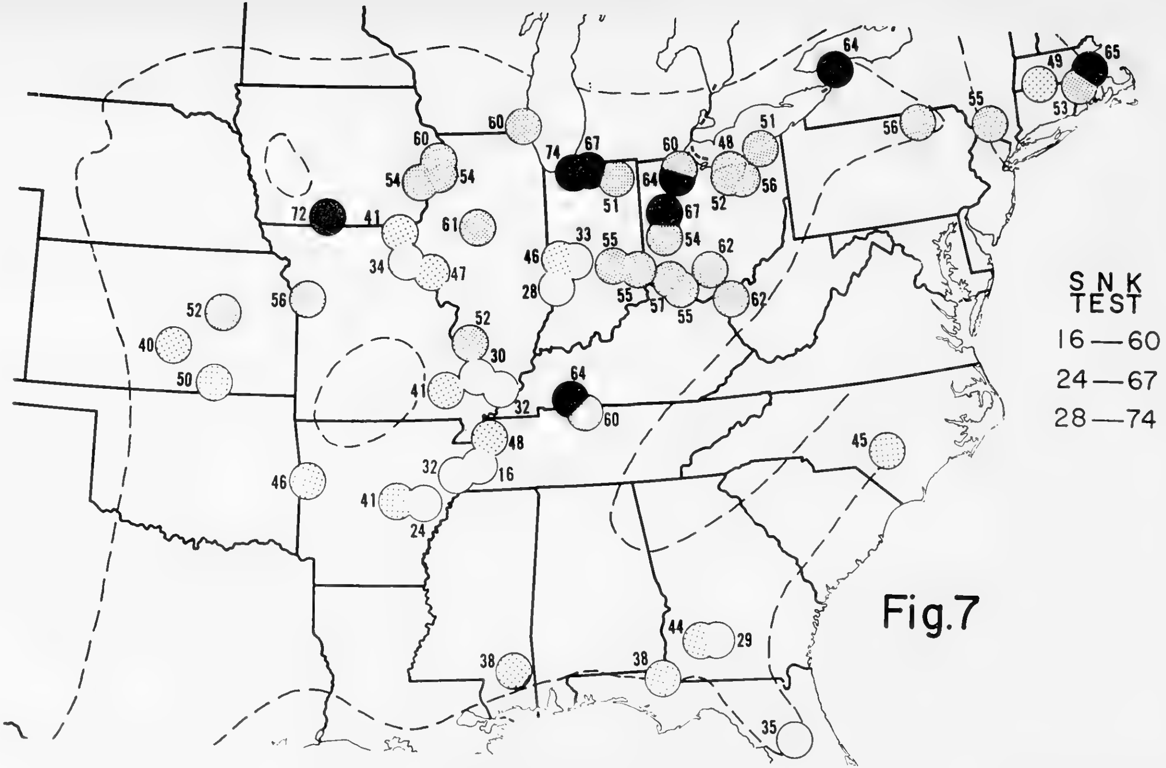

Fig.7

FIG. 7. Geographic distribution map of means of the character "antennal segment VI length" for the 57 localities containing alates. Explanation as in Figure 2.

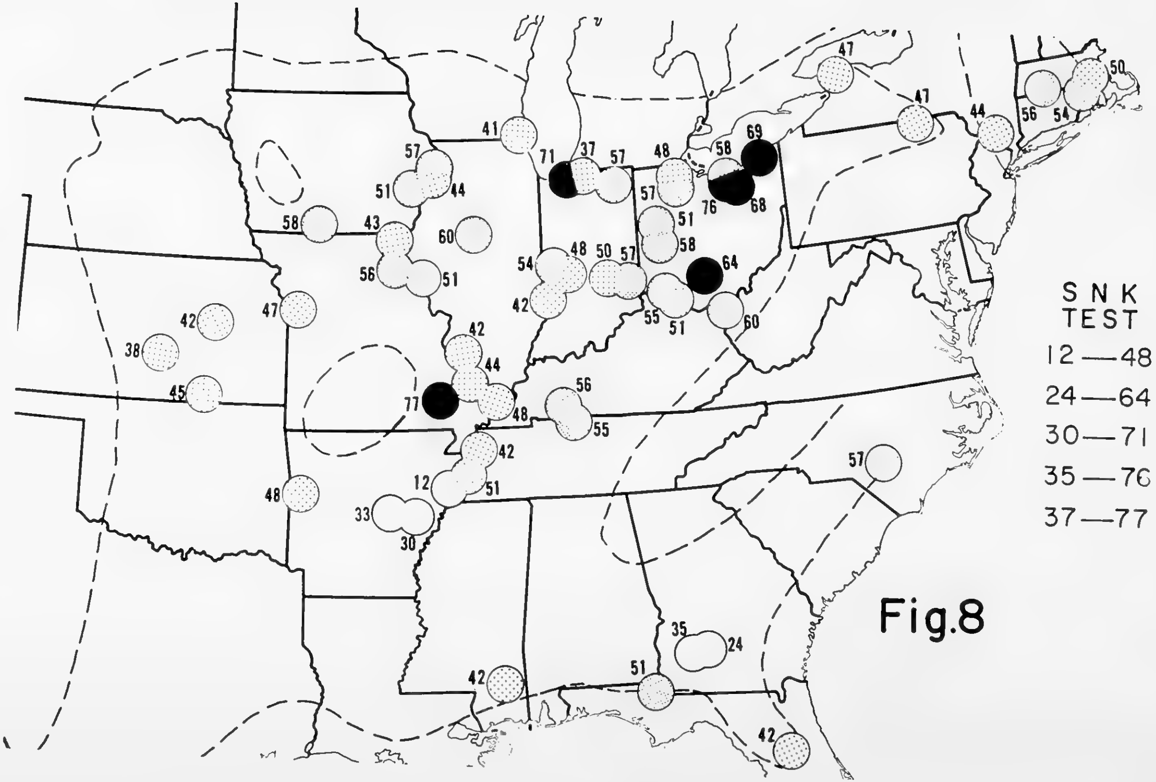

FIG. 8. Geographic distribution map of means of the character "number of sensoria on antennal segment III" for the 57 localities containing alates. Explanation as in Figure 2.

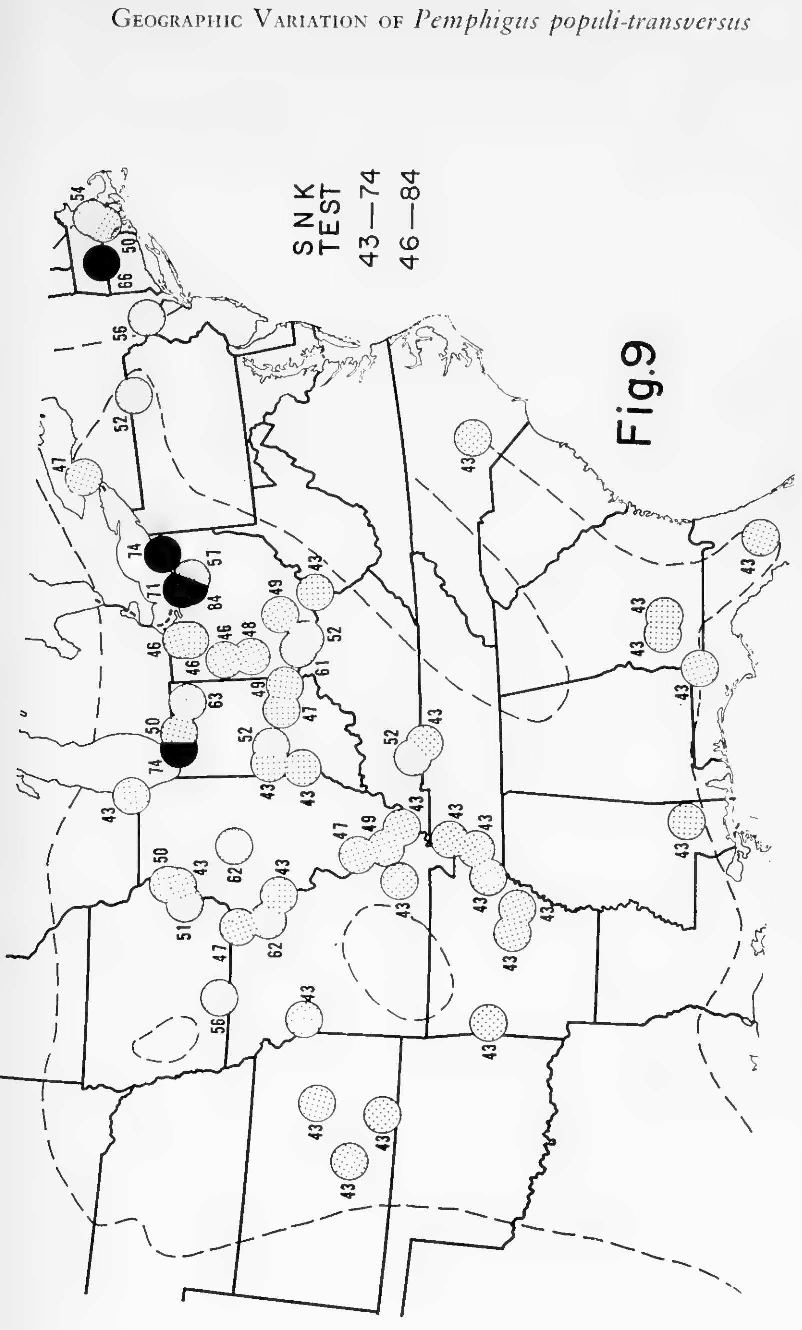

Fig.9

FIG. 9. Geographic distribution map of means of the character "number of sensoria on antennal segment IV" for the 57 localities containing alates. Explanation as in Figure 2.

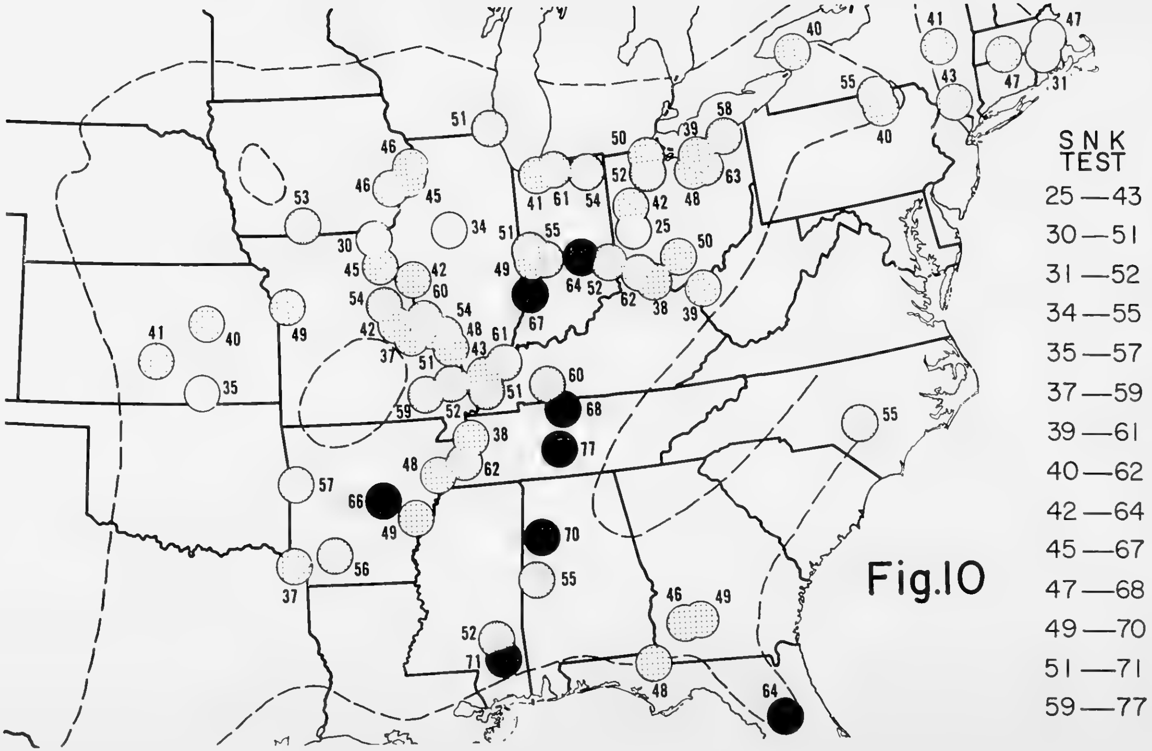

FIG. 10. Geographic distribution map of means of the character "stem mother total length" for the 74 localities containing stem mothers. Explanation as in Figure 2.

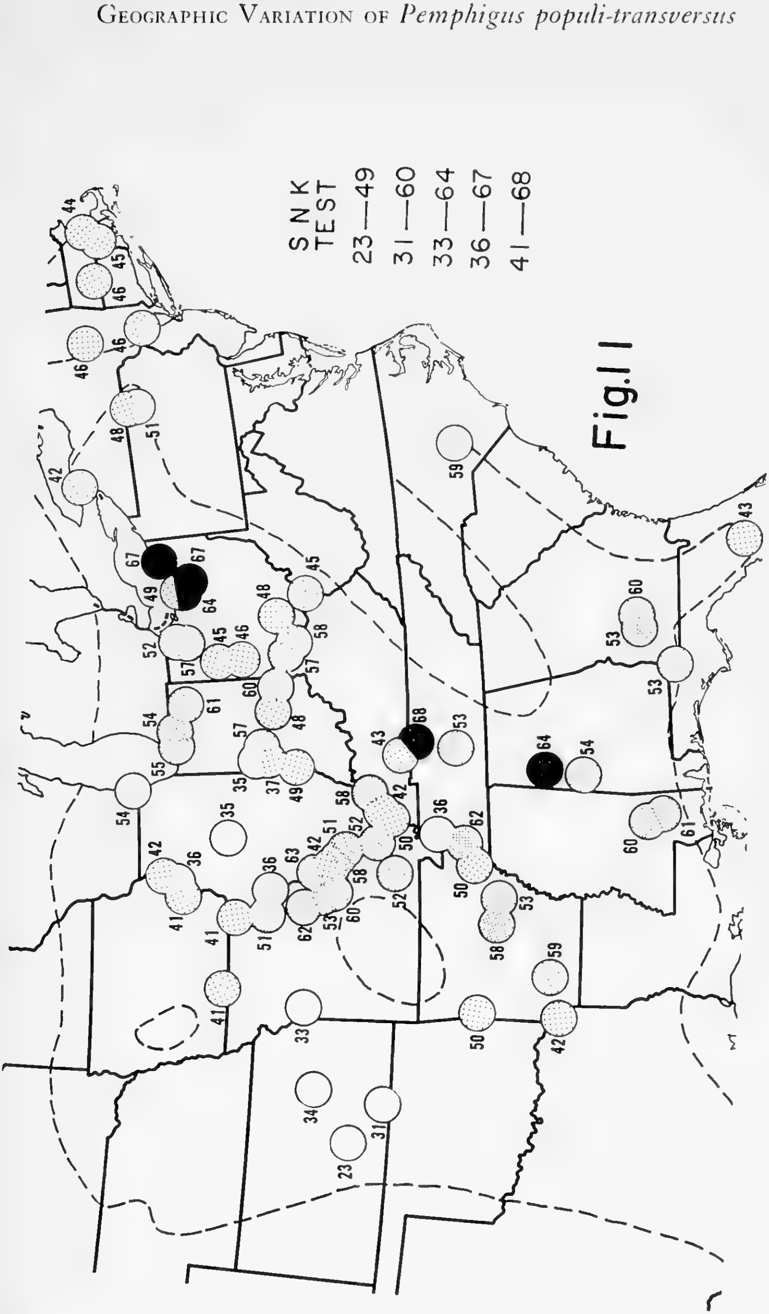

Fig. 11. Geographic distribution map of means of the character "stem mother head width" for the 74 localities containing stem mothers. Explanation as in Figure 2.

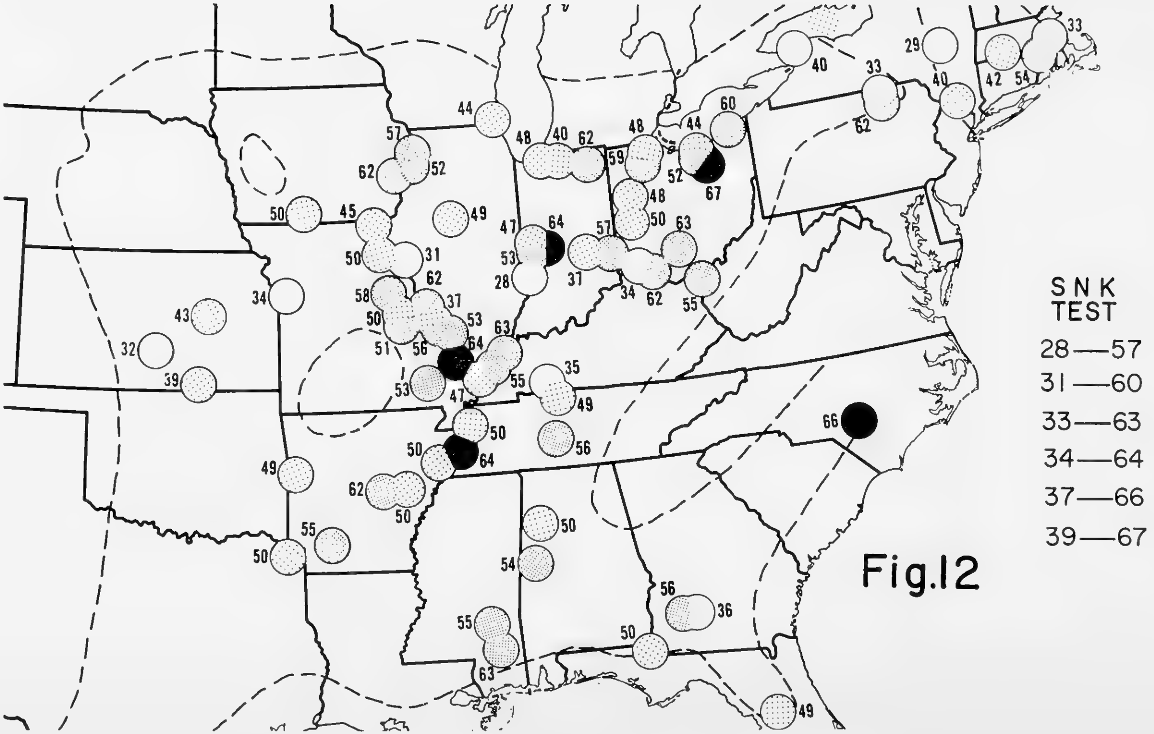

FIG. 12. Geographic distribution map of means of the character "stem mother femur length" for the 74 localities containing stem mothers. Explanation as in Figure 2.

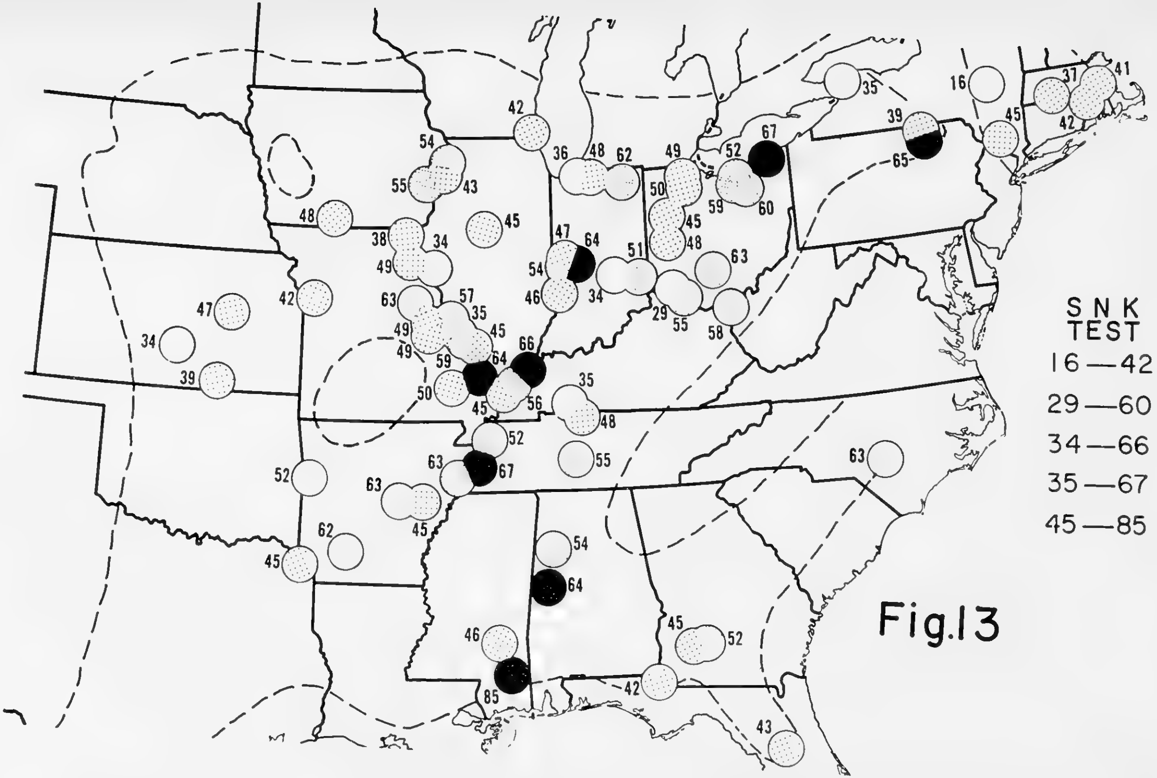

Fig. 13. Geographic distribution map of means of the character "stem mother tibia length" for the 74 localities containing stem mothers. Explanation as in Figure 2.

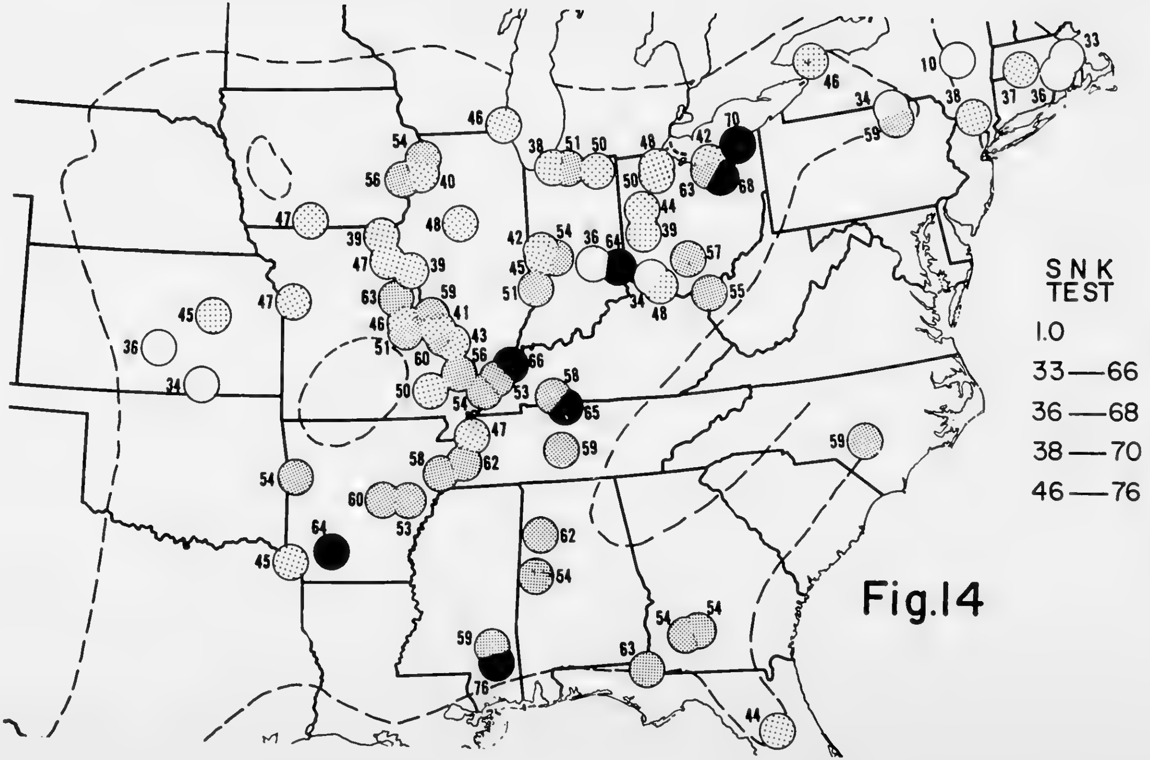

Fig.14

Fig. 14. Geographic distribution map of means of the character "stem mother antennal segment III length" for the 74 localities containing stem mothers. Explanation as in Figure 2.

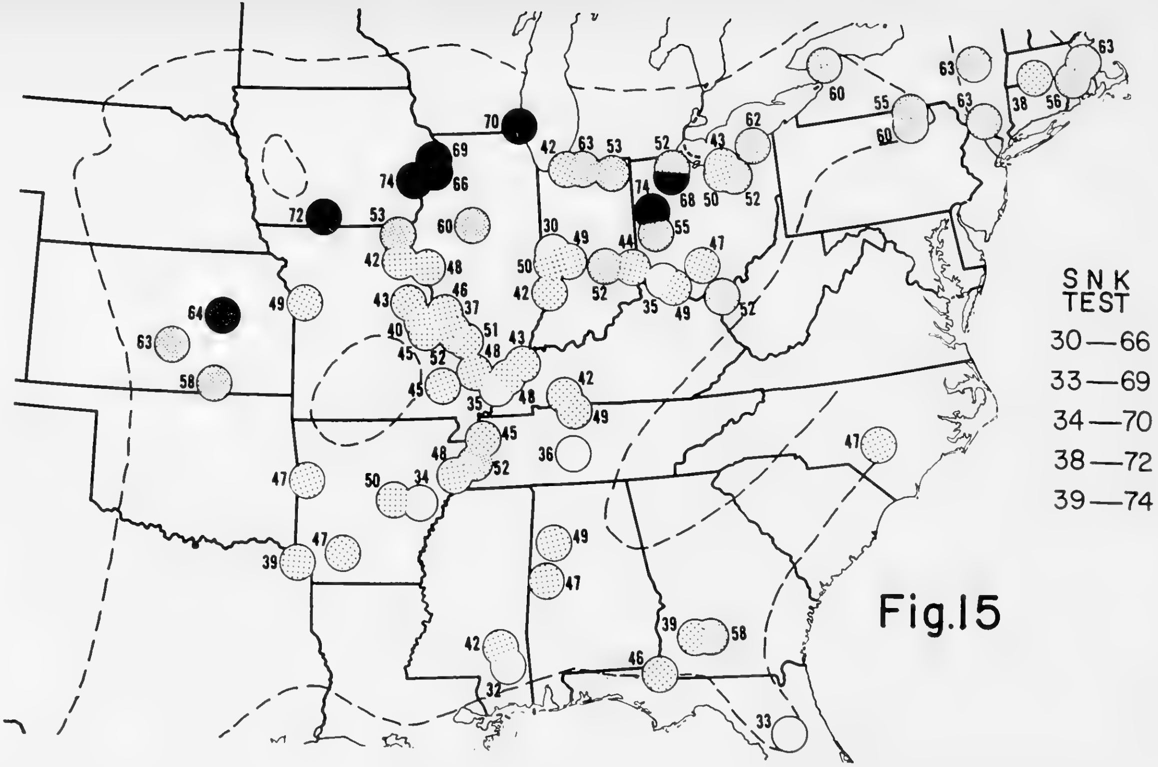

Fig. 15. Geographic distribution map of means of the character "stem mother antennal segment IV length" for the 74 localities containing stem mothers. Explanation as in Figure 2.

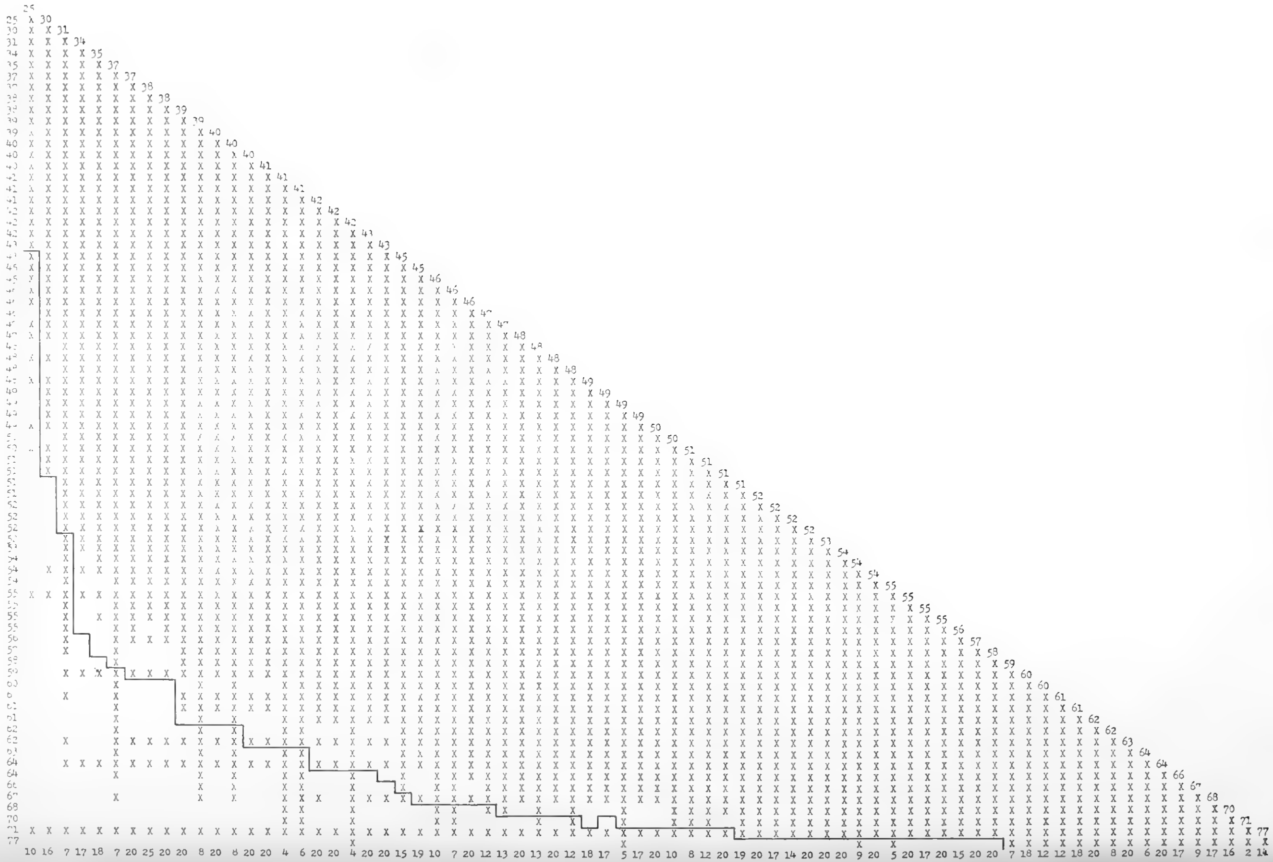

FIG. 16. Diagrammatic representation of the results of an SNK analysis for stem mother total length based on unequal sample sizes compared with the results when employing an average sample size. The numbers at the left hand margin and along the principal diagonal of the half matrix are the mean probit scores for the character (compare Figure 10). The numbers along the bottom of the half matrix indicate the sample size of the corresponding mean along the principal diagonal. In order to test whether any two means are significantly different look up the lower mean along the principal diagonal and run down the column to the level of the higher mean along the left hand margin. In case of several probit means of equal score employ the mean with the appropriate sample size. If both ends are marked by X the means are not significantly different. If the end representing the higher mean lacks an X the means are significantly different. Thus for example mean 30 is not significantly different from mean 47, but is significantly different from mean 48. The line running from the left hand margin in zig-zag fashion to the bottom of the matrix represents the boundary of not significant sets based on an SNK test using the method of equal sample sizes and substituting average sample size n_o for n. All X's outside this boundary are not significant differences which would be considered significant when using average n_o; blank areas within the boundary are significant differences between means which would not show up with the average method. For further discussion see text.

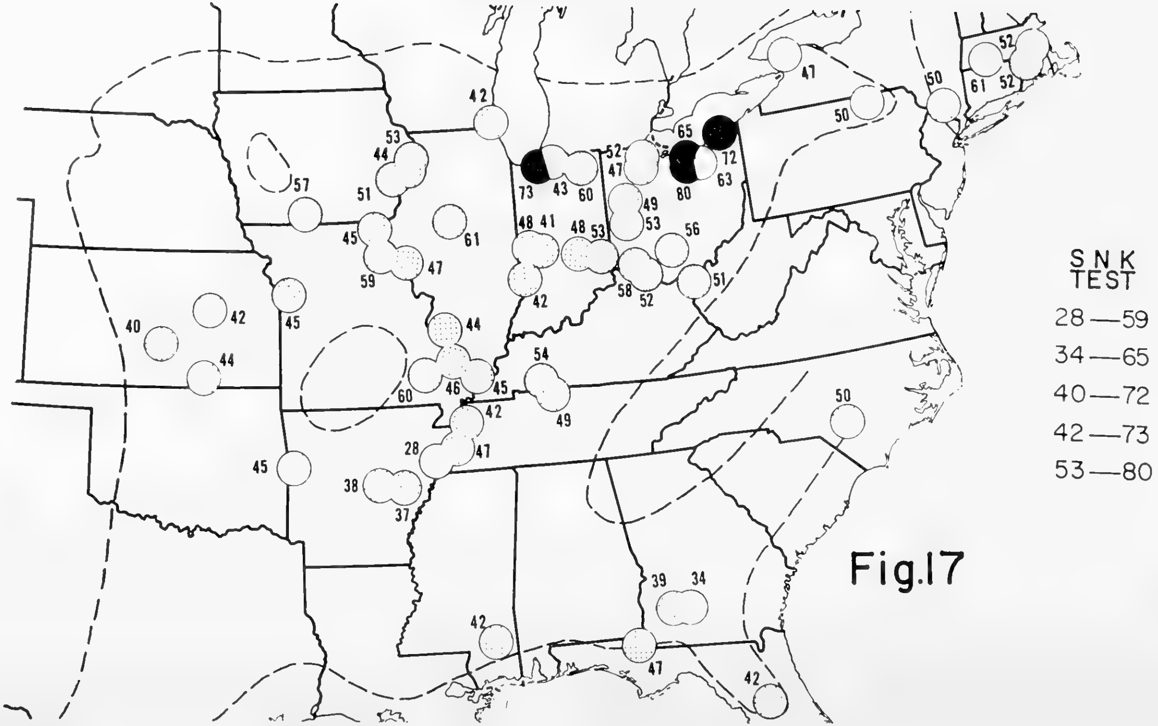

Fig.17

Fig. 17. Geographic variation of interlocality factor I. Explanation as in Figure 2.

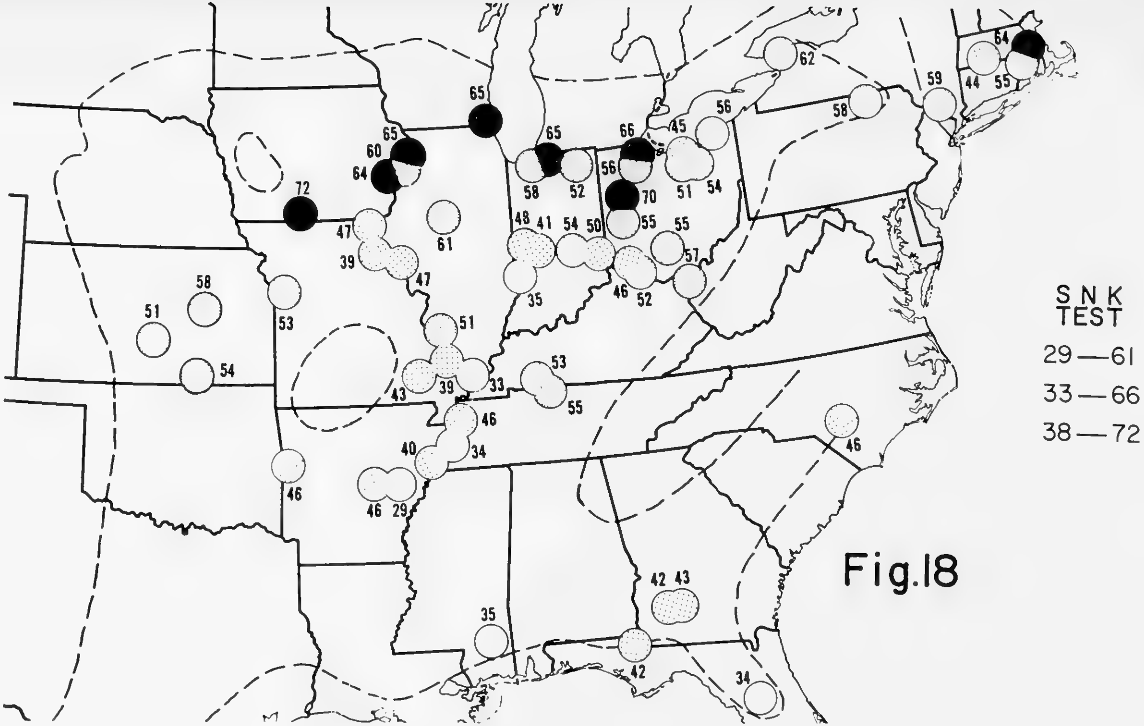

Fig.18

FIG. 18. Geographic variation of interlocality factor II. Explanation as in Figure 2.

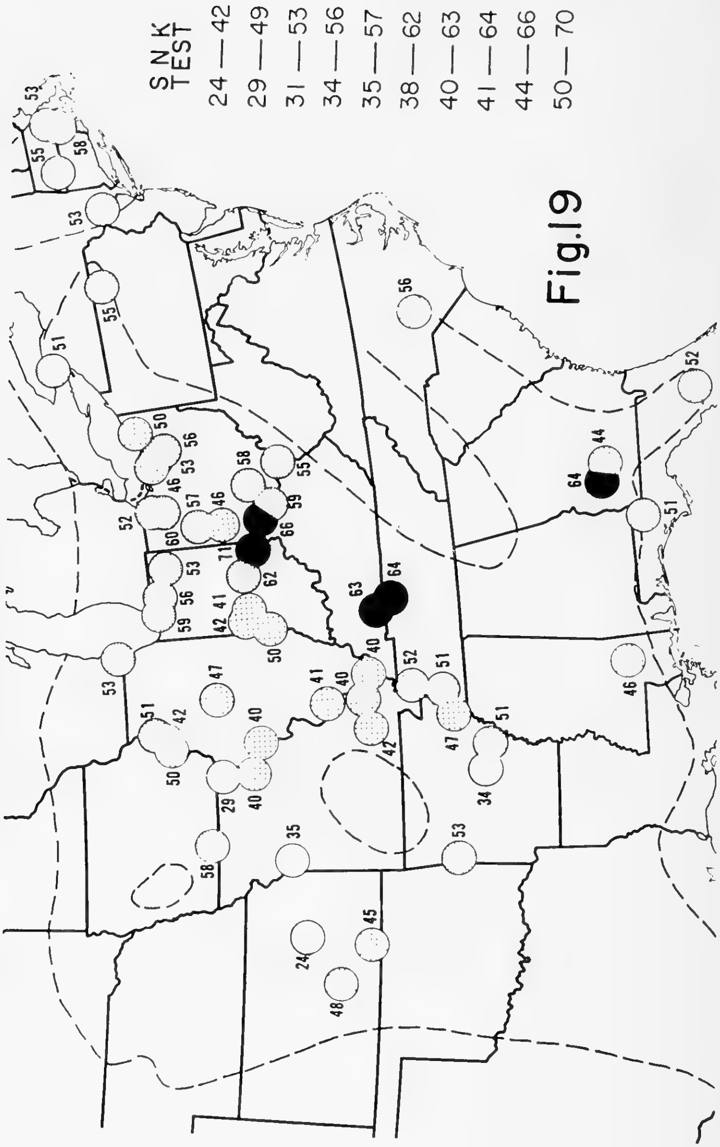

FIG. 19. Geographic variation of interlocality factor III. Explanation as in Figure 2.

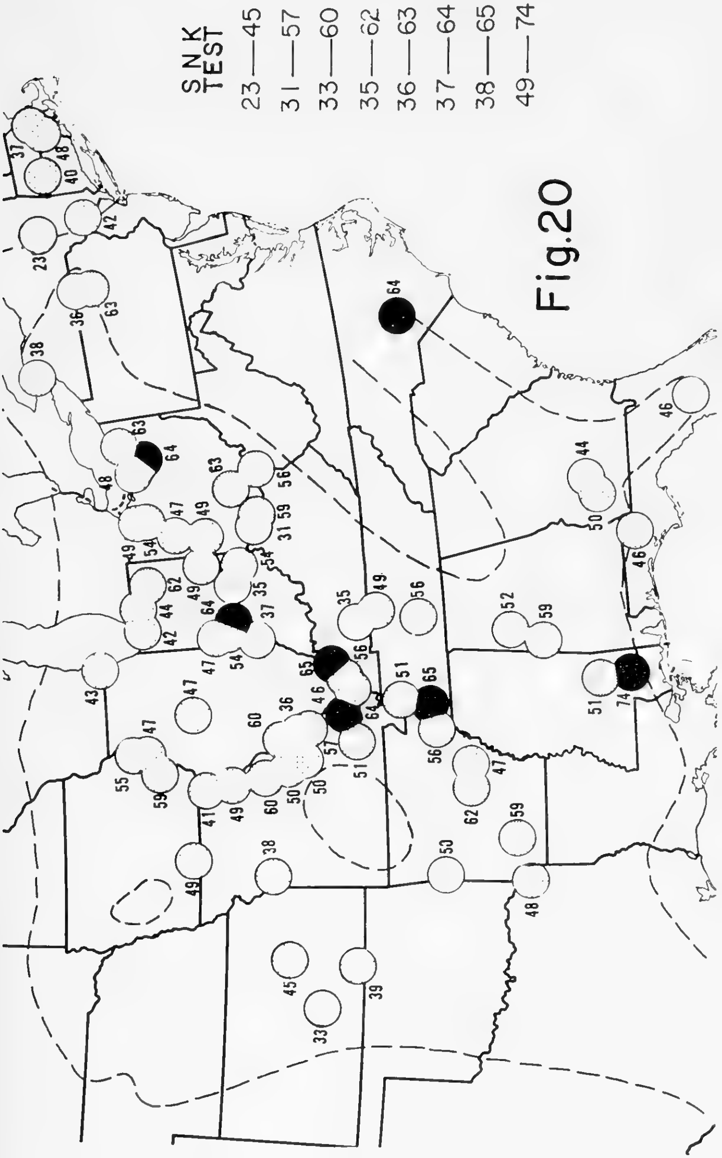

Fig. 20. Geographic variation of interlocality factor F-1. Explanation as in Figure 2.

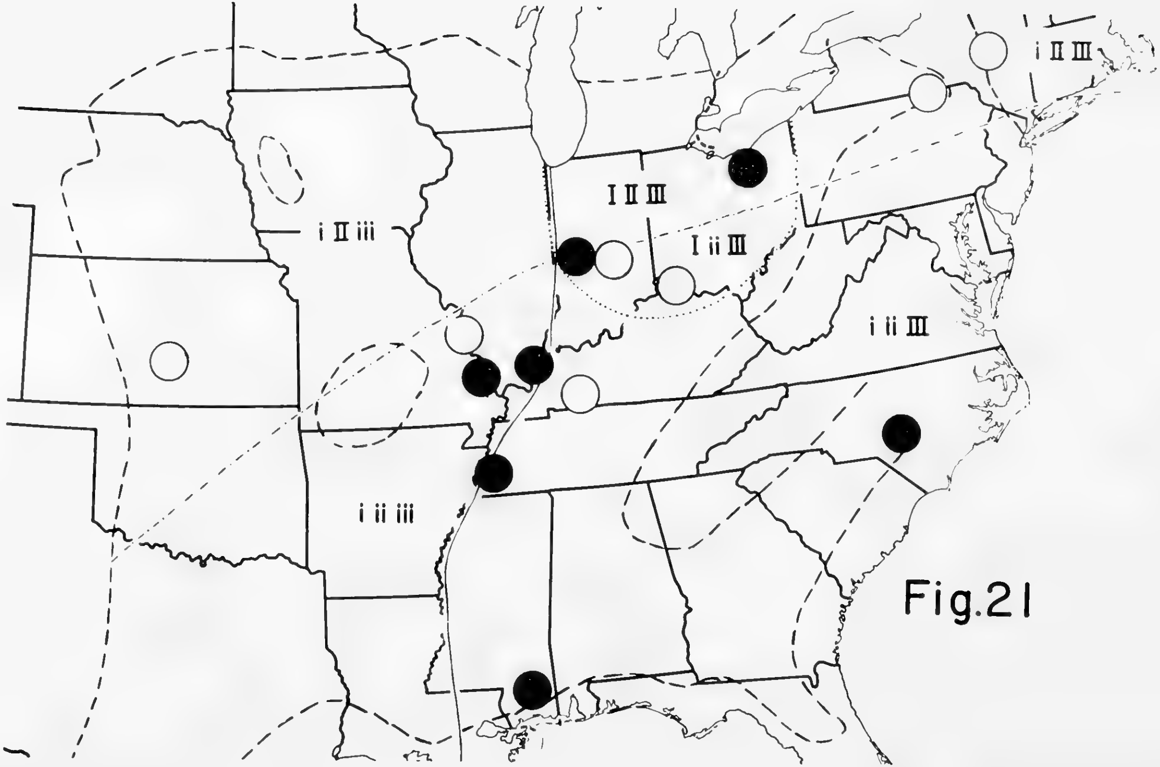

Fig.21

FIG. 21. Attempt to categorize distinct infraspecific populations on the basis of the four factors shown in Figures 17-20. The infraspecific populations are divided by approximate boundaries separating high and low areas for factors I, II and III. These boundaries are symbolized by dotted, dot-dashed and solid lines, respectively. Such boundaries were impossible to devise for factor F-1, which has patchy high and low means. To give some idea of the variation of this factor, we have copied the extreme means (black and white circles) from Figure 20 onto this map. Symbols identifying the infraspecific populations indicate magnitude of factor scores, i, ii, and iii indicating the low levels of the three factors while I, II, III represent the high levels of these factors. While means in these groups are generally not significantly different from those in other groups, it is safe to say that all means representing extreme highs or lows are significantly different from the opposite extremes for their factor.

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VOL. XLVI PAGES 253-302 OCTOBER 28, 1965 No. 6

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This study was made under a grant (GB-1349) from the National Science Foundation.

ABSTRACT

This paper deals with caecilians of southeastern Asia and the African islands of São Thomé and Rolas in the Gulf of Guinea. Four species are redescribed: *Ichthyophis glutinosus* (Linnaeus), *Ichthyophis hypocyaneus* (Van Hasselt), *Ichthyophis weberi* Taylor, and *Schistometopum brevirostris* (Peters). A neotype is designated for *I. weberi.* The following are described as new: *Ichthyophis atricollaris* (Borneo), *I. elongatus* (Sumatra), *I. biangularis* (Borneo), *I. pesudangularis* (Ceylon), *I. asplenius,* Borneo, *I. forcarti* (Ceylon), *I. orthoplicatus* (Ceylon), *I. billitonensis* (Billiton); and *Schistometopum ephele* São Thomé.

Ichthyophis hypocyaneus and *Schistometopum brevirostris* are rehabilitated names removed from the synonymy of *Ichthyophis glutinosus* and *Schistometopum thomense* respectively.

INTRODUCTION

In the preparation of a taxonomic treatment of the Gymnophiona of the world, I have been reviewing the caecilians in many of the museums of the world and collecting in those areas where members of this order are to be found. As was to be expected certain forms, presumably undescribed, have been encountered and a part of them are herein described.

A neotype is designated for *Ichthyophis weberi* whose type was destroyed in the Bureau of Science in Manila in World War II.

I have had the fortune to study the type of *Caecilia hypocyanea* Van Hasselt preserved in the Leiden Museum. This is, I believe, a recognizable species and is removed from the synonymy of *Ichthyophis glutinosus*, a species that has been a most remarkable catch-all during taxonomic history. Another species, described as *Siphonops brevirostris* Peters and later placed in the synonymy of *Schistometopum thomense,* is resurrected and designated *Schistometopum brevirostris.* Unfortunately however the type of *brevirostris* was not available for examination when I was last in Berlin.

A list of forms treated in this paper are:

Ichthyophis glutinosus (Linnaeus)
Ichthyophis hypocyaneus Van Hasselt
Ichthyophis atricollaris sp. nov.
Ichthyophis elongatus sp. nov.
Ichthyophis biangularis sp. nov.
Ichthyophis pseudangularis sp. nov.
Ichthyophis asplenius sp. nov.
Ichthyophis forcarti sp. nov.
Ichthyophis weberi Taylor
Ichthyophis orthoplicatus sp. nov.
Ichthyophis billitonensis sp. nov.
Schistometopum ephele sp. nov.
Schistometopum brevirostris Peters

ACKNOWLEDGMENTS

In my caecilian studies of the past three years I have placed myself under obligation to many persons and institutions. This very considerable list will appear in the general work which I have in preparation. Those persons and institutions that have helped with this preliminary study or who have provided specimens are mentioned here.

I desire to acknowledge my deep obligation for information or for many kindnesses while visiting their museums; and my grateful thanks for the loan of specimens and the privilege of describing new forms:

To Dr. Hialmar Rehndahl and Miss Greta Vestergren of the Royal Natural History Museum, Stockholm, Sweden, for pertinent information on the type of *Caecilia glutinosa* (Linnaeus).

To Dr. L. D. Brongersma, Director of the Leiden Museum, who loaned the type of *Caecilia hypocyanea* Van Hasselt, and permitted me to describe the Bornean *Ichthyophis atricollaris* and *Ichthyophis asplenius* from the Leiden Museum collections, and who furnished much helpful information regarding the work of Kuhl and Van Hasselt in Java, and the publications on their collections; also to Dr. H. Boschma and Dr. M. Boeseman of Leiden for many courtesies at the Museum.

To Dr. George S. Myers, Division of Systematic Biology, Stanford University, and Dr. Alan E. Leviton, Associate Curator of Zoological collections for loan of material from the Stanford collections, especially the only known specimens of *Ichthyophis weberi* (practically topotypes), one of which has been named a neotype of the species.

To Dr. Lothar Forcart of the Museum of Natural History, Basel, Switzer-

land for the loan of significant specimens with the privilege of describing *Ichthyophis forcarti,* and *Ichthyophis pseudangularis.*

To Dr. Josef Eiselt of the Natural History Museum in Vienna for loans and the privilege of describing *Ichthyophis elongatus;* and also for other specimens.

To Miss Alice G. C. Grandison for the privilege of describing *Ichthyophis biangularis;* also for the loan of a number of other significant specimens.

To Mr. Hellenius of the Amsterdam Zoological Museum for the loan of specimens, one of which, *Ichthyophis billitonensis,* is described as new.

To Dr. Enrico Tortonesi, Director of the Civic Museum of Genoa for the loan of significant specimens, one of which has been named the type of a new species, *Schistometopum ephele;* and one a specimen of *S. brevirostris* Peters which convinces me that Peters' species merits specific designation.

To the Director of the Zoological Survey of India and Miss Mira B. Kirpalani for the loan of specimens, one of which is named the type of *Ichthyophis orthoplicatus.*

Ichthyophis glutinosus (Linnaeus)

FIGS. 1, 2, 3.

? *Serpens caecilia ceylonica* Seba, Locupletissimi rerum naturalium thesauri accurata descriptio, et iconibus artificiosissimis expressio, per universam physices historiam, vol. 2, 1735, p. 26, pl. xxv, fig. 2 (Ceylon).

Caecilia glutinosa Linnaeus, Museum S.R.M. Adolphi Friderici Regis Svecorum—in quo Animalia rariora imprimis et exotica: Quadrupedia Aves, Amphibia, Pisces, Insecta, Vermes describuntur et determinantur labine et svetice cum Iconibus jussu Reg. a. Car, Linnaeo, 1754, p. 19 (("In Indiis"); Caroli Linnaei Systema Naturae per Regna tria Naturae secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locus, Ed. 10, reformata, 1758, vol. 1, p. 229 (type-locality "In Indiis"); Andersson, Bihang Till. K. Svenska Vet. Akad. Handlingar, Bd. 24, Afd. 4, No. 6, 1899, p. 6 (type of *glutinosus*).

Ichthyophis glutinosus Taylor, Univ. Kansas Sci. Bull., vol. 40, Apr. 20, 1960, pp. 38-39.

The name *Ichthyophis glutinosus** has been used in more than a hundred articles applying to perhaps ten or more different species. Some of these may actually deal wholly or in part with *glutinosus* but most of them do not. To make an authoritative assignment of each, it would be necessary to examine the material studied or referred to by each author.

In a paper dealing with Asiatic caecilians published in the University of Kansas Science Bulletin (Vol. 40, April. 20, 1960, pp. 37-120), I pointed out that the Linnean description of *Caecilia glutinosa* was somewhat inadequate to identify certainly this species among the several forms that exist in Asia.

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* See Bourret, Les Batraciens de l'Indochine (l'Institut Oceanographique de l'Indochine) 1942, p. 136, for a listing of articles.

Thus Linnaeus states that he is unable to observe tentacles (*"Cirrhos nullo observare potui"*); teeth are not mentioned as occurring on the lower jaw; no mention is made of the presence of scales; characteristics of the nuchal collars are not mentioned and the locality given *"Habitat in Indiis"* might be anywhere in India, Ceylon, southeastern Asia or Islands of the Indo-Australian Archipelago.

Seemingly the type was not seen by subsequent writers on caecilians until studied by Andersson when he published his "Catalogue of Linnean type specimens of snakes" in 1899.* Andersson gives the length as 400 mm. (Linnaeus had said *"Longitudo pedem superat"*), and gives 355 as his count of transverse folds, Linnaeus' count having been 350.

In 1959 I appealed to Dr. Hialmar Rendahl of the Royal Natural History Museum, Stockholm, Sweden for further data on the type specimen. The matter was placed in the hands of Miss Greta Vestergren. She has had the kindness to forward certain data on the type which I present here:

"I must call your attention to the fact, that the specimen in question is not in exceedingly good condition. The snout is broken, most of the teeth in the upper jaw are lost, and moreover the specimen seems to have been dried partially, on account of which the fold-limits on the anterior part of the ventral surface are rather difficult to distinguish."

"Measurements in mm.:

"Total length 394; length from front of vent to tip of tail, 5.4; length of head from tip of snout to first groove, 14; width of head at first groove, 12.2; width of body at near middle, 17.2; distance between eye and tentacle, 2 mm. Tentacle to nostril? (snout broken); level of eyes to tip of snout, 6.2; diameter of eye, 0.7; distance between eyes, 7.5.

"Scales begin in the first and second folds, each fold having two scalerows. The third fold has three scalerows, the fourth fold four rows; while throughout almost all of the remaining folds of the body there are six scalerows." Thus the scalerows total something more than 2000.

"The count of the transverse folds on the middle of the right side of dorsum (including tail) is 359; on the middle of the left side, 367; lower on sides, 355-365; count on venter 357 (?).**

"Accurate count of the teeth was difficult to obtain and those that follow must be regarded as approximations: maxillary-premaxillary, total, 18-18; vomeropalatine, 16-17; dentary teeth, 20-17, spenial teeth, 11-12.

"The details of the color-markings are as follows:

A yellowish lateral stripe 4.5 mm. wide reaching to the tip of the tail; it does not connect with any yellowish spot at vent; the stripe is broken on the

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* Bihang Till K. Svenska Vet.-Akad. Handlingar Bant. 23, Afd. 4, No. 6, 1899, p. 6.

** These differences in counts are due to splitting of the folds. The counts range from 355 to 367 at various points.

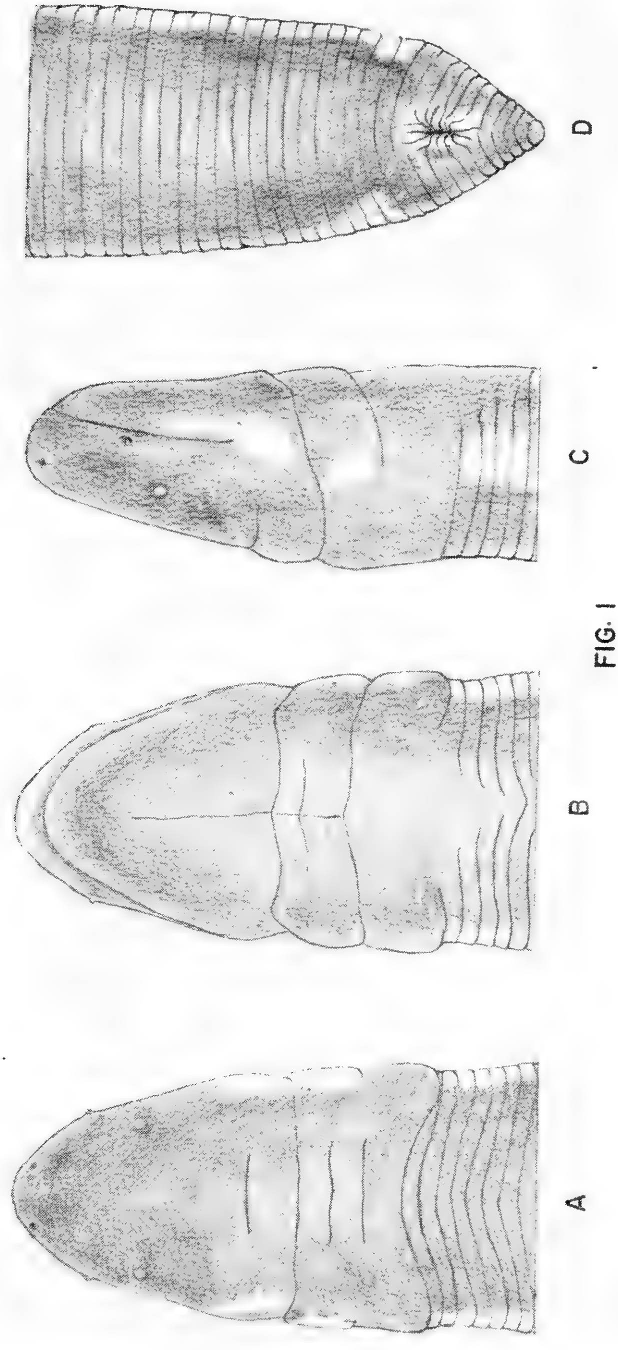

FIG. I

FIG. 1 *Ichthyophis glutinosus* (Linnaeus). Basel Museum No. 1, Ceylon. A, dorsal view of head; B, ventral view of head; C, lateral view of head; D, terminus of body and subcaudal region. Width of head at first nuchal groove, 12.5 mm.

neck by dark color, but narrowed, reaches beyond this, at least to the tentacle. At the jaw-angle the yellow divides, one narrow branch passing along the edge of the lower jaw to the tip. The stripe widens somewhat on the neck. The color of the entire ventral surface is a lighter brown than the brown of the dorsum. The eye is distinct on the left side (scarcely so on the right), and surrounded by a light ring. There is no light anal spot. It is impossible to say whether or not light spots were present on tentacles and nostrils. No glands are evident at the sides of vent. The sex is indeterminable.

"Concerning the folds it might be added that they are complete under the abdomen at least on the hinder two thirds. As I mentioned previously, the fold-limits are rather indistinct on the mid-ventral region of the anterior part of the body. The folds form a sharp angle on the abdomen pointing backwards except for an area in front of vent. On the anteriormost part of the back they may form an angle."

Diagnosis: A relatively short thick-bodied species, the body width in total length 19 to 21 times in adults; transverse primary and secondary body folds approximately from 348 to 369 ventral count, 354 to 382 dorsal count (rarely counts may be higher or lower). Color in life bluish gray to ultramarine often turning brown in preservatives. Eyes represented by grayish-white areas without visible details of lens or pupil; scalerows six or seven in each fold throughout most of the body, averaging a total of 2000 or more scalerows. Splenial teeth 11-11 to 14-14.

Description of species (from Musée d'Histoire Naturelle Bale (Suisse) No. 1, Ceylon, collected and studied by Paul and Fritz Sarasin): Body somewhat flattened; head rather small, the eyes small, evidenced only by a slightly elevated gray area (no details of lens or pupil discernible); tentacle near edge of lip, separated from eye by a distance of 2 mm., from nostril by 3.8 mm.; distance between eyes, 7 mm.; distance from level of eyes to tip of snout, 6.1 mm.; eye to nostril, 5 mm.; eye to mouth-angle 4 mm.; two nuchal collars, the first limited by the first groove going straight across throat and curving back a little and passing completely around occiput; second groove curving strongly forward on throat and up on sides of head to about level of jaw; third groove limiting second collar moderately distinct around neck; from tip of snout to first groove (lateral measurement), 13 mm. (median ventral, 11 mm.), (dorsal, 13 mm.); to second groove (lateral), 17 mm.; (ventral, 14 mm.); to third groove (lateral), 20.3, (ventral, 21 mm.); (dorsal, 18 mm.). The first collar has a faint median transverse dorsal groove; the second collar has two posterior folds, first reaching down to mouth level, the second reaching venter.

Total transverse folds following the two collars, 342 (dorsal count), 328 (ventral count); nine folds confined to tail. The grooves and folds on anteriormost dorsal part of body curve forward mesially and sometimes form a slight angle on dorsal part of body; but ventrally in anterior half of body the grooves are dim or interrupted, although the folds can be seen to cross completely and form a backward-directed angle; posteriorly the grooves are clearly seen and tend to go straight across venter for some distance in front of vent; two slight elevations present on sides of vent suggesting glands.

One to four scalerows in the folds of the first three centimeters of body; beyond this, folds with five to seven (sometimes eight) scalerows, reaching a total of approximately 2000 scalerows. Anteriorly scales very small, transversely widened; posteriorly they are larger, more nearly cycloid, but in any fold the scales of one row may vary in size and overlap laterally, or in places they may not even touch.

Dentition: Maxillary-premaxillary, 20-21; vomeropalatine, 20-20; dentary, 18-19; splenial, 12-12. The teeth relatively small for the size of the species, the anterior dentaries a trifle larger than the premaxillaries; tongue broad, with some longitudinal plicae, covering splenial teeth completely, the edges free; choanae somewhat elongate, oval, the greatest width of one, in distance between them, approximately three times.

Color: Above bluish-gray uniform on all dorsal surfaces; venter slightly lighter but almost same shade; a yellow (now faded) lateral stripe about 2.8 to 3.2 mm. wide extending posteriorly to or almost to extreme tip of tail but not joining a dull cream spot on vent; anteriorly on collars the stripe is interrupted completely, but anterior to collar it widens and bifurcates, one upper part reaching a short distance along the upper jaw, and lower part passes on lower jaw for a distance; ill-defined light spots on tentacle and nostril.

Measurements in mm.: Total length, 303; tail, 5.7; width of head at eye, 9; width of head at first groove, 12.5; length of head to first groove (lateral measurement), 13; width of body, 16; width in length, 19 times.

Variation: The specimen described agrees in most characters with the type. The change from the ultramarine or bluish gray color to the brown color of the type appears in some recently collected specimens. It is conditioned by the character of the preserving fluid and perhaps also to light exposure and slight desiccation. This is true also of many species of *Ichthyophis* that are of a violet or lilac color in life. However, in many if not most cases the original color or a part of it remains.

In several species the three or four anterior folds following the collars may form a more or less distinct forward-directed angle. At least one species (herein described) has folds forming distinct dorsal angles throughout much of the body.

Several species of the genus have the primary and also the secondary folds (of which there may be three or four to each primary) tending to split

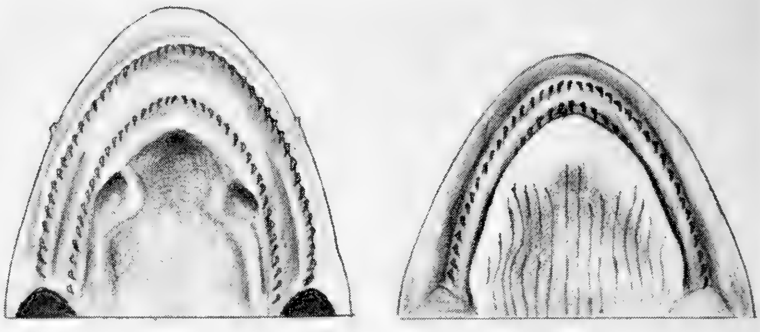

FIG. 2

FIG. 2. *Ichthyophis glutinosus* (Linnaeus). Basel Museum No. 1, Ceylon. A, palatal region of mouth and upper jaw; B, lower jaw and tongue.

dorsally or laterally. Counts made at different levels vary considerably, sometimes as much as a difference of twenty.

The larvae of *glutinosus* are relatively wider than those belonging to most other species of *Ichthyophis.* The eyes are represented by circular milky-white spots, slightly elevated, and a whitish stripe tends to connect eye to tentacle. A light area is present below and about the nostril. A low fin begins at the 16th preterminal fold, and extends to the tip of the tail and slightly below it. Two separate lateral gill-slits are present on each side. The neuromast system of the head and neck is more or less complete in the following specimen: (Natural History Museum Basel, No. 8, Ceylon): Total length, 121 mm.; width of head, 6.2; head length, snout tip to 1st nuchal groove, 7.2; width of body, 7.5; width in length, 16 times.

The penis, developed in the posterior part of the gut, is extrusible. A figure is given here showing its general appearance in situ, unextruded (from Basel Museum, No. 4).

Variation in measurements etc. are indicated in the following table of data.

Remarks: Another species, of a violet to lilac color, occurs also in Ceylon. It reaches a length perhaps as great as *glutinosus* but is slenderer and has fewer transverse folds.

As more than a single species was available to the Sarasin brothers, who seemingly were unaware of these differences, it is not impossible that their work is based on more than a single species.* However I have no certain evidence that this is the case.

---

* As has been suggested by Dr. L. S. Ramaswami, Current Science, vol. 16, Jan., 1947, p. 8-10.

TABLE 1. Measurements and data on *Ichthyophis glutinosus.*

Museum Number	Basel 4 (6124)	K.U. 31291†	K.U. 31290†	K.U. 31283†	K.U. 31293†
Sex	♂	♀	♀	♂	♀
Total Length	343*	320	300	275	263
Tail length	7.2	6.7	7	6	6
Width of head	....	10.6	10.2	9.6	8.8
Width of body	17	14.4	13.8	13.3	12.2
Width in length, times	20	22	21.7	20.6	21.5
Snout to 1st groove	....	14	13.2	12	13
Snout to 2nd groove	....	18.2	16	16	15.3
Snout to 3rd groove	....	22.6	20	21	18.2
Eye to eye	....	6.8	6.6	6.3	6.2
Eye level to snout tip	....	5.6	5.8	5.8	5.5
Tentacle to eye	....	1.8	1.8	1.8	1.7
Tentacle to nostril	....	3.7	3.6	3.7	3.35
Total folds	355	349-361	348-360	352-354	369-382
Tail folds	9	7.8	8	9	7-8
Max.-premax. teeth	....	23-23	23-23	26-27	20-21
Vomeropalatine	....	24-25	23-23	24-24	25-26
Dentary	....	22-22	21-21	20-20	21-22
Splenial	....	12-12	14-14	11-13	13-14
Posterior scalerows	7	6	6	6	6

* Estimated length, head missing and perhaps certain anterior body folds.

† Kansas Univ. Specimens from Tonacumbe Estate, Numunukula, Ceylon. W. W. Phillips, collector.

Ichthyophis hypocyaneus Van Hasselt (in Boie)

Ichthyophis Hasselti Fitzinger, Neue Classification der Reptilien nach ihren natürlichen Verwandtschaften, Wien, 1826, p. 63 (*nomen nudum*; Java).

Caecilia—Van Hasselt, Algemeene Konst Letter-Bode voor Het Jaar 1823, No. 41, Vrijdag den 10 den October (Letter, Kuhl and Van Hasselt); (Reprint of above in French), Bull. Sci. Nat. et Geol., 2nd sec., vol. 2, Paris, p. ...... (dated Ceram Province of Bantam, Feb. 1, 1823).

Caecilia hypocyanea Van Hasselt, in H. Boie, in F. Boie, Isis, 1827, p. 565; I. Müller, Isis, vol. 22, 1829, p. 875; *ibid.,* vol. 24, 1831, pp. 707-710; S. Müller, Zeitschr. für Phys., vol. 4, p. 195; Arch. Anat. Phys., 1835, p. 391, pl. 8, figs. 12-14; Schlegel, Abbildungen neuer oder unvollständig bekannter Amphibien nach der Natur oder dem Leben entworfen herausgegeben und mit erläuternden 1837-1844, p. 119, pl. 39, fig. 1 (entire animal depicted).

Epicrium glutinosum: Duméril and Bibron, Erpétologie générale, vol. 8, 1841, pp. 286-287 *(part.).*

Ichthyophis glutinosus: Boulenger, Catalogue of the Batrachia Gradientia *s.* Caudata and Batrachia Apoda in the collection of the British Museum, ed. 2, 1882, pp. 89-91 (*part.* but not the figure).

The first description of this species appeared under its generic name only and is a *descriptio nudus.* This was in a letter of Van Hasselt's that was

FIG. 3

FIG. 3. *Ichthyophis glutinosus* (Linnaeus). Basel Museum No. 4, Ceylon. Penial organ, as seen from a ventral view, lying on the floor of the cloacal region. (Much enlarged.)

published (Algemeene Konst en Letter-Bode, voor Het Jaar 1823, No. 41, Vrijdag den 10 den October. Letter Kuhl and Van Hasselt) in which mention is made of a caecilian. I have not seen this publication but translated into French it was reprinted in the Bulletin des Sciences Naturelles et de Geologie, (deuxieme section) Bulletin Universal des Sciences et de l'Industrie, vol. 2, Paris. The title was "Fourth letter upon the reptiles of Java. Dated in Ceram [Serang] Province de Bantam."

I have seen the French translation, part of which, dealing with the caecilian, is here given in free English translation.

"I found this reptile in the wet and marshy places on the northern coast of Bantam [Java]. The Malays call it *Octur-doeël* and do not fear it. Its tongue is not extensile or visible except when the mouth is open and must be regarded as rudimentary. The teeth are very small, curved backwards and arranged in several rows. The eyes are hidden under the skin and are very small. The head is equally small and of a width equal to the trunk. In front of the eyes there are small elongations of the skin *(tentacles)* one half-line in length, which the animal is able to evert. The anus is found near the terminus of a very short tail rounded to a point, which appears to have a great sensitiveness. The scales are invisible at least in a living (fresh) state, and the skin is smooth and viscous, ringed by transverse grooves quite similar to those of annelids. The rings in the anterior part of the body are interrupted below. The color above is a dark olive and below steel-blue. The sides of the body are decorated by two longitudinal lines of ochreous yellow spots. Length to vent, 0.78 *sic*;* of the tail, .02.

A larval specimen of a caecilian in the Vienna Museum now bears the following data: "*Epicrium hasselti,* Wagler, Java, 1825, III, 68." The present catalogue number is 9097. The catalogue shows that it was obtained from the Leiden Museum by Natterer in March 1825 and thus may have been seen by Fitzinger. A *nomen nudum* may not be considered as having a type, else this specimen would be so considered. The specimen seemingly was one sent from Java by Van Hasselt.

The "legal" description of *Caecilia hypocyanea* was published in 1827 in a paper prepared largely if not wholly by H. Boie, who had access to Van Hasselt's notes, but which was actually published by his brother, F. Boie. The fact that he has added Van Hasselt's name after the scientific name makes it necessary that Van Hasselt be regarded as the author of the name. It is true that when his description was originally published *(loc. cit.)* under the generic designation *Caecilia* it was a *descriptio nudas* and the type-description must date from F. Boie's work in 1827. Van Hasselt had given it a name in his unpublished notes.

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*In the original Dutch publication this number was given 0.98 and is presumably correct. I am uncertain as to the unit of measurement used.

Schlegel, *loc. cit.* gives certain pertinent data, stating that Van Hasselt saw two specimens from Bantam. One was about 10 inches long (taken on muddy soil). The back was brilliant black-olive while on the underside it was steel-colored. The lateral stripes were ochre-yellow. The other was a young specimen, somewhat red-brown on the dorsal side and olive on the venter, which had been caught in the Loudemanik River. He states that Van Hasselt does not mention gill-slits or a fin. The young breathe by gills but these are lost as the animals become developed. It is probable that Schlegel did not know of the specimen sent to Vienna.

Now it would appear that the larva mentioned is the specimen in the Leiden Museum earlier studied by Müller (Isis, 1831, vol. 24, p. 710). He had observed its gill-slits and noted its other characteristics such as the branchial arches. He concluded that despite the resemblance of these animals to reptiles, they were really amphibia and for the known caecilians he proposed the name Gymnophides as the first Order of the Amphibia.

This small specimen is still extant (Leiden Museum number 2409).* It measures 115 mm. in length and has approximately 311 transverse body folds. A part of the neuromast system is still in evidence on the head. The dental formula: Maxillary-premaxillary, 13-14; vomeropalatine, 18-18; dentary, 16-17; splenial, 8-8. There are actually two gill-slits on each side, the anterior one the smaller.

Van Hasselt's notes sent from Java and preserved in the Leiden Museum have been copied for me by Dr. Brongersma, Director of the Leiden Museum:

1. He refers to the preceding small specimen giving it a specific name stating that it was found in the Loudemanick River in July, and then a question—"the young of the following?" Then follows a short Latin description of the specimen.
2. *Caecilia hypocyanea* Ceram [Serang] January, Octur-Doeël [native name]. Then follows a statement in Dutch, "Lives in muddy regions and it is said to enter into the anus of chickens."

Then follows a description in Latin.

In a previous paper I have stated that Van Hasselt described the species *C. hypocyanea* from the specimen in the Vienna Museum. This I believe now to be an error and must conclude that the type actually is a Javanese specimen, now catalogued in the Leiden Museum as No. 2408. This specimen is redescribed here.

Diagnosis: A species with a very narrow lateral stripe broken minutely in several places, appearing to be composed of a series of ochre-yellow spots; blackish olive dorsally, steel-blue ventrally in life. Transverse body folds, 314-316*; distance of tentacle from eye about one half its distance from

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* In Van Hasselt's notes the young specimen is given a name but he suggests that it may be the young of the following species *C. hypocyanea.* Fortunately the name has not been published since it is indeed the young of *C. hypocyanea.*

nostril. Maxillary-premaxillary teeth, approximately 20-20; splenials, 11-11. Folds incomplete anteriorly, passing completely across back posteriorly, forming an angle ventrally. The width in length about 26 times.

Description of type (Leiden No. 2408): Head wider than neck but less than width of body; eye (lens and iris distinct) surrounded by a slightly darker ring and a minute outer ring consisting of a circle of yellowish-white glandules; tentacle close to edge of lip, preceding eye, its distance from eye (1.45 mm.) about half its distance from nostril (2.9 mm.); distance between eyes (5.8 mm.) greater than length of snout from level of eyes to tip. Two collars not strongly defined; first nuchal groove passes around back of head; second ascends sides to a point above mouth angle; second collar fuses with first dorsally and has one or two transverse folds on its posterior dorsal part. Anterior skin of head, neck and part of body glassy smooth. Following the collars, 314-316 transverse primary and secondary folds, incomplete dorsally on anterior third of body, and likewise incomplete on median ventral part; on middle third folds practically complete, those above slightly sinuous, those below forming an angle pointing backwards. On posterior third folds and grooves pass nearly directly around body, or more anteriorly may have an indistinct angle below while in front of vent they may actually curve forward; six or seven folds confined to tail which terminates in a small pointed tip; vent longitudinal its sides denticulate, the area slightly swollen.

Scales appear in the first or second fold, two rows being present in tenth fold; two rows present at middle of body with some small scattered scales; four rows in posterior folds.

Dentition: Maxillary-premaxillary teeth, 20-20; vomeropalatine, 19-19; dentary, 19-19; splenial, 11-11; latter teeth as large as the dentary teeth, and at least a part of the vomeropalatine series as large as the maxiliary-premaxillaries.

Color: In life, dark olive above, steel-blue below with broken ochre-yellow lateral lines. The specimen is now brown, the neck being darkest; head somewhat olive-gray above; venter a lighter shade of brown except that on under part of tail and a little area in front of the vent the color is bluish gray. The narrow lateral yellowish lines are rather dim and the numerous breaks in it are hardly discernible.

Measurements in mm.: Length snout to vent, 258; tail length, 5; width of head, 8; width of neck, 6.8; width at middle of body, 10; tip of snout to first groove (lateral), 10; to second groove, 12.8; to 3rd groove, 16.8.

Remarks: The characteristics of the folds broken above and below suggest a relationship with the Bornean *asplenius.* However the presence of splenial teeth would seem to deny such a relationship.

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* Van Hasselt's count of the folds was 320. This no doubt has included the two collars and the two folds across the second collar.

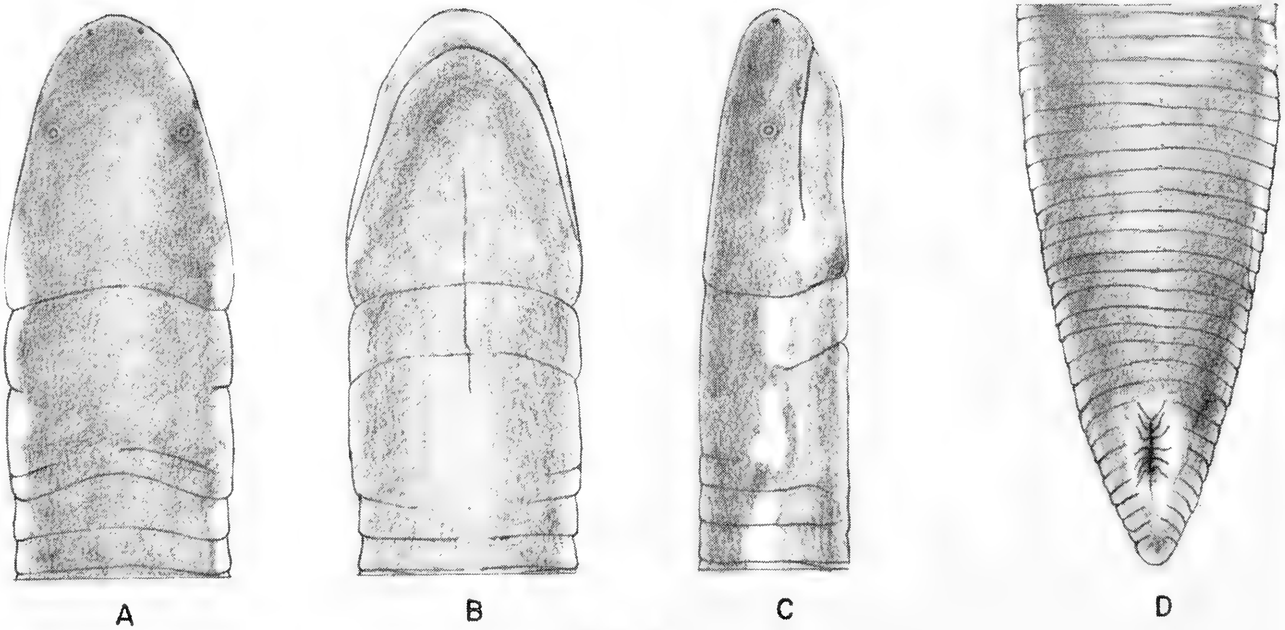

FIG. 4

FIG. 4. *Ichthyophis hypocyaneus* Van Hasselt. Type. Leiden Museum No. 2408. A, B, C, three views of the head; D, terminus of body and subcaudal region. (Actual width of head, 8 mm.)

Ichthyophis atricollaris sp. nov.

FIGS. 5, 6.

Type: Rijksmuseum van Natuurlijke Historie, Leiden, Holland, No. 10684; Long Bloee, Boven Mahakkam, Borneo.

Paratypes: Nos. 6912 D, Upper Mahakkam, and 10685, Long Bloee, Boven Mahakkam, Borneo.

Diagnosis: A broad yellow stripe extending from second collar, terminating at level of vent; head nearly uniform dark brownish violet lacking light spots at eye, tentacle and nostril; neck nearly uniformly dark above and below, the collars only dimly indicated; body dorsally uniform brownish violet slightly lighter below and on chin and neck. Primary and secondary folds, 263-300 (ventral count), 275-310 (dorsal count), complete above throughout, incomplete on anterior fifth of venter, the grooves not crossing above or below on anterior two thirds of body. Splenial teeth present, 8-8.

Description of type: Head short, rather broadly oval anteriorly; eyes small, the distance between them (6 mm.) greater than length from anterior level of eyes to tip of snout; tentacle from mouth (0.25 mm.), the distance from eye (1.52 mm.), much less than its distance from nostril (3 mm.); snout projects one millimeter beyond the mouth. First and second collars distinguishable on sides of neck but more or less fused together dorsally, less so ventrally. Primary and secondary folds together number 263 (ventral count), 275 (dorsal count), the folds complete, except for those on anterior midventral region, the grooves however distinct on sides and on latter third of body; eight folds ventrally, ten dorsally on tail, the vent interrupting only three folds below. Scales begin at about the 25th fold, one or two scales being present near middorsal line; at middle of body three or four rows varying somewhat in the same fold dorsally and laterally; posterior fifth of body with seven to eight rows.

Dentition: Maxillary-premaxillary teeth, 22-22; vomeropalatine, 22-23; dentary, 19-20; splenial, 8-8. Dentary teeth largest. Choanae relatively small, the transverse diameter of one (.4 mm.) in distance between them (2.5 mm.), about 6 times; splenials on a high splenial ridge about on same plane as dentary teeth.

Color: Above brownish violet, the edges of the transverse primary and secondary folds a little lighter, especially so in the latter half of body; ventral surface a lighter shade; head lighter than dorsum, nearly uniformly colored above and below, with a vague suggestion of a lighter eye circle and a scarcely discernible lighter region about nostril; a vague small yellowish spot near mouth-angle; a white spot surrounding vent; a lateral yellow stripe from second collar to level of vent, the edges barely visible from above, narrowing a little anteriorly.

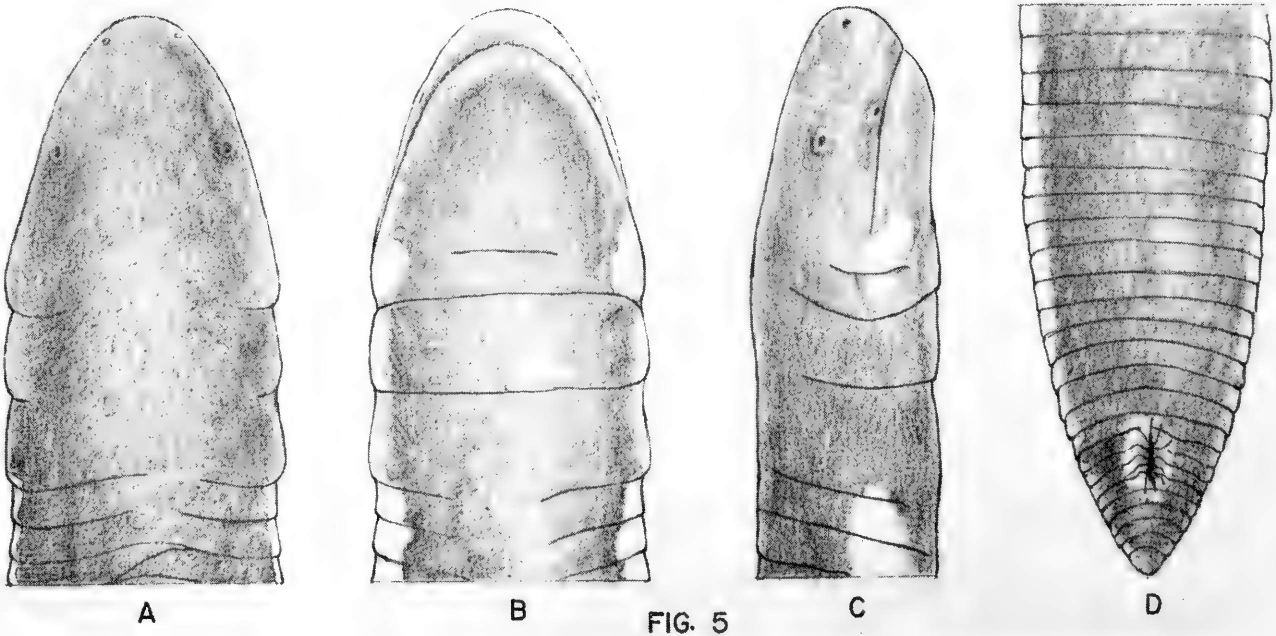

FIG. 5

FIG. 5. *Ichthyophis atricollaris* sp. nov. Type. Leiden Museum No. 10684. A, B, C, three views of the head; D, subcaudal region. (Actual width of the head, 9.9 mm.)

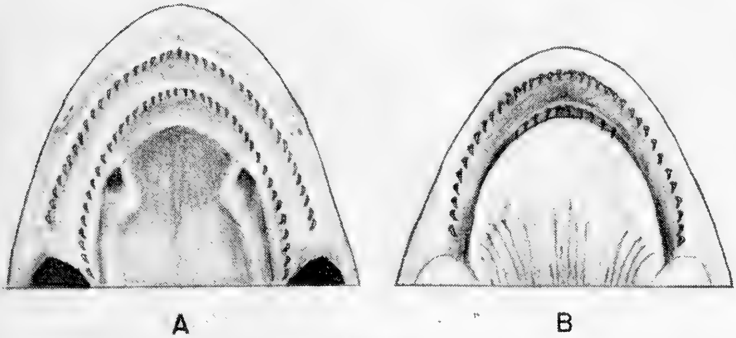

FIG. 6

FIG. 6. *Ichthyophis atricollaris* sp. nov. Type. Leiden Museum No. 10684, Long Bloee, Boven Mahakkam (river), Borneo. A, upper jaw and palatal region of mouth; B, lower jaw and tongue. (Actual width of head, 9.9 mm.)

Variation: Variation in measurements and tooth numbers is given in the following table. In color there is a strong similarity. The dark neck is the same in all, the yellow streak stopping abruptly at the 2nd collar. Dorsal folds tend to cross the back in a straight line.

In none of the specimens are the collars strongly marked, but the smallest shows the first plainly on the underside of the neck. No. 10685 has a short longitudinal whitish line under the first collar. This specimen also has the folds somewhat less distinct than the others.

TABLE 2. Table of measurements of *Ichthyophis atricollaris*.

Number Museum	10684 Leiden	10685 Leiden	6912(D) Leiden
Total length	285	255	204
Tail length	4.8	5.1	4
Width of body	11	9.5	8
Width of head	9.9	9	7.7
Snout tip to 1st groove	10	11	9
Snout tip to 2nd groove	13.7	13.2	11
Snout tip to 3rd groove	17.2	17	13.4
Tentacle to eye	1.52	1.5	1.25
Tentacle to nostril	3	2.5	2.4
	V D	V D	V D
Total folds	263-275	300-310	293-303
Folds on tail	8-10	8-9	8-8
Maxillary-premaxillary teeth	22-22	25-27	24-24
Vomeropalatine	22-23	20-20	20-19
Dentary	19-20	19-19	18-19
Splenial	8-8	8-5+	8-8
Width in length (times)	26	26.8	25.5

In all the angle of the folds on the venter is less acute than in most other species now recognized in the genus *Ichthyophis.*

The type specimen was taken on the Upper Mahakkam River, at Long Bloee, by the Nieuwenhuis Borneo Expedition. The paratype No. 10685 is from the same locality and No. 6912 (D) from Boven Mahakkam; the exact locality may or may not be known.

Three other species were taken in the same general area. At least two other species seemingly were taken at the same place since No. 6912 is one of a series of five caecilians bearing this same number and locality.

Ichthyophis elongatus sp. nov.

Figs. 7, 8.

Holotype: Naturhistorische Museum Wien. No. 9094. Padang, Sumatra.

Paratype: N.M.W. No. 9092, Domenik, Sumatra.

Diagnosis: Head a little wider than body. Transverse folds, 274-290, three confined to tail; folds not complete across anterior two thirds of body; maxillary-premaxillary teeth, 28-32; splenial, 14-16; latter half of body with six scalerows in each fold; *body width in length 37 to 40 times;* a narrow lateral yellow stripe. Tip of tail acuminate.

Description of type: Head rather wider than body; eyes distinct with a narrow white ring; distance of tentacle to eye (1.65 mm.) a little less than half its distance to nostril (3.45 mm.); eye to nostril, 4.5 mm.; tentacle from lip, 0.3 mm.; first nuchal groove distinct below and on sides, dimly visible, curving forward on back of head; second groove distinct below and on sides; third groove visible across back and on venter except in mid-ventral region; the two collars fused together dorsally, the second divided dorsally by a transverse groove visible below only at sides.

Folds following collars, 274 (dorsal count), 277 (ventral count), the folds and grooves incomplete on the dorsal surface; anteriorly separated by a distance of three millimeters which gradually narrows until near middle of body, they become complete; except for two anterior centimeters, the folds are complete ventrally, forming an acute angle pointing backwards for about seven eights of the body length. The ventral grooves are not in evidence and the complete fold and angle often cannot be discerned unless the specimen is somewhat desiccated. Only three folds on tail, two and a half interrupted by the longitudinal vent; a pair of glandular swellings near anterior end of vent.

Small scales begin on second collar; at middle of body seven rows present, the scales large, variable in size, and these continued to near vent; seven or eight rows posteriorly.

Dentition (of type and paratype): Maxillary-premaxillary, 32-32, 29-28; vomeropalatine, 27-27, 30-30; dentary, 29-29, 27-27; spenial, 14-14, 16-16.

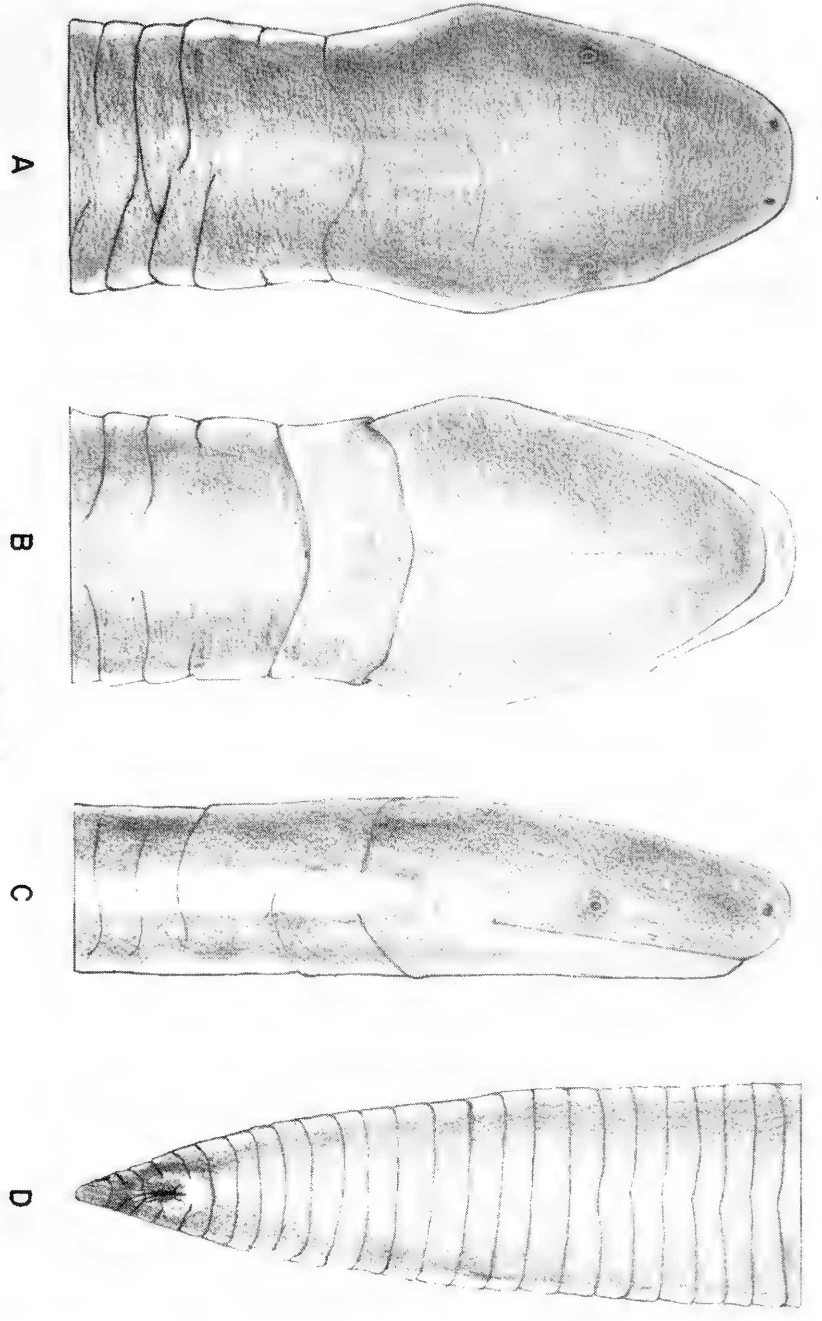

FIG. 7

Fig. 7. *Ichthyophis elongatus* sp. nov. Type. Vienna Museum No. 9094, Padang, Sumatra. A, B, C, three views of the head; D, subcaudal area. (Actual width of head, circa 10 mm.)

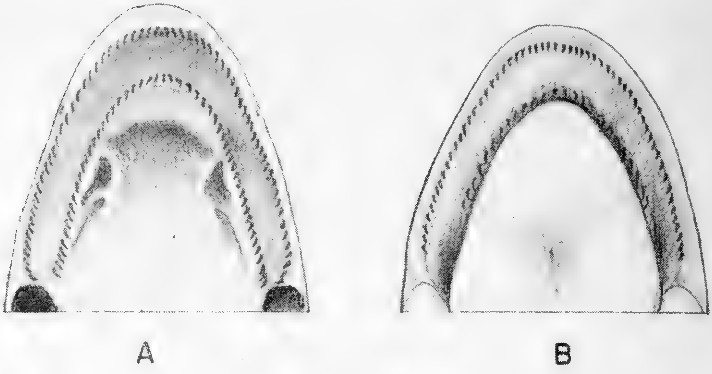

FIG. 8

Fig. 8. *Ichthyophis elongatus* sp. nov. Type. Vienna Museum No. 9094, Padang, Sumatra. A, Upper jaw and palatal view of mouth. (Actual width of head, circa 10 mm.)

Choanae semilunate, lateral, the diameter of one in distance between them, 4½ times; tongue narrowed anteriorly, not covering spenials.

Color: Dark lilac dorsally, somewhat grayish lilac of a slightly lighter shade ventrally; a yellow to cream lateral stripe about one millimeter wide reaching to near eye, terminating anterior to vent, the stripe broken on second collar; a white spot surrounding vent; a light ring about eye; a light spot at nostril and tentacle, and a light area above tentacle; top of head somewhat brownish.

Measurements in mm. (type and paratype): Total length, 300, 280; tail length, 3.4, 3.5; width of body, 7.6, 8; width in length (about), 40 times, about 37 times; snout to first groove, 12, 11.2; to second groove, 14.9, 15.9; to third groove, 19, 19.8; eye to eye, 6, 6; eye level to snout tip, 5.4, 5.

Variation: The transverse body folds of the paratype are 287 (dorsal count) and 290 (ventral count). The tail has three folds with a fourth indistinctly indicated near the tip. In both, the body and tail are narrowed, the width of the tail at vent being three millimeters. It is flattened ventrally ending in a fine point.

In the paratype the general lilac color is of a lighter shade and the lateral stripe is somewhat more distinct and a trifle wider at least at certain points; the head is somewhat lighter in color and the tip of the snout is cream. The second collar dorsally is about one half divided by a transverse groove.

Remarks: Incomplete dorsal folds appear in another species, occurring in Borneo, which, however, lacks vomerine teeth; the number of dorsal folds is 264-270; and the width in length is about 24 times instead of 37 to 40 times.

Ichthyophis biangularis sp. nov.

Figs. 9, 10.

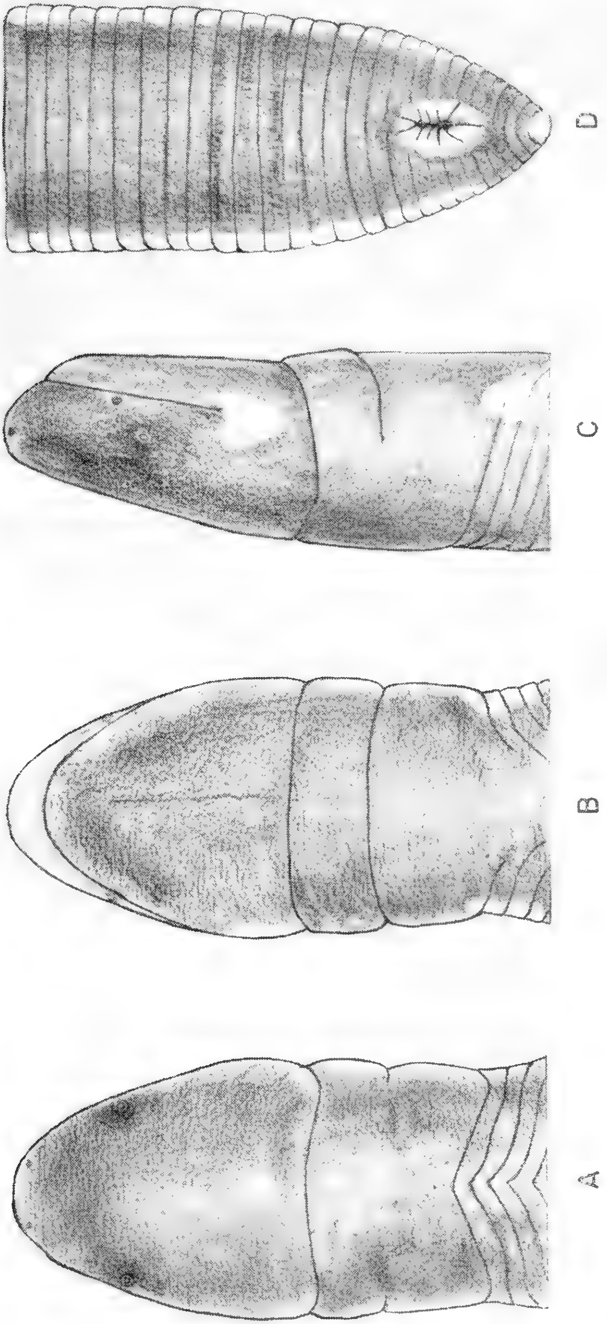

FIG. 9

FIG. 9. *Ichthyophis biangularis* sp. nov. Type. British Museum No. 72. 2. 19. 59, A. Matang Mt. Sarawak, Borneo. A, B, C, three views of head; D, subcaudal area. (Width of head, 8.2 mm.)

Holotype: British Museum No. 72.2.19.59,A, Matang (Mt.) Sarawak, Borneo; Everett, Coll.

Diagnosis: Eye distinct in socket; tentacle twice as close to eye as to nostril; total folds behind collars, 330-333, with ten confined to tail; *transverse folds distinctly angular above as below,* throughout most of body; body width in body length about 26 times. Scales begin in first transverse fold, four rows at middle of body, four rows posteriorly. Color blackish slate above and below with a yellow lateral line terminating anteriorly at second collar; yellow spot at mouth angle not dividing.

Description of type: (Skin partly removed from head.) Eye dimly distinct with a slightly lighter ring about it; tentacle much closer to eye (1.2 mm.) than to nostril (2.4 mm.); eye to nostril, 3.5 mm. First and second collars fused above; collars distinct below, the first groove seemingly interrupted on dorsal surface; second groove distinct below and on sides, scarcely visible from above, bordered below by a light line. Third groove distinct above interrupted mid-ventrally where the second collar fuses with the first and second transverse folds.

Counts of transverse folds vary but little. Two counts show, dorsally, 333, ventrally, 330; ten folds on tail (from anterior edge of vent), four interrupted by vent, six more or less complete behind vent; folds forming a distinct angle dorsally and a somewhat more acute angle ventrally, except on the fifth of body preceding vent where dorsal and ventral grooves and folds run nearly directly across.

Scales begin in the first folds following collars, at least two rows present on the dorsal surface; at mid-body there are three well-defined rows, and a fourth complete or incomplete; posteriorly there are four well-developed rows.

Dentition: The teeth have been exposed and lost or removed. The following counts are close approximations: Maxillary-premaxillary teeth, 25-26; prevomeropalatine, 24-24; dentary, 19-19; splenial, 2-2.

Color: Generally blackish slate, the venter scarcely less dark than dorsum; a dull narrow, irregular-edged stripe on sides, beginning at second collar and terminating posteriorly behind level of vent; a yellowish-cream spot at jaw angle not branching; a white spot about vent, a very narrow dim light ring about eye, and a lighter spot at tentacle (skin in area about nostrils removed).

Skull: The exposed parts of the skull show the eye in a circular socket completely separated from the fenestral opening of tentacle; no diastema between the squamosal and parietal bones; eye socket between maxillary, squamosal and a small supraocular; a preocular and a septomaxilla or "lateral nasal"; nasal fused with prefrontal; frontals and parietals distinct, no ethmoid visible; premaxillaries distinct with premaxillary teeth, 8-8, followed by 17 or 18 maxillary teeth on each side; tentacular aperature pierced in maxillary.

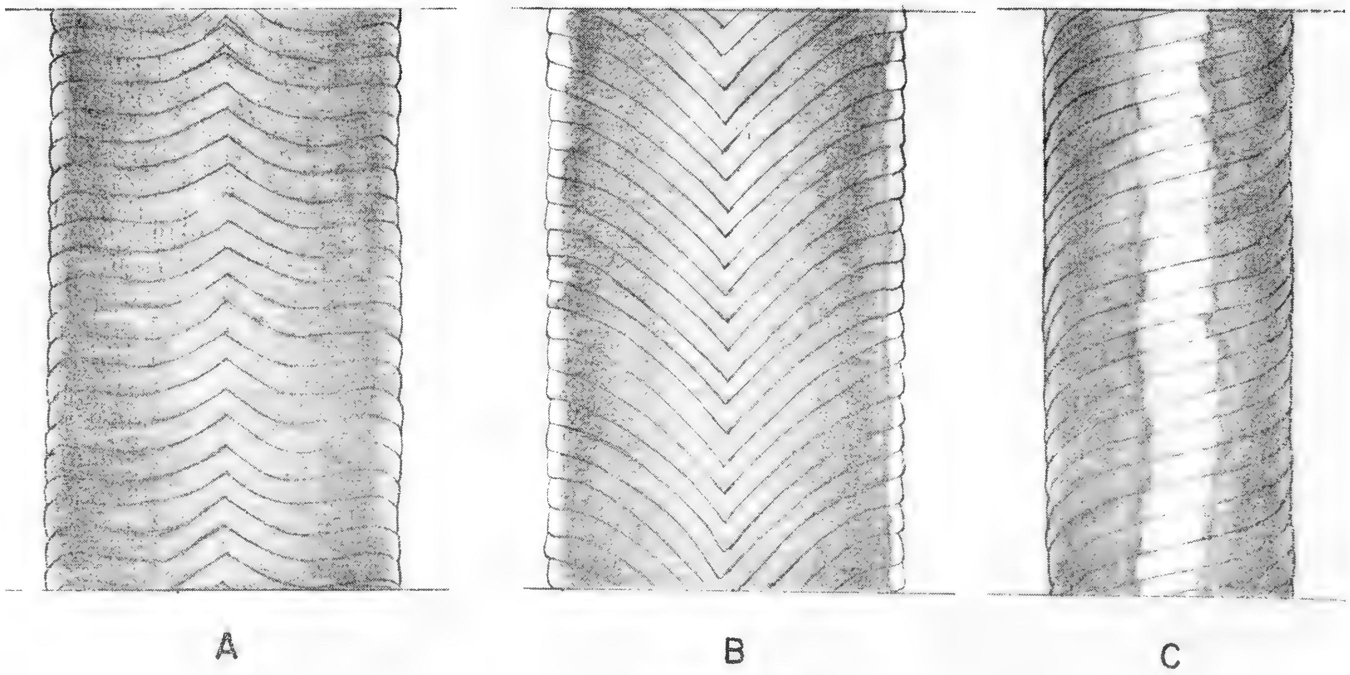

FIG. 10

Fig. 10. *Ichthyophis biangularis* sp. nov. Type. British Museum No. 72. 2. 19. 59, A. Matang Mt. Sarawak, Borneo. A, B, C, three views of dorsal, ventral and lateral views of the anterior part of body showing biangulate condition of the transverse body folds. (Width of body at this point, circa 9.2 mm.)

Measurements in mm.: Total length, 258; tail, 5.8; width of body, 9.8; width of head, 8.2; tip of snout to first groove, 10; to second groove, 12.5; to third groove, 16.5. Width in length, 26.3 times.

Remarks: The type number (BM 72.2.19.59) originally included three specimens. The other two are larvae and in my opinion do not belong to the species described here. The two larvae likewise represent two species. The larger larva, here designated A, has 261-256 transverse folds. The folds cross the back and are perhaps slightly angulate in the anterior folds. The smaller one, here called B, has the folds failing to cross the median dorsal part of the body. It may be the young of *Ichthyophis asplenius* herein described.

The name *biangularis* is from Latin, *bi*=two, *angulus*=angle.

Ichthyophis pseudangularis sp. nov.

FIGS. 11, 12, 13.

Holotype: Musee d'Histoire Naturelle Bale (Suisse) No. 4412. Collected in Ceylon by Paul and Fritz Sarasin.

Diagnosis: A medium-sized species having a yellow lateral stripe extending the length of the body, more or less broken on collars, and a yellow cream spot at jaw angle dividing and sending a branch onto lower jaw; transverse folds, 269-271, five confined to tail; tentacle twice as close to eye as to nostril; body width in total length about 26 times; splenial teeth 10-9; dorsal transverse folds curving forward on median line, somewhat angular anteriorly, strongly angular on venter except on posterior fifth of body.

Description of type: Head somewhat bluntly conical; eyes small but distinct, in a socket; tentacle to eye, 1.5 mm., to nostril, 2.9 mm.; distance between eyes (straight line), 5.3 mm.; level of eyes to tip of snout, 4.6 mm.; nostrils plainly visible from above; a slight median elevation on dorsum extending along body for about half its length; a dorsolateral ridge on sides of body extending to tail, making body somewhat quadrangular in cross-section; tentacle very close to edge of lip; eyes lateral.

First nuchal groove passes completely around head; second groove distinct across throat reaching up on sides to level of mouth-angle; third groove indistinct; the two collars fused dorsally, the second with two transverse folds on its posterior part, neither of which cross venter.

Folds following collars 269-272 (variable at different body levels), the dorsal folds running somewhat forward and forming a distinct angle or sharp curve pointing forward becoming somewhat more obtuse towards middle of body; ventrally folds form an acute angle pointing backwards except on posterior fifth of body in which the folds pass nearly straight across dorsally and ventrally. A few folds following collars are incomplete ventrally.

Scales appear on the second collar; in the tenth fold there are at least

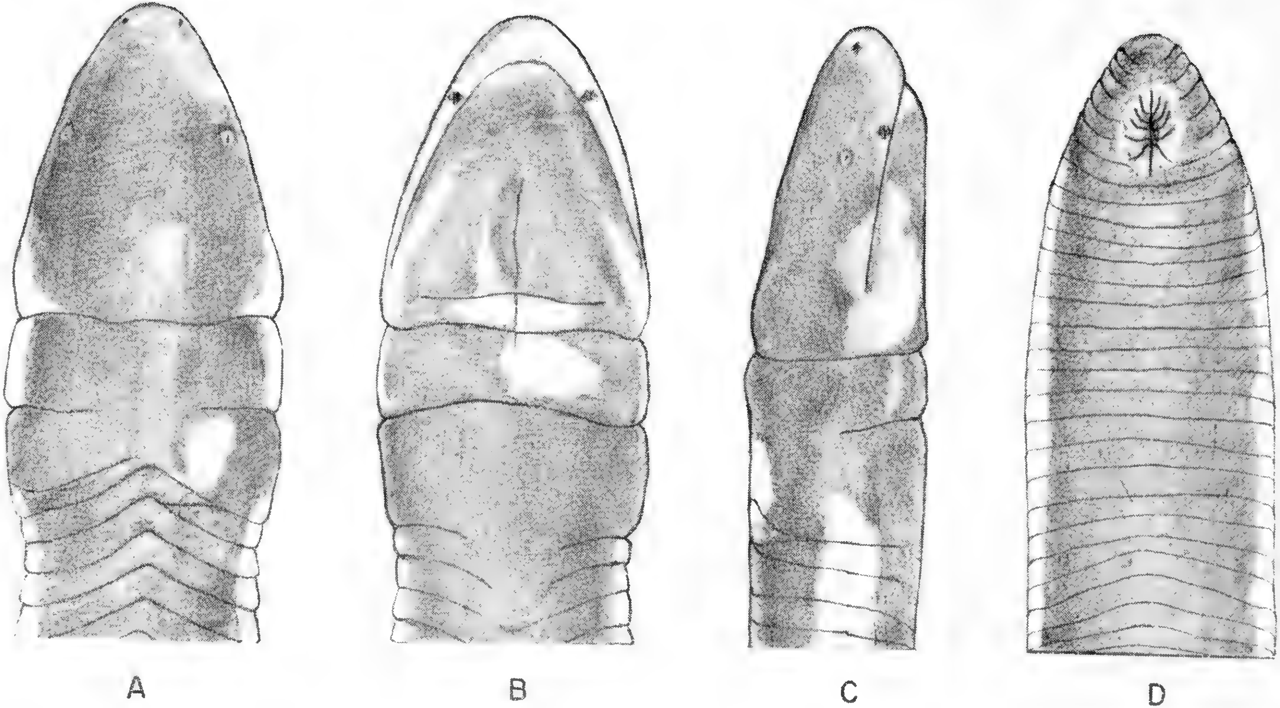

FIG. 11

Fig. 11. *Ichthyophis pseudangularis* sp. nov. Type. Basel Museum No. 4412. Ceylon. A, B, C, three views of head; D, subcaudal area. (Actual width of head, 8.5 mm.)

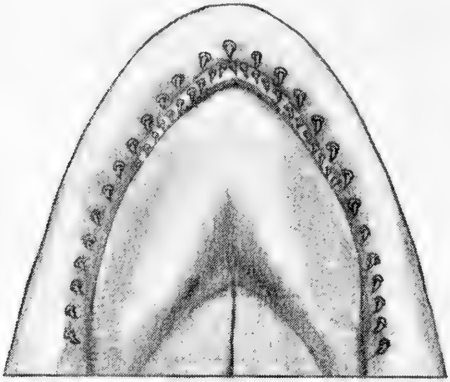

FIG. 12

FIG. 12. *Ichthyophis pseudangularis* sp. nov. Type. Basel Museum No. 4412, Ceylon. A, view of lower jaw and tongue.

two incomplete scalerows. In latter half of body there are six more or less complete rows of scales in each fold.

Dentition: Maxillary-premaxillary teeth, 18-19; vomeropalatine, 22-22; dentary, 18-18; splenial, 10-9. The anterolateral dentaries are the largest teeth.

Tongue somewhat swollen laterally, the tip not covering the splenials.

Color: Above slate to lavender slate; somewhat brownish slate on venter; a narrow yellow to cream lateral stripe more or less interrupted on collars, terminating posteriorly behind level of vent; posterior to angle of jaw a yellowish cream spot which bifurcates sending a branch along lower jaw, the yellow not reaching eye along upper jaw. Some indistinct cream marks on chin, and one asymmetrical spot above second collar: a small cream spot at vent, one at tentacle, and one at nostril. Tip of snout light cream.

Measurements in mm.: Total length, 225; tail, 3.5; width of body, 8.6; width of head at first collar, 8.5; width in length, 26 times.

Remarks: The name *pseudangularis* is from Greek, *pseudo,* false and Latin, *angulus,* angle.

Ichthyophis asplenius sp. nov.

FIGS. 14, 15.

Holotype: Rijksmuseum van Natuurlijke Historie, Leiden, No. 6912 B. From, Boven Mahakkam, Borneo.

Paratype: R.N.H. Leiden, No. 6912 A. Topotype. Museo Civico Genova No. 32195, Sarawak, Borneo.

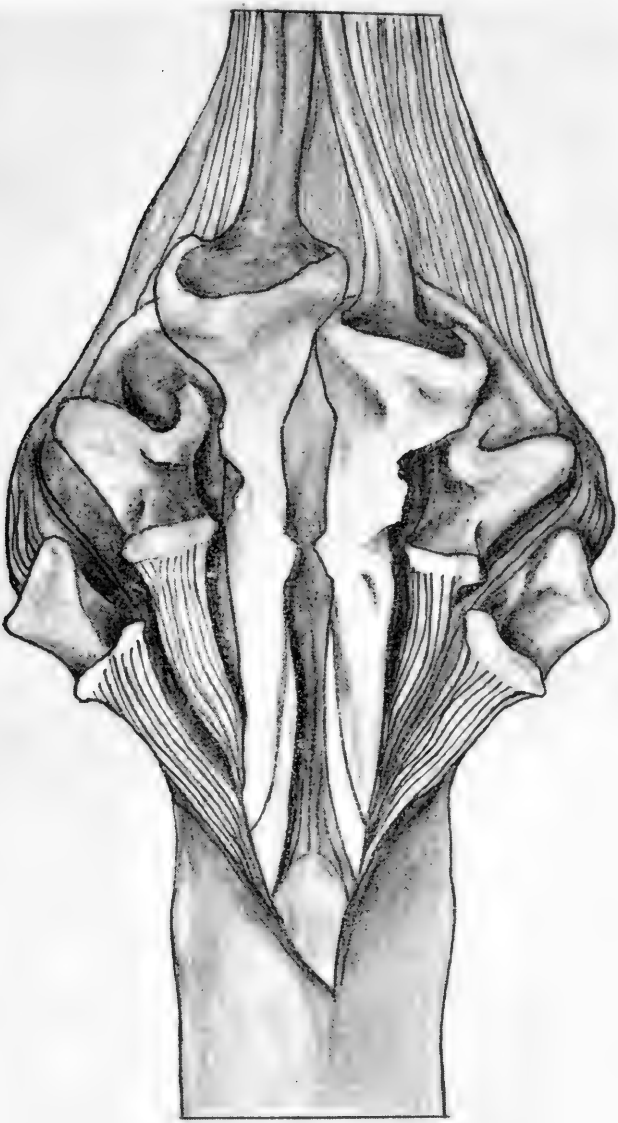

FIG. 13

FIG. 13. *Ichthyophis pseudangularis* sp. nov. Type. Basel Museum No. 4412, Ceylon. Penial organ seen from ventral view, lying in cloacal region. (Much enlarged.)

Diagnosis: A moderately broad lateral yellow stripe broken or not on collar. Eye in socket, the tentacle much closer to eye than to nostril; width

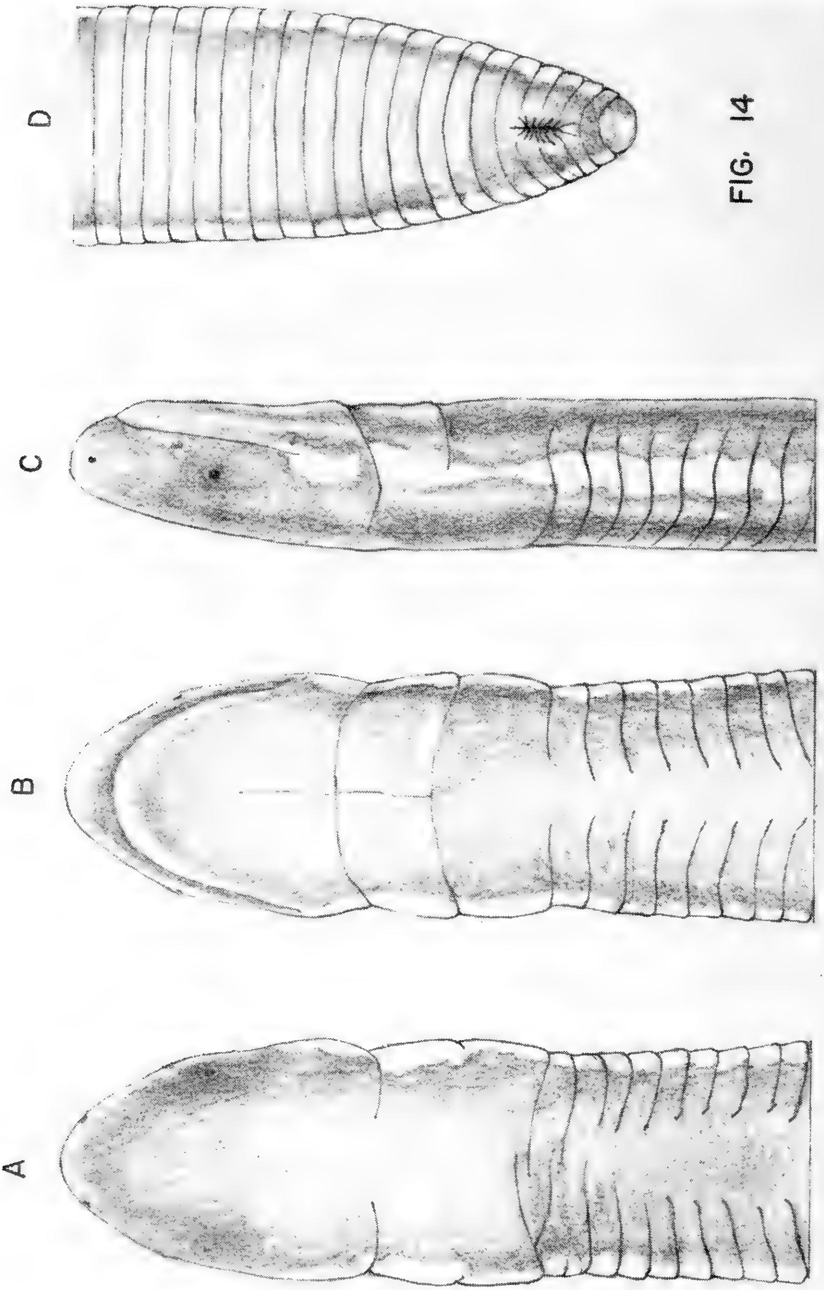

FIG. 14

Fig. 14. *Ichthyophis asplenius* sp. nov. Type. Leiden Museum No. 6912 D. Boven Mahakkam (river), Borneo. A, B, C, three views of head; D, subcaudal area. (Actual width of head, 6.5 mm.)

in length, 23-26 times; total folds, 247-270; no splenial teeth in transformed specimens; grooves and folds do not cross the back except in the posterior half of body, some folds tending to form angles directed forward; throughout most of body, grooves do not cross venter but the folds are complete, forming a ventral angle pointing backwards except on latter fourth of body where they, with the grooves, pass directly across.

Description of the type: Head moderate. Eye visible, somewhat elevated but dim; distance between eyes (4.4 mm.) considerably greater than distance from level of eyes to tip of snout; snout projecting about one millimeter beyond mouth; distance of tentacle from eye (1.2 mm.) much less than distance to nostril (2.15 mm.); eye to nostril, 3 mm.; tentacle to edge of lip, 0.2 mm.; nostrils nearly terminal but visible from directly above head.

First and second collars fused above, distinct below; first nuchal groove complete below, broken in middorsal region of head; second groove preceded below by a slight fold, visible laterally when seen from above; third groove vaguely marked above and on sides; second collar fused below with the following body fold. A fold, similar to a body fold is present dorsally on back of first collar. Primary and secondary folds following collars are 264-270, the folds and grooves incomplete across back on anterior half of the body being separated on median line anteriorly by a distance of three to three and a half millimeters, the distance between growing gradually shorter until folds become complete near the middle of body. The grooves are complete only on latter fourth of body; ventrally folds form a backward-pointing angle except on latter fifth of body where the grooves run straight across venter; five folds on tail, three of which are behind vent; vent longitudinal, short; glandular swellings at side of vent not evident.

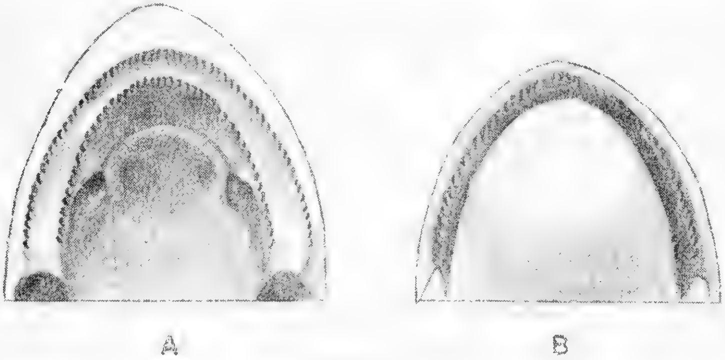

FIG. 15

FIG. 15. *Ichthyophis asplenius* sp. nov. Type. Leiden Museum No. 6912 D, Boven Mahakkam (Upper Mahakkam river), Borneo. A, upper jaw and palatal region of the mouth; B, lower jaw and tongue. (Actual width of head, 6.5 mm.)

Very small scales present in the 30th fold and there may be a few scattered scales preceding this; at middle of body about three rows where the scales can be traced to the mid-ventral line; posteriorly four rows present with occasional scales that may tend to form a fifth row.

Dentition: (of type and paratype respectively): maxillary-premaxillary teeth, 26-26, 27-28; vomeropalatine, 26-27, 29-29; dentary, 25-25, 25-25; splenial, 0-0, 0-0. The teeth all small, the dentary teeth perhaps the largest; the vomeropalatine teeth minute.

Color: Generally rather dark brownish lilac, very nearly the same shade above and below; a yellowish lateral stripe, with rather uneven edges, about 1.5 mm. wide beginning on head at tentacle and extending to level of vent. Head slightly olive-brown; only a suggestion of a light spot at vent; a very faint ring about eye; tip of snout light.

Measurements in mm. (of type and topotypic paratype): Total length, 207, 202; tail length, 3, 3.2; width of body, 8.8, 8.2; width of head, 6.5, 6.6; between eyes, 4.8, 4.4; eye level to tip of snout, 3.5, 3.5; eye to tentacle, 1.2, 1.25; tentacle to nostril, 2.2, 2.5.

Variation: The Sarawak paratype in Genova measures 191 mm., the tail, 3.3 mm.; it lacks splenial teeth and has the typical incomplete folds. Near the middle of the body where the folds are complete the folds tend to form a slight median angle directed forward; the incomplete folds tend to curve forward somewhat. The ventral count of the folds is 247, the dorsolateral count 254. The width of the body (7.2) in the total length is a little more than 26 times.

The character of incomplete folds in the anterior part of the body occurs in a Sumatran form herein described. This latter form however differs in having a slightly higher average number of folds. The body width in length is nearly 40 times instead of 23-26 times, and there is present a series of 14-14, 16-16 splenial teeth. The head is proportionally larger and wider.

When the folds first meet on the back near the middle of the body they may tend to form an obtuse angle or a median curve.

Remarks: Number 5 (Basel Natural History Museum), and number 9090 (Vienna Museum) are two problematical specimens both purporting to be from Ceylon that seem to show a relationship with *Ichthyophis asplenius.* They agree in two significant characters: the incomplete folds above and below on a considerable part of the body, and the complete absence of splenial teeth. There are certain small differences and a rather considerable difference in the other three tooth-series. Thus the maxillary-premaxillary teeth are 26-26 to 28-28; vomeropalatine, 26-27 to 29-29; the dentary, 25-25. If the localities of these two specimens are correct it shows two forms occupying ranges in the easternmost and westernmost points in the range of the genus, and lacking, as far as known, in any closely related forms in the area that separates them.

Other data on these two specimens No. 5 and No. 9090 respectively are: Total length, 220 ♀ and 203 ♀; tail length, 3.7, 3; head width, 7, 6.2; body width, 8.8, 7; width in length, 25, 29 times; tip of snout to first nuchal groove, 8, 7.8; to second groove, 11.8, 10; to third groove, 15, 13; eye to eye, 5, 4.3; level of eyes to snout tip, 3.85, 3.45; tentacle to eye, 1.1, 1.1; tentacle to nostril, 2.1, 2.2; total folds ventral and dorsolateral counts, 277-288, 275-281; tail folds, 4, 5-6. There are four or five rows of scales in the posterior folds.

It would not be impossible that each of these specimens bears an incorrect locality label. However I have no evidence that this is true. Rediscovery of this form in Ceylon is necessary before one can deal with these specimens with certainty.

A series of five Malayan specimens from the National Museum of Singapore (formerly Raffles Museum) are referred to this species. On the Loan Invoice these are listed: No. 2 (R 8928, 7.12.42, Forest Research Institute, Kepong; No. 3 (R 9246. 30. 12. 49.) Forest Research Institute, Bukit Lapong; No. 4 (R 8081. 269. 49.) Forest Research Institute, Kepong; No. 5, Forest Research Institute, Bukit Lapong, Selangor: No. 10 (28. 5. 31.)Tg. Rambutan, Perak, Malaya.

These specimens are from 209 to 242 mm. in length, the width in length 27 to 30 times. There is but little difference in the dorsal and ventral counts of the folds (primaries and secondaries together which are not distinguishable. The counts vary from 251 to 279. There is no trace of splenial teeth. All are of the same brown color with a rather broad yellow lateral stripe from head to tail. The grooves are present laterally but grooves and folds are broken dorsally on much of the anterior third of the body. I do not consider these as paratypes.

Ichthyophis forcarti sp. nov.

Figs. 16, 17.

Holotype: Musee d'Histoire Naturelle Bale (Suisse) No. 4411, Ceylon, Paul and Fritz Sarasin, collectors.

Diagnosis: Transverse folds 346-348, forming a sharp median curve (rarely angulate), pointing forward on anterior half of body, posteriorly crossing body nearly in a straight line; ventrally folds form an angle pointing backwards except in posterior part where they pass directly across; splenial teeth, 5-5. Folds and grooves complete above and below; eye distinct, the tentacle twice as close to eye as to nostril; body width in length 27 times; a narrow irregular-edged yellow lateral line from the second collar to close to tip of tail.

Description of type: Head not wider than neck and body, the eyes distinct in sockets, the distance between them (5.5 mm.) greater than distance from eye level to snout tip (4 mm.); tentacle much closer to eye (1.5 mm.) than to

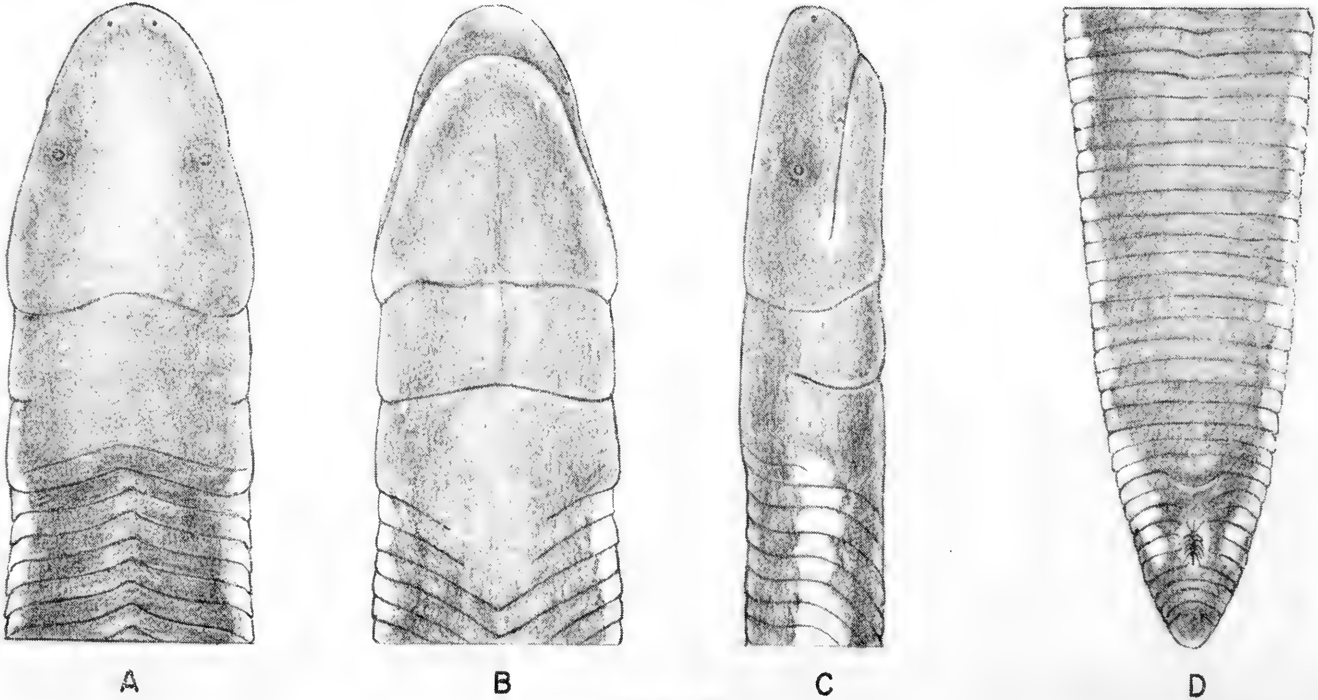

FIG. 16

FIG. 16. *Ichthyophis forcarti* sp. nov. Type. Basel Museum No. 4411, Ceylon. A, B, C, three views of head; D, subcaudal area. Actual width of head, 8.5 mm.)

nostril (2.65 mm.); eye to nostril, 3.5 mm.; tentacle to lip, 0.2 mm.; first and second collars fused above, distinct below, the nuchal grooves shallow, bordered by a slightly lighter line; second collar with one transverse fold above on posterior part, below mesially fused to first transverse fold posterior to second collar; 346-348 transverse folds complete above and below except anterior three or four on median ventral surface; nine folds on tail, the two preceding vent forming an angle directed backward into vent; four or five complete folds behind vent. Five or six anterior folds form angles dorsally.

Scales begin on back of second collar (the surface of body is slightly dehydrated and scales visible throughout); at middle of body maximum scale-rows in each fold, four or five; at posterior part, five rows, only a part of which are complete on sides and ventrally.

Dentition: Maxillary-premaxillary teeth, 25-26; vomeropalatine, 24-24; dentary, 18-19; splenial 5-(?). The teeth are small without much contrast in size except splenials, which are much smaller and arise at a much lower point than dentaries; splenials scarcely reach level of the bases of dentary teeth. Choanae lateral, directed forward, the transverse diameter of one contained in the distance between them somewhat more than three times; tongue plump, rounded anteriorly, covering splenials which scarcely reach surface of gums.

Color: Lilac-brown above and below, the head slightly olive-brown, somewhat dimly mottled; a lateral yellow stripe beginning behind second collar and terminating behind vent; light yellow mark at mouth-angle; a small circular light mark above eye; a small light spot at tentacle, one below nostril and one surrounding vent, the latter narrowly separated from the

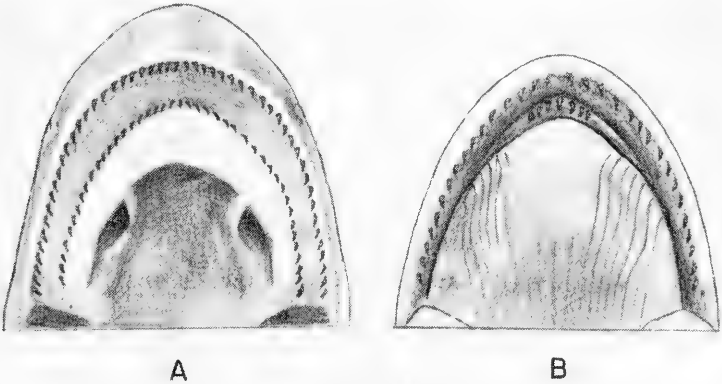

FIG. 17

Fig. 17. *Ichthyophis forcarti* sp. nov. Type. Basal Museum No. 4411, Ceylon. A, upper jaws and palatal region of mouth; B, lower jaws and tongue. (Actual head width, 8.5 mm.)

lateral stripes. In the present slightly dehydrated state each fold shows a narrow light line caused by the scales and glands showing through the skin.

Measurements in mm.: Total length, 236; tail, 4; width of body, 8.6; width of head, 8.5; snout tip to first groove, 10.3; to second groove, 13.5; to third groove, 16.2; width in length, 27.4 times.

Remarks: The exact locality at which this specimen was taken is seemingly no longer known.

The species is named for Dr. Lothar Forcart of the Natural History Museum of Basel.

Ichthyophis weberi Taylor

FIGS. 18, 19.

*Ichthyophis weberi** Taylor, Philippine Journ. Sci., vol. 16, no. 3, March, 1920, pp. 227-228 (type-locality, Malatgan River, Palawan, Philippine Islands, C. M. Weber, collector); Dept. Agri. Nat. Resour., Bureau of Science, Manila, publ. 15, Dec. 15, 1921, pp. 26-27 (reprinting of the type-description); Univ. Kansas Sci. Bull., vol. 40, Apr. 20, 1960, pp. 43-44 (removed from synonymy).

Ichthyophis monochrous: Van Kampen *(part.),* The Amphibia of the Indo-Australian Archipelago, Leyden, 1923, pp. 3-4, 282; Inger, *(part.),* Fieldiana: Zoology, vol. 33, no. 4, July 23, 1954, pp. 207, 209.

Diagnosis: A small species reaching a length of 256 mm.; above uniform dark lilac to violet, the ventral surface a little lighter and showing a slightly brownish lilac shade; cream spot at vent; eye in a socket, visible through skin. Transverse folds (primaries, secondaris and tertiaries indistinguishable from each other superficially), from 304-322, ventral count to 313-329, dorsal count; splenial teeth absent in adult, present in at least some larva. Body width in total length about 25 times. Vertebrae, 104-108.

Description of the neotype: (Stanford University No. 21758): Head rather short (10 x 8.5 mm.), rather flattened; distance between eyes (in straight line), 5.85 mm.; length from level of eyes to tip of snout, 4.9 mm.; nostrils plainly visible from above, directed upward and slightly backward; tentacle, small rather conical, close to lip (0.25 mm.), its distance from eye (1.8 mm.) much less than its distance from nostril (3.2 mm.); snout projecting about 1 mm. beyond mouth; eye from mouth, 1.4 mm., from nostril, 3.9 mm.

Two collars, first strongly defined on throat but first groove, while distinct laterally, is incomplete above; second groove distinct laterally, scarcely visible from above; third groove limiting second collar is visible laterally but incomplete below and only dimly visible above; an indistinct groove separates a transverse fold on the back part of second collar.

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* The holotype of this species was destroyed in the Second World War during one of the final battles in Manila, which partially destroyed the Bureau of Science. I hereby designate Stanford University, No. 21758 from near Iwahig, Palawan (virtually a topotype) as a neotype.

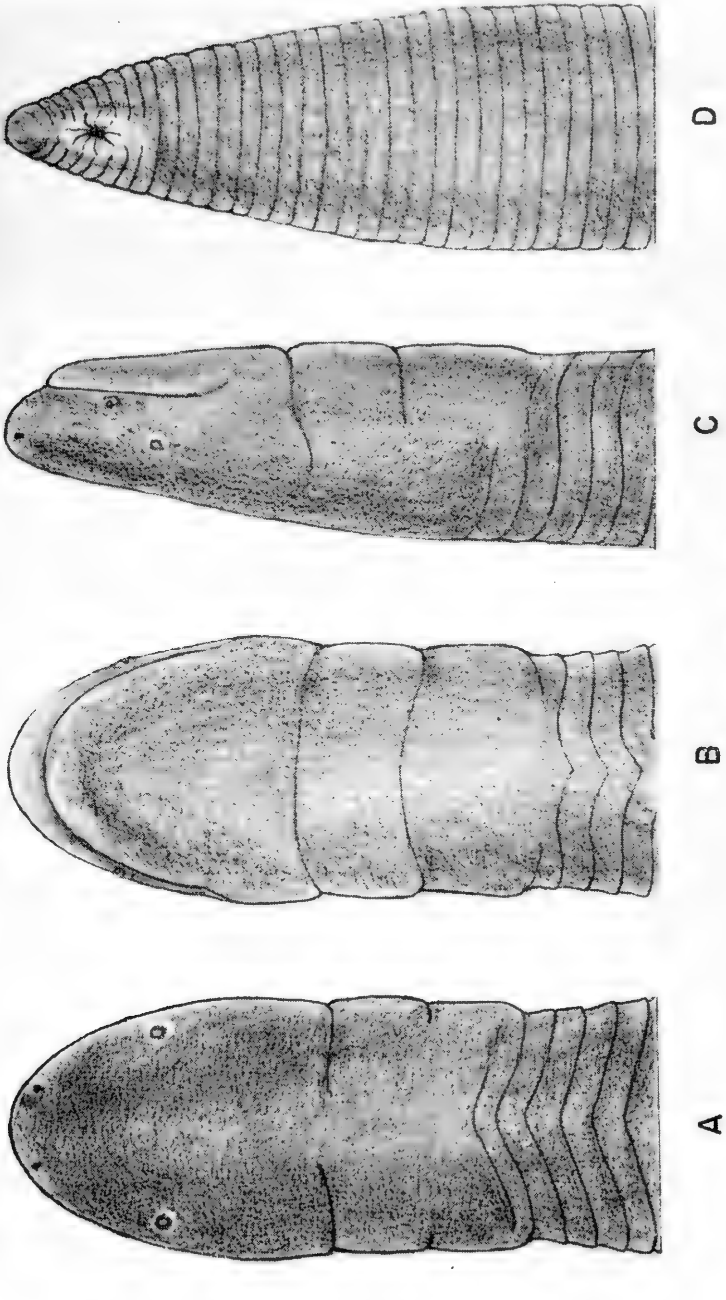

FIG. 18

FIG. 18. *Ichthyophis weberi* Taylor. Neotype. Stanford University No. 21758, near Iwahig, Palawan, P.I. A, B, C, three views of head; D, terminal part of body and subcaudal region. (Actual width of head, 8.5 mm.)

The folds following second collar, 304 (ventral count), 313 (dorsolateral count); folds immediately following the second collar, incomplete below, but complete dorsally; on middle third of body folds incomplete or dim on middle of dorsum; on latter third both folds and grooves more or less distinct, definitely so on posterior part. All folds, except a number preceding vent, form a well-defined ventral angle; tail very short, six folds present, four or five interrupted below by vent; sides of vent with eight or nine denticulations; an anal gland on either side of the vent, slightly elevated.

Scales begin immediately following the collars, one or two rows being present, the largest scales reaching a length of half a millimeter, the smaller ones 0.1 to 0.2 mm.; at middle of body three rows of larger scales present; on posterior fifth there are three or four rows (the fourth row not necessarily complete) and usually the scales not contiguous or overlapping, but generally large.

Dentition: Maxillary-premaxillary teeth, 25-25, small, of nearly equal size; vomeropalatine, 27-27, slightly smaller; dentary, 22-22, the last six to eight of the series a little larger than all the other teeth; no trace of splenials. Palate high, the choanae rather large, subtriangular directed outward and forward, the distance between them more than two and one-half times width of a choana. Tongue large, flat anteriorly, covering entire surface between the dentary series.

Color: Above nearly uniform violet to lilac; on ventral surface lighter with a suggestion of brownish; a whitish mark on vent. Tip of snout vaguely lighter; no spot at eye or tentacle; lower jaw not or but vaguely lighter than chin.

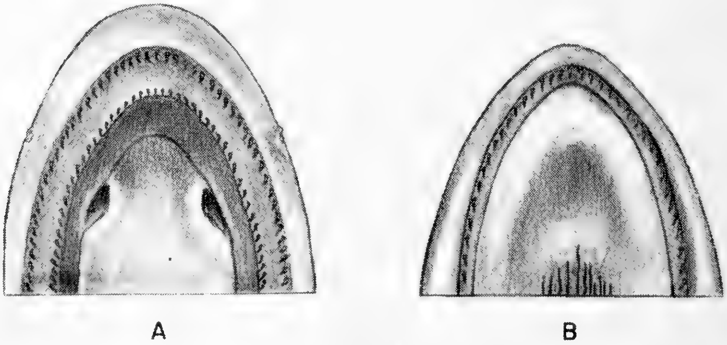

FIG. 19

FIG. 19. *Ichthyophis weberi* Taylor. Neotype. Stanford University Museum No. 21758, near Iwahig, Palawan, P.I. A, upper jaw and palatal region; B, lower jaw and tongue. (Width of head, 8.5 mm.)

Measurements (see table):

TABLE 3. Table of measurements and data on *I. weberi.*

Number	21758 ♂ * Neotype	21760 ♀	21762 ♂ *	21764	21759 Larva	Type
Total length	256	226	230	209	148.5	250
Tail length	4	3.1	3.1	3.3	4.5	2.5
Width of body	10	9.1	7.5	7.6	6.8	....
Width of head	8.5	8	8.6	7.8	7	....
Length of head to 1st groove	10	9.6	10.2	9.7	6	....
Eye to eye	5.8	4.8	5.4	5.25	4	....
Eye level to snout tip	4.9	4.4	4.8	4.9	2.3	5
Tentacle to eye	1.8	1.35	1.35	1.28	in eye spot	1.5
Tentacle to nostril	3.2	2.75	3.1	2.8	.	....
Snout to 1st groove	10	9.6	10.2	9.7	6	....
Snout to 2nd groove	13.7	12.8	12.8	11.3	7.3	....
Snout to 3rd groove	17	16.4	16.3	15.2	10	....
Total folds:						
dorsolateral	304	332	312	316	320	324
ventral	313	327	324	321	329	....
Tail folds	6	6	6	6	6	....
Maxillary-premaxillary teeth	25-25	25-25	25-26	24-25	15-14	....
Vomeropalatine	27-27	24-24	25-25	23-24	15-15	....
Dentary	22-22	18-18	21-22	21-21	13-13	....
Splenial	0-0	0-0	0-0	0-0	5-5	0-0
Vertebrae	107	108	105	105	105	....

* Numerous small ventral papules present on folds, preceding vent.

Variation: There are a few differences between the type and the neotype. The ventral groove mentioned in the type is probably due to preservation. Only the larva, No. 21759, shows a similar groove, obviously caused by preservation. The length of the tail of the type was said to be 2.5 mm. I suspect this measurement was made from the posterior rather than the anterior end of the vent. The color (above "yellowish brown") was probably due to changes brought about by fixation. The individual glandules that appeared in the type as "minute rounded yellowish dots" were doubtless made apparent by a slight surface dehydration. In the specimen reported here, the rounded glandules are dimly visible under magnification and larger elongate glandules are dimly visible bordering the grooves.

It would appear that the splenials are present in some larvae and that these are lost during transformation, as occurs in salamanders. One recently transformed specimen of the series, No. 21761, still shows two of the splenials still present. These I presume would soon have been lost. All others of the series of ten (except a larva) show a complete absence of splenials. The specimen with the highest number of teeth (No. 21766 ♀ measuring 258 mm. in length) is the largest of the series, the formula being, 28-28, 26-27, 28-28, 0-0.

The extruded tentacle is flattened, rather than conical.

Remarks: The coloration of the larva is darker above than that of the two largest specimens listed but scarcely darker than the two medium-sized ones. These are slaty violet dorsally and somewhat darker above than the neotype; the ventral coloration however is very similar. All the specimens have the head bent down at an angle. Whether this is a result of fixation, I cannot say.

Ichthyophis orthoplicatus sp. nov.

FIGS. 20, 21.

Holotype: Zoological Survey of India, Calcutta, No. 17010, Pattipola, Central Province, Ceylon; F. H. Gravely, collector,* Aug. 2, 1915.

Diagnosis: A short, relatively broad species, the width in length approximately 19 times; unicolor lilac-slate, lacking any trace of a lateral stripe. Total folds on body and tail posterior to the collars, 291 to 295, seven confined to tail. *Grooves and folds not angulate on venter;* splenial teeth, 10-10; eye visible in a socket; tentacle a little more than twice as close to eye as to nostril; no diastema between squamosal and parietal bones.

Description of the type: Head oval, the distance between eyes (straight line), 5.5 mm.; from eye-level to tip of snout, 4.7 mm.; distance of tentacle from eye, 1.25 mm.; from nostril, 2.9 mm.; tentacular opening a horseshoe-shaped groove, separated from the edge of lip by a distance of 0.55 mm.; nostrils visible from above; first collar vaguely indicated laterally but the first and second grooves cannot be discerned above or below (probably visible in well-preserved specimens); third groove limiting the second collar not or scarcely discernible (probably because of the dehydration of the specimen); evidence of lateral longitudinal swellings on each side of the combined collars; seemingly there is one or more folds (grooves) on the dorsal posterior part of second collar. Total number of folds behind collars varies from about 291 to 295, of which six (or five) are confined to tail. Latter somewhat compressed laterally, flattened below, terminating in a point; anterior ventral folds incomplete for one fifth of body length; elsewhere folds and grooves above and below pass almost directly across dorsum and venter, no folds showing ventral angles. Vent longitudinal, the edges denticulate, interrupting three or four folds.

Dentition: Maxillary-premaxillary teeth, 23-22; prevomeropalatine, 20-20, smaller than preceding; dentary, 20-20, somewhat larger than the maxillary; splenial, 9 (or 10)-10, some equaling dentaries in size. Tongue rounded anteriorly not covering splenial teeth; choanae rather large, the diameter of one in distance between them, about three times.

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* *Ichthyophis monochrous (part.)* Deraniyagala, Ceylon J. Sci. (B), vol. 17, pt. 3 (May 19, 1933).

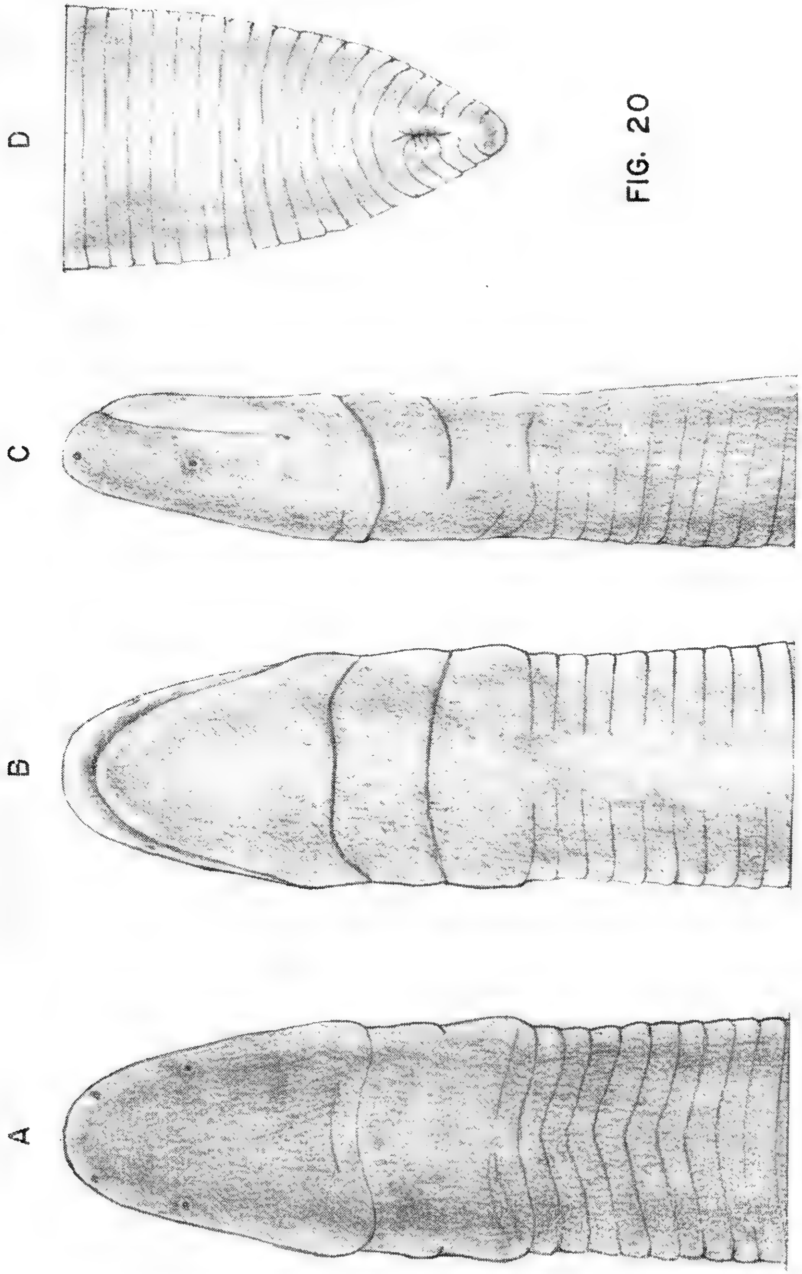

FIG. 20

Fig. 20. *Ichthyophis orthoplicatus* sp. nov. Type. Zoological Survey of India, Calcutta No. 17010, Pattipola, Ceylon. A, B, C, three views of head; D, terminal part of body and subcaudal area. (Actual width of head, 7.9 mm.)

Color: Above and below lilac-slate (more brownish where dried), and seemingly not lighter on ventral surface; a very dim lighter ring about eye, and scarcely discernible lighter areas about tentacle and nostril; a light spot at vent, but no anal glands visible. Head somewhat olive above.

Measurements in mm.: Present shrunken length about 222 (estimated true length 235); tail length, 4; head width, 7.9; approximate body width, 12.5; width in length (approx.) 18 times.

Remarks: The type specimen is strongly contracted, the vertebrae forming a strongly sinuous line.

Rhinatrema, a South American genus of caecilians, which likewise has a species with a lateral stripe, differs from *Ichthyophis* in having all grooves and folds passing directly around the body. As far as I know, the present species is the only species of *Ichthyophis* known in which the folds (and grooves) fail to form a ventral angle throughout most of the body. However, for a greater or lesser distance preceding the vent (one fourth or less of the length) the folds and grooves of all species of *Ichthyophis* pass straight across the venter.

Deraniyagala, Ceylon J. Sci. (B), vol. 17, pt. 3, May 19, 1933, writes of the type specimen:

"*Ichthyophis monochrous.* This is the only specimen in the Colombo museum and has 298 annuli."

The few differences between Mr. Deraniyagala's description and that given here are insignificant. His count of folds perhaps includes the two anterior collars.

Kelaart (Prodromus Faunae Zeylanicae, 1852), mentions a mutilated *Ichthyophis* from Kandy "of a brown color above and a pale yellow brown

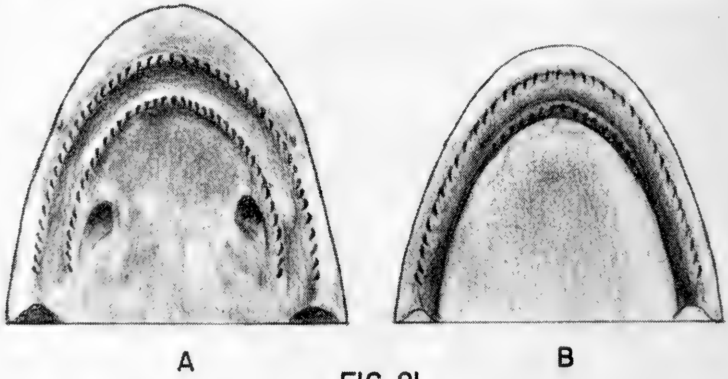

FIG. 21

FIG. 21. *Ichthyophis orthoplicatus* sp. nov. Type. Zoological Survey of India, Calcutta, No. 17010, Pattipola, Ceylon. A, upper jaw and palate of mouth; B, lower jaw and tongue. (Actual width of head, 7.9 mm.)

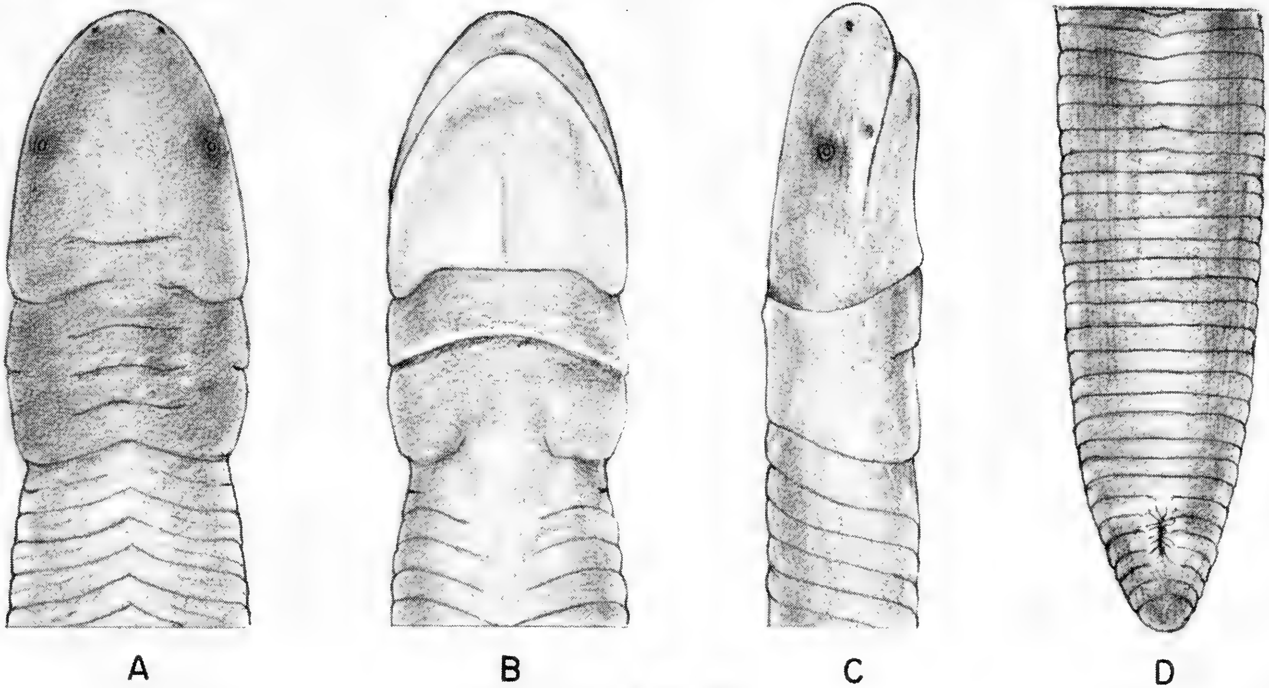

FIG. 22

Fig. 22. *Ichthyophis billitonensis* sp. nov. Type. Amsterdam Museum No. 5209, Billitan Island, Java Sea. A, B, C, three views of head; D, terminal part of body and subcaudal area. (Actual width of head, 5.8 mm.)

beneath, without the side streak of *Ichthyophis glutinosus*." He also states that Dr. Templeton found a new species in the island. These specimens are probably no longer in existence.

The species is named *orthoplicatus,* from Greek *orthos*=straight, plus Latin, *plicatus,* fold.

Ichthyophis billitonensis sp. nov.

Figs. 22, 23.

Holotype: Zoölogisch Museum, Amsterdam, No. 5209, Billiton Island, Indo-Australian Archipelago.

Diagnosis: Probably a small species (type 135 mm.). Total transverse folds, 251-254, five on tail, angulate on venter except on last fifth of body and tail; dorsally sinuous, a few slightly angulate anteriorly, others curving forward somewhat; posteriorly folds pass directly around body; eye distinct; tentacle nearly twice as close to eye as to nostril; splenial teeth, 1-1, relatively large. Collars distinct ventrally, fused dorsally; second nuchal groove below preceded by a narrow curved white fold (groove); scales relatively large, about three rows in each posterior fold.

Description of type: Head bluntly conical, the gape short; area above jaw-angles somewhat thickened; eye very distinct, probably functional; tentacle much closer to eye (1 mm.) than to nostril (2 mm.); eye to nostril, 2.7 mm.; tentacle from edge of lip, 0.25 mm.; nostrils visible from above, directed upward. First collar distinct below, fused to second collar above; first and second transverse grooves very distinct below, the second tending to form a slight fold which is curved, and white in color; dorsally first nuchal groove is interrupted for three and one-half millimeters; second barely discernible on sides when seen from above; third groove sharply marked dorsally, while ventrally it is indistinct; second collar fused posteriorly with the median ventral parts of two or three transverse folds; the collars, fused dorsally, have two longitudinal swellings separated mesially by a median longitudinal elevation.

Following the collars, there are 251-254 transverse primary and secondary folds complete around the body, except first three or four anterior folds on ventral surface; five or six folds confined to tail, two or three of which are behind vent. Tongue somewhat oval, anterior part normally covering splenials which are slightly exposed above gums.

Dentition: Maxillary-premaxillary teeth, 21-21; prevomeropalatine, 17-18; mandibular, 18-17; splenial, 1-1. Choanae large with somewhat elevated rims directed forward and laterally, the distance between them 1.4 mm., the transverse diameter of one (0.43 mm.), in this distance about three times; moderately large scales appear in first fold; at middle of body scales in two large and one small incomplete row; posteriorly there are three large rows and a few scattered smaller scales in each fold.

Color: Generally brown; head rather olive-brown, the collars dark brown; body above brown, the ventral regions a lighter brown; a light spot at vent, tentacle and nostril. A minute lighter ring surrounds eye; an indistinct lighter area above jaw-angle. At the present time there is indication of a yellowish line around each fold, probably due to a slight dehydration, thus causing the edges of the scales to be visible (not impossibly visible in life).

Measurements in mm.: Total length, 135; tail, 2.3; width of body, 6.7; width of head, 5.8; snout to first groove, laterally, 7; to second groove, 9.2; to third groove, 11; eye to eye, 3.3; eye level to tip of snout, 3; width in length, 20 times.

Remarks: Despite the small size of this specimen it gives evidence, in the distinctness of the folds and the development of the teeth and scales, of maturity.

The absence of a lateral stripe suggests a relationship with the *monochrous* group but in many ways it resembles the *glutinosus* forms. The retention of only two splenial teeth is unusual in this genus.

The species is named for its place of origin, the island of Billiton situated in the northern part of the Java Sea, between Sumatra, Borneo, and Java. Sometimes this name is spelled Belitung.

*Schistometopum ephele** sp. nov.

FIGS. 24, 25, 26.

Type: Museo Civico di Storia Naturale, "G. Doria," Genova, No. 8773; Agua Ize (400-700M.) Ihla São Thomé, Gulf of Guinea.

Paratype: B.M. 1933.11.16. 1-4 ♀ Ihla São Thomé.

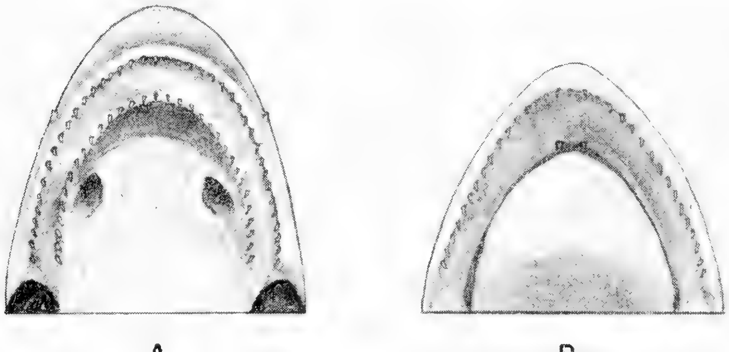

FIG. 23

FIG. 23. *Ichthyophis billitonensis* sp. nov. Type. Amsterdam Museum No. 5209, Billiton Island, Java Sea. A, upper jaw and palate; B, lower jaw and tongue. (Actual width of head, 5.8 mm.)

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* From Latin *ephelis*=freckled.

FIG. 24. *Schistometopum ephele* sp. nov. Type. Museo Civico Genova No. 8773, Agua Ize, São Thomé, Gulf of Guinea. Photograph of type about natural size.

Diagnosis: A *Schistometopum* with a proportionally smaller, more-pointed head than *thomense.* Color light yellowish-brown with dark lilac-brown flecks over dorsum and sides of body; fewer flecks on venter chin and throat; primary folds, 97-106; secondary, 40-52.

Description of the type: Head relatively very small; eye small, distinct in socket; distance between eyes (3.1 mm.), equal to length of snout in front of eyes (3.1 mm.); tentacular aperture small, separated from eye by 0.6 mm.; from nostril by 2.5 mm.; from mouth by 0.35 mm.; eye from nostril, 3.2 mm.; nostrils barely visible from directly above, practically terminal. Two collars; first collar sharply defined by a deep groove fore and aft surrounding neck, curving very slightly forward both dorsally and ventrally; a short indefinite transverse groove visible above and below; a distinct fold across chin preceding first groove; second collar a little wider ventrally than dorsally, with a distinct transverse groove above as long as width of body, not present ventrally; third groove, limiting collar, complete. Primary folds 97, all complete above and below, the grooves likewise distinct; secondaries, 40; total folds, 137; at first the grooves marking the secondaries are short; eight are complete.

Scales present, one or two appearing low on sides at about the 33rd fold; a single row complete around body where secondaries begin. In posterior portion where secondaries are complete, three scalerows present.

Dentition: Maxillary-premaxillary teeth 16-16; vomeropalatine, 18-18; dentary, 11-11; splenial, 10-9; dentary teeth longest, all directed backwards somewhat; splenials elevated to nearly same level as dentaries. Tongue not covering splenials, and lacking lateral beadlike elevations and grooves.

Color: Light yellowish brown with lilac-brown flecks and marks.

Measurements in mm. (type and paratype): Total length, 186, 340; width of head at first groove, 6, 9.4; width of body (middle), 9.2, 15.5; tip of snout to first nuchal groove, 7.2, 11; to second groove, 9.2, 13; to third groove, 12, 17; width near terminus of body, 6.9, 13.

Variation: The dental formula of the paratype is approximately 16-15; 18-18; 9-9; 8-9. There are 100 primary folds and 36 secondary; there is a slight lateral dorsal swelling (muscular) on each side of the head preceding the first groove. This is discernible also in the type. The snout projects very slightly beyond mouth. The vent is transverse, denticulated, but no anal glands are in evidence.

Distribution: Known only on Ihla São Thomé.

Remarks: This type was collected by the Leonardo Fea Expedition. In the British Museum one specimen is designated a paratype. This is a large specimen but considerably desiccated. A second specimen bearing the same number may likewise belong here (348 mm. long and dissected partially). Two other specimens under this number are completely yellow and are referred to *S. thomense.*

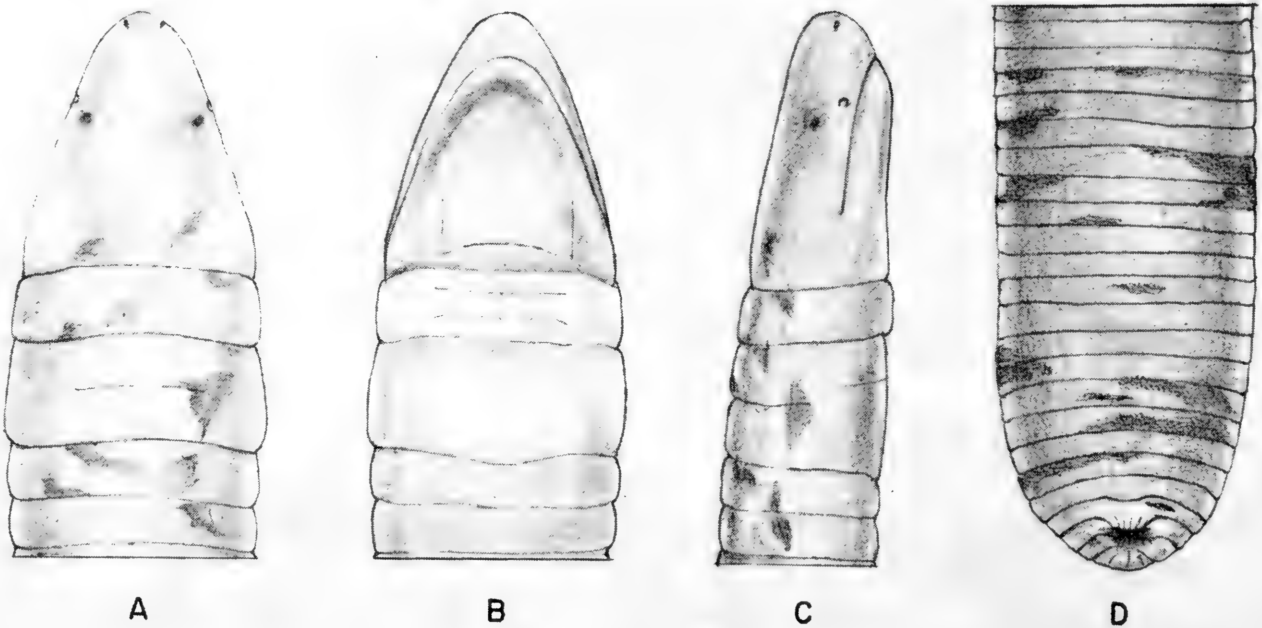


FIG. 25

FIG. 25. *Schistometopum ephele* sp. nov. Type. São Thomé Island, Gulf of Guinea. A, B, C, three views of head; D, terminal part of body, ventral view. (Actual width of head, 6 mm.)

B.M. Museum, No. 1927.2.10.1 from the same locality may also belong with this species.

Schistometopum brevirostris Peters

FIGS. 27, 28.

Siphonops brevirostris Peters, Monatsb. Akad. Wiss., Berlin, 1874, pp. 617-618, pl. 1, fig. 2 (type-locality, Westkuste, Africa. Later reported by Peters as "aus Guinea"; Gorham, 1962, gives Rolas Is., Gulf of Guinea, but I have overlooked the source of this information).

Dermophis brevirostris, Peters, Monatsb. Akad. Wiss. Berlin, 1879, p. 937 (aus Guinea); *ibid.,* 1880, p. 223 (*Dermophis brevirostris* gleich *Siphonops thomensis* Bocage).

Diagnosis: Head elongated somewhat; diameter of body in total length 35 times. Color bluish gray, the grooves lighter; splenial teeth, 4-5.

Description of species: (from Museo Civico di Storia Naturale "G. Doria," Genova, Italy, No. 28881, from São Thomé): Body moderately slender and seemingly flattened somewhat throughout (rather than cylindrical); head slender, oval; the eyes distinct, minute, the distance between them equal to the length of snout from level of eye; snout extends beyond mouth, 0.6 mm.; tentacular aperture about one third diameter of eye, its distance from eye, 0.78, from nostril, 3.35; from lip, 0.5 millimeters. Two distinct collars; the first nuchal groove curves forward dorsally passing under chin in advance of the dorsal portion, the width of the first collar greater ventrally; first collar with a short transverse medial groove above and below; second collar nearly same width above and below, also with a dorsal transverse

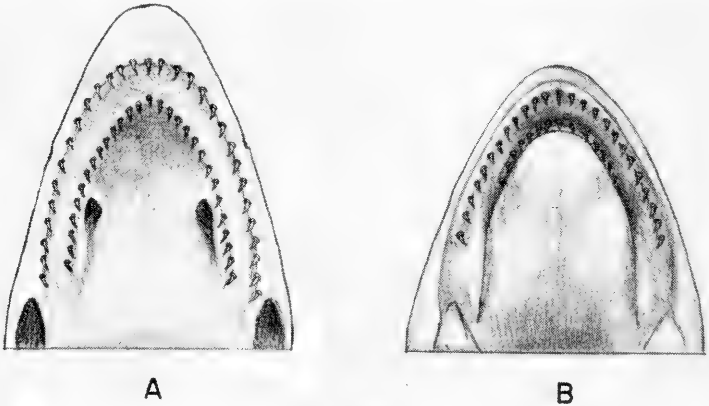


FIG. 26

FIG. 26. *Schistometopum ephele* sp. nov. Type. Museo Civico Genova No. 8773, São Thomé Island, Gulf of Guinea. A, upper jaw and palatal region; B, lower jaw and tongue. (Actual width of head, 6 mm.)

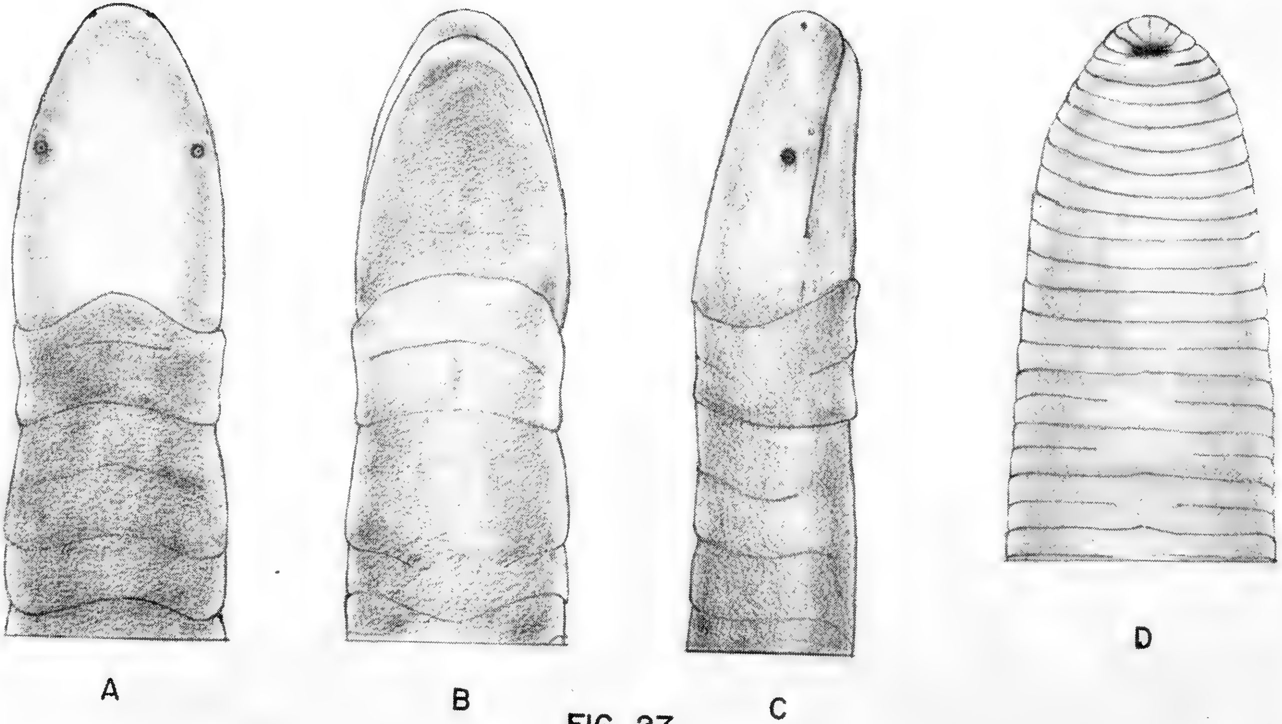


FIG. 27

FIG. 27. *Schistometopum brevirostris* (Peters). Museo Civico Genova No. 28881, São Thomé Island, Gulf of Guinea. A, B, C, three views of head; D, terminus of body, ventral view. (Actual width of head, 6 mm.)

median groove but none on ventral part; the third nuchal groove incomplete below; second collar fused to the following first primary fold ventrally.

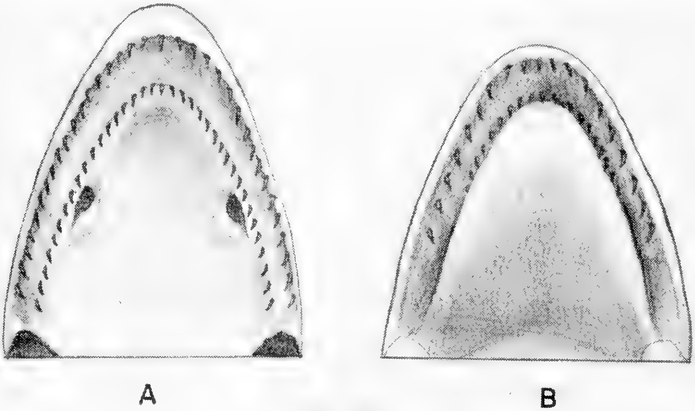
Total primary folds 101, complete above and below; secondaries, 38, the last nine complete; a pair of ventral longitudinal grooves beginning just in front of third transverse nuchal groove, cross the collars run forward on chin but fail to meet anteriorly; a small transverse ventral groove across back part of chin preceding the first nuchal groove.

Scales begin about the 20th fold, where one or two very small transversely widened scales are present; at middle of body a short lateral row present; at beginning of the secondaries a nearly complete row around body, the largest scales nearly one mm. in length; in each fold posteriorly there are four somewhat irregular rows, the largest scales a little more than 1.75 mm. in width; some are subcircular in shape. Skin glands not conspicuous, but in primary grooves a row of glandules usually evident, and at least posteriorly some very minute pores are evident under a lens. Terminus of body tapering, the vent transverse, its two sides denticulate, with a pair of small anal glands preceding it; from vent to terminus, 1.6 mm.

Dentition: Maxillary-premaxillary teeth, 15-16; prevomeropalatine, 20-20; dentary, 11-14; splenial, 9-9.

Color: In preservative, body light gray, becoming brownish anteriorly when removed some minutes from liquid. Head above and on sides nearly uniform cream to fawn, contrasting strongly with color on first collar; lower jaws light, the area between them gray brown; posterior part of body perhaps a little lighter than anterior.

Measurements in mm.: Total length, 236; width of body, 9.5; width of


A

B

FIG. 28

Fig. 28. *Schistometopum brevirostris* (Peters). Museo Civico Genova No. 28881, São Thomé Island, Gulf of Guinea. A, upper jaw and palate; B, lower jaw and tongue. (Actual width of head, 6 mm.)

head at first nuchal groove, 6; tip of snout to 1st groove, 9; to second groove, 11.2; to third groove, 14.9; eye to eye, 3.85; eye-level to tip of snout, 4.1; body width in length, 24.8 times.

Variation: A specimen in the British Museum (No. 1927.2.10.1 from São Thomé) is somewhat darker gray than the specimen described and the grooves are somewhat lighter. The width in length (9.8 and 261 mm.) contained 26.6 times. There are 106 primary folds and 52 secondaries; the dental formula: m-p., 16-17; v.p., 19-18; d., 11-11; sp., 10-11.

Remarks: I would interpret Peters' counts, in my own terms of reference as: four folds for the two collars; followed by 132 primaries and secondaries of which the last 14 are complete; when the secondaries begin these folds are alternately incomplete and complete. Thus there are 96 primaries following the collars, and 36 secondaries.

I have referred these specimens to Peters' *S. brevirostris,* although I have not compared them with the type. Peters did not distinguish between primaries and secondaries, or between these and the two collars. The type, if still extant, was not available for examination in 1962.

THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

CATALOGUE OF THE TYPES IN THE SNOW ENTOMOLOGICAL MUSEUM

Part IV (Orthoptera)

By

George W. Byers and Lanny B. Carney

CATALOGUE OF THE TYPES IN THE SNOW ENTOMOLOGICAL MUSEUM.

Part V (Acarina)

By

George W. Byers and Calvin L. Wong

Vol. XLVI Pages 303-315 October 28, 1965 No. 7, 8

THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. XLVI Pages 303-307 October 28, 1965 No. 7

Catalogue of the Types in the Snow Entomological Museum
Part IV (Orthoptera)[1]

By

George W. Byers and Lanny B. Carney

ABSTRACT

Types of 69 species and subspecies of Orthoptera are catalogued, with references to original description (except for species represented by paratypes only), number and condition of specimens, and type numbers as recorded in the catalogue of types in the Snow Entomological Museum.

INTRODUCTION

Although there has never been a staff member of the Snow Entomological Museum working primarily on the taxonomy of the Orthoptera, there has long been an interest in building a good representative collection of these insects. A few papers dealing with the Orthoptera have been published by Museum personnel, notably those on the Oedipodinae of Kansas, by R. H. Beamer, and the Melanopli of Kansas, by P. W. Claassen, which papers appeared in 1917, in volume 11 of the University of Kansas Science Bulletin.

A number of specialists on the Orthoptera have, through the years, made use of the collection in the Snow Museum, returning to the Museum certain type specimens representing new species revealed by their studies. Outstanding among these specialists are James A. G. Rehn and Morgan Hebard, both of the Academy of Natural Sciences of Philadelphia. By similar means, or by exchange, the Museum has come into possession of types (principally syntypes or paratypes from extensive series) of species described by S. H. Scudder, T. H. Hubbell, and others.

In the following list of type specimens, we have arranged the families and suborders according to the system proposed by Rehn and Grant, in their

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[1] Contribution number 1239 from the Department of Entomology, The University of Kansas, Lawrence, Kansas.

Monograph of the Orthoptera of North America (Volume 1, 1961, Monogr. Acad. Nat. Sci. Philadelphia, 12). Beneath the family headings, the types are arranged alphabetically by genus, then species, in two separate lists. The first includes holotypes, allotypes, and syntypes (cotypes), as well as paratypes if these are present in addition, and gives a reference to the original description of each species. The second list includes species represented by paratypes only and omits literature references. Both lists indicate the sex of the types and the condition, if the specimens are seriously damaged. (Missing parts are indicated only when absent from both sides of the specimen.) The type number from the Catalogue of Types in the Snow Entomological Museum is given for each species.

We have not included any secondary types, such as homotypes, plesiotypes or metatypes. The lists also include only those type specimens that are actually present in the Museum as of 1964. In some cases an original description indicated one or more types were deposited in the Snow Museum, but none—or a lesser number than that indicated—was actually found in the collection. Of the types listed by Hunter (1913, Univ. Kansas Sci. Bull., 8[1]:16), only that of *Lactista arphoides* was not found.

Only original combinations of generic and specific names have been used, as it was deemed impracticable to attempt to give the current generic assignment or synonymic status of every species.

ACKNOWLEDGMENTS

We wish to thank Dr. Harold J. Grant, Jr., and Dr. Theodore J. Cohn for assistance with various details in the preparation of the catalogue. Financial support from the General Research Fund of the University of Kansas, which has made possible the completion of this work, is gratefully acknowledged.

Suborder Caelifera

Superfamily Acridoidea

Tetrigidae—Paratypes

Apotettix eurycephalus brevipennis Hancock. 1 ♂, 1 ♀ (antennae missing from both). 5424.

Paratettix hesperus Morse. 1 ♂, 1 ♀ (♀ lacks antennae). 1295.

Tettigidea lateralis cazieri Rehn & Grant. 4 ♂, 2 ♀. 5421.

Acrididae

Aeoloplides rotundipennis Wallace, 1955, Ann. Ent. Soc. Amer., vol. 48, no. 6, pp. 464-466. ♂ holotype, ♀ allotype, 32 ♂, 12 ♀ paratypes. 5685.

Cordillacris pima Rehn, 1907, Proc. Acad. Nat. Sci. Phila., vol. 59, pp. 69-71. ♀ holotype (both hind tibiae and tarsi lacking). 1315.

Melanoplus blatchleyi Scudder, 1898, Proc. U.S. Nat. Mus., vol. 20, no. 1124, pp. 322-323. 1 ♂, 1 ♀ syntypes (antennae missing in both). 1302.

Melanoplus gladstoni Scudder, 1897, Proc. Amer. Philos. Soc., vol. 36, no. 154, p. 23. 1 ♂ syntype. 1303.

Melanoplus huroni Blatchley, 1898, Psyche, vol. 8, no. 264, pp. 195-196. 1 ♀ syntype (five legs missing, wings damaged). 1314.

Melanoplus insignis Hubbell, 1932, Misc. Publ., Mus. Zool. Univ. Mich., no. 23, pp. 56-58. ♂ holotype, ♀ allotype. 2231.

Melanoplus packardi[2]

Melanoplus snowii Scudder, 1898, Proc. U.S. Nat. Mus., vol. 20, no. 1124, pp. 274-275. ♂ holotype (no legs or antennae), ♀ allotype (no front or middle legs, no antennae). 1301.

Trimerotropis snowi Rehn, 1905, Trans. Kans. Acad. Sci., vol. 19, pp. 223-224. ♀ holotype. 1298.

Acrididae—Paratypes

Aerochoreutes carlinianus strepitus Rehn. 1 ♂ (hind legs missing), 1 ♀. 5412.

Agroecotettix modestus crypsidomus Hebard. 1 ♂, 1 ♀. 1310.

Appalachia arcana Hubbell & Cantrall. 1 ♂, 1 ♀. 4550.

Aptenopedes aptera borealis Hebard. 1 ♀. 3052.

Aptenopedes aptera saturiba Hebard. 1 ♂, 1 ♀. 3053.

Aptenopedes aptera simplex Hebard. 2 ♂, 2 ♀. 3051.

Aptenopedes hubbelli Hebard. 2 ♂, 2 ♀. 3054.

Aptenopedes nigropicta Hebard. 2 ♂. 3055.

Aptenopedes robusta Hebard. 1 ♂, 2 ♀. 3056.

Aptenopedes sphenarioides appalachee Hebard. 2 ♂, 2 ♀. 3057.

Barytettix cochisei Gurney. 1 ♂ (antennae missing). 5415.

Bradynotes chilcotinae Hebard. 1 ♂, 1 ♀. 1309.

Circotettix crotalum Rehn. 1 ♂, 1 ♀. 1300.

Circotettix nigrafasciatus Beamer. 14 ♂, 6 ♀. 1299.

Conalcaea cantralli Gurney. 1 ♂. 5409.

Conalcaea coyoterae Hebard. 1 ♀. 927.

Eumorsea balli Hebard. 1 ♂. 2267.

Melanoplus beameri Hebard. 16 ♂, 17 ♀. 1313.

Melanoplus bruneri Scudder. 1 ♂, 2 ♀ (antennae lacking in ♂, 1 ♀). 1305.

Melanoplus elongatus Scudder. 1 ♀ (antennae missing). 928.

Melanoplus indigens digitifer Hebard. 5 ♂, 5 ♀. 3058.

Melanoplus intermedius Scudder. 1 ♀. 1306.

Melanoplus macclungi Rehn. 46 ♂, 51 ♀. 5418.

Melanoplus mastigiphallus Strohecker. 1 ♂, 1 ♀. 3641.

Melanoplus oreophilus Hebard. 1 ♂, 2 ♀. 933.

Melanoplus viridipes eurycercus Hebard. 1 ♂, 1 ♀. 1312.

---

[2] Two male and three female specimens labelled as part of Scudder's type series are some of those listed by Scudder, 1898, in Proc. U. S. Nat. Mus., vol. 20, but are not regarded by us as original types of this species, which was described in 1878 (Proc. Boston Soc. Nat. Hist., vol. 19, p. 288).

Oedaleonotus fratercula Hebard. 1 ♂, 1 ♀ (antennae missing). 2266.
Phrynotettix robustus manicola Rehn & Grant. 1 ♂. 5423.
Phrynotettix robustus occultus Rehn & Grant. 1 ♂. 5892.
Psoloessa thamnogaea Rehn. 1 ♂. 3807.
Psychomastax psylla robusta Hebard. 1 ♂. 5417.
Schistocerca ceratiola Hubbell & Walker. 3 ♂, 2 ♀. 4551.
Stenobothrus olivaceus Morse. 1 ♂. 1804.
Zapata salutator Rehn. 1 ♀ (antennae missing). 5426.

Suborder Ensifera

Tettigoniidae

Plagiostira gracila Rehn, 1905, Trans. Kans. Acad. Sci., vol. 19, p. 227. ♀ holotype. 5411.

Tettigoniidae—Paratypes

Arethaea ambulator Hebard. 1 ♂, 1 ♀. 2274.
Arethaea coyotero Hebard. 1 ♂, 1 ♀. 2272.
Arethaea mescalero Hebard. 2 ♂ (one without legs). 2273.
Brachyinsara hemiptera Hebard. 1 ♂, 1 ♀. 3049.
Decticita balli Hebard. 1 ♂. 3050.
Dichopetala gladiator Rehn & Hebard. 1 ♂, 1 ♀. 1307.
Idionotus tehachapi Hebard. 1 ♂, 1 ♀. 2271.
Insara tessellata Hebard. 3 ♂ (all lacking antennae). 2270.
Inscudderia walkeri Hebard. 1 ♂, 1 ♀. 1308.

Gryllacrididae

Ceuthophilus paucispinosa Rehn, 1905, Trans. Kans. Acad. Sci., vol. 19, pp. 227-228. ♀ holotype. 1291.

Ceuthophilus tuckeri Rehn, 1907, Ent. News, vol. 18, no. 10, pp. 445-446. ♂ holotype (both hind legs missing). 1292.

Phrixocnemis franciscanus Rehn, 1905, Trans. Kans. Acad. Sci., vol. 19, pp. 228-229. 1 ♂, 1 ♀ syntypes. 1293.

Phrixocnemis socorrensis Rehn, 1905, Trans. Kans. Acad. Sci., vol. 19, pp. 229-230. 1 ♂, 1 ♀ syntypes (♀ missing both antennae). 5431.

Udeopsylla serrata Rehn, 1905, Trans. Kans. Acad. Sci., vol. 19, pp. 230-231. ♂ holotype. 1294.

Gryllacrididae—Paratypes

Ammobaenetes lariversi Strohecker. 1 ♂, 1 ♀ (♀ missing both antennae). 3642.
Ceuthophilus wichitaensis Hubbell. 1 ♂, 1 ♀. 5413.
Stenopelmatus intermedius Davis & Smith. 1 ♂, 1 ♀. 1290.

Gryllidae—Paratypes

Cycloptilum bidens Hebard. 3 ♂, 3 ♀. 1803.
Cycloptilum spectabile Strohecker. 1 ♂, 1 ♀. 3640.
Oecanthus californicus pictipennis Hebard. 1 ♂ (antennae damaged). 5560.

Gryllotalpidae—Paratypes

Scaptericus acletus Rehn & Hebard. 1 ♂, 1 ♀. 3808.

Suborder Dictyoptera

Superfamily Mantodea

Manteidae

Stagmomantis gracilipes Rehn, 1907, Proc. Acad. Nat. Sci. Phila., vol. 59, pp. 67-68. ♂ holotype (head and abdomen damaged). 1289.

Superfamily Blattodea

Blattidae

Latiblattella lucifrons Hebard, 1917, Mem. Amer. Ent. Soc., no. 2, pp. 43-46. ♂ holotype, ♀ allotype. 1287.

Blattidae—Paratypes

Pseudomops septentrionalis Hebard. 4 ♂, 1 ♀. 1288.

THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. XLVI Pages 309-315 October 28, 1965 No. 8

Catalogue of the Types in the Snow Entomological Museum Part V (Acarina)[1]

By

George W. Byers and Calvin L. Wong

ABSTRACT

Types of 113 species of Acarina are catalogued, with references to original description (except for species represented by paratypes only), number and sex or stage of specimens, and type numbers as recorded in the catalogue of types in the Snow Entomological Museum.

INTRODUCTION

Most of the species of mites (Acarina) represented in the Snow Entomological Museum by type specimens were named and described during recent years by staff members and students or former students of the Department of Entomology of The University of Kansas. These acarologists are W. T. Atyeo, R. E. Beer, J. Boczek, J. G. Borland, J. M. Brennan, E. A. Cross, D. A. Crossley, B. Greenberg, C. C. Hall, E. W. Jameson, Jr., E. H. Kardos, D. S. Lang, L. J. Lipovsky, R. B. Loomis, D. S. Narayan, and K. A. Wolfenbarger. The few types representing other species were obtained by exchange or were received as gifts.

In the following list of type specimens, the families are arranged alphabetically. Under the family headings, the genera and then the species are likewise arranged alphabetically, in two lists. The first list includes species represented by holotypes, allotypes, syntypes or lectotypes and indicates paratypes if these are present in addition. This list contains references to the original description of each species and to the designation of a lectotype, where applicable. The second list is of species represented by paratypes only

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[1] Contribution No. 1228 from the Department of Entomology, The University of Kansas, Lawrence, Kansas.

and omits literature references. Both lists indicate the sex or stage of the types. The type number from the Catalogue of Types in the Snow Entomological Museum is given for each species. On the labels of the microscope slides carrying certain of the types, there appears another number, which refers to a catalogue of specimens of Acarina prepared and slide-mounted at The University of Kansas.

No kinds of types other than those already noted are included in this catalogue. Only those type specimens actually present in the collection as of 1964 are listed.

The combinations of generic and specific names appearing here are those originally used by the authors indicated; a few of the species have subsequently been removed to other genera, but it seems best, in the interest of stability, to record only the original combinations. In one instance of primary homonymy, however, the main entry has been made under the replacement name, although the original combination is listed, as well.

ACKNOWLEDGMENTS

We wish to thank The University of Kansas for financial support, provided from the General Research Fund, which has made possible the preparation of this catalogue. Assistance relating to certain included types was given by Dr. Richard B. Loomis of Long Beach State College, California, whose help is gratefully acknowledged. We also acknowledge with thanks the assistance of Miss Linda Hardee and Miss Judy Jobson in cataloguing, copyreading, and typing the manuscript.

Cheyletidae

Cheletophyes knowltoni Beer & Dailey, 1956, Univ. Kans. Sci. Bull., vol. 38, pt. 1, no. 5, pp. 409-417. ♀ holotype, ♂ allotype, 34 ♂, 38 ♀ paratypes. 6251.

Diplogyniidae—Paratypes

Neolobogynium lateriseta Hicks. 1 ♀. 6321.

Eriophyidae

Aceria slykhuisi Hall, 1958, Jour. Kans. Ent. Soc., vol. 31, no. 3, pp. 233-235. ♀ holotype, ♂ allotype, 4 ♂, 16 ♀ paratypes. 5759.

Catharinus axonopi Boczek, 1960, Jour. Kans. Ent. Soc., vol. 33, no. 1, pp. 11, 12. ♀ holotype, ♂ allotype, 3 ♀ paratypes. 6252.

Latonotus wegoreki Boczek, 1960, Jour. Kans. Ent. Soc., vol. 33, no. 1, pp. 9-11. ♀ holotype, ♂ allotype, 3 ♀ paratypes. 6253.

Tegonotus guavae Boczek, 1960, Jour. Kans. Ent. Soc., vol. 33, no. 1, pp. 11-14. ♀ holotype, ♂ allotype, 5 ♀ paratypes. 6254.

Laelaptidae

Laelaps stegemani Hefley, 1935, Jour. Kans. Ent. Soc., vol. 8, no. 1, pp. 22-24. ♀ holotype. 3789.

Labidostomidae

Labidostomma barbae Greenberg, 1952, Jour. N.Y. Ent. Soc., vol. 60, no. 4, pp. 198-200. ♂ holotype, 2 ♂ paratypes. 5405.

Labidostomma caloderum Greenberg, 1952, Jour. N.Y. Ent. Soc., vol. 60, no. 4, pp. 197-198. ♂ holotype, 1 ♂, 1 ♀ paratypes. 5404.

Labidostomidae—Paratypes

Labidostoma circinus Atyeo & Crossley. 2 ♀. 6255.
Labidostoma fictiluteum Atyeo & Crossley. 1 ♂, 1 ♀. 6256.
Labidostoma malleolus Atyeo & Crossley. 2 ♀. 6257.
Labidostoma multifarium Atyeo & Crossley. 2 ♀. 6258.

Macrochelidae—Paratypes

Macrocheles rodriguezi Oliver & Krantz. 1 ♂, 1 ♀. 6322.

Myobiidae—Paratypes

Radfordia bachai Howell & Elzinga. 1 ♂, 12 ♀. 5686.

Penthaleidae

Penthaleus crinitus Narayan, 1957, Jour. Kans. Ent. Soc., vol. 30, no. 3, pp. 111-113. ♀ holotype, 4 ♀ paratypes. 6259.

Podapolipodidae

Podapolipus komareki Storkan, 1927, Zool. Anzeiger, vol. 71, pp. 19-22. 15 ♂, 17 ♀, 54 larval syntypes. 6260.

Pterygosomidae

Pimeliaphilus rapax Beer, 1960, Jour. Parasitol., vol. 46, pp. 434-440. ♀ holotype, ♂ allotype, 3 ♂, 1 ♀, 2 larval, 17 nymphal paratypes. 6261.

Scutacaridae

Nasutiscutacarus ampliatus Beer & Cross, 1960, Jour. Kans. Ent. Soc., vol. 33, no. 2, pp. 54-57. ♀ holotype, 3 ♀ paratypes. 6262.

Nasutiscutacarus anthrenae Beer & Cross, 1960, Jour. Kans. Ent. Soc., vol. 33, no. 2, pp. 51-54. ♀ holotype, 7 ♀ paratypes. 6263.

Tarsonemidae

Hemitarsonemus peregrinus Beer, 1954, Univ. Kans. Sci. Bull., vol. 36, pt. 2, no. 16, pp. 1300-1308. ♂ holotype, ♀ allotype, 2 ♂, 3 ♀ paratypes. 5428.

Rhynchotarsonemus niger Beer, 1954, Univ. Kans. Sci. Bull., vol. 36, pt. 2, no. 16, pp. 1221-1229. ♂ holotype, ♀ allotype, 4 ♂, 2 ♀, 3 larval paratypes. 5416.

Steneotarsonemus fulgens Beer, 1954, Univ. Kans. Sci. Bull., vol. 36, pt. 2, no. 16, pp. 1281-1285. ♂ holotype, ♀ allotype, 2 ♂, 10 ♀ paratypes. 5425.

Steneotarsonemus hyaleos Beer, 1954, Univ. Kans. Sci. Bull., vol. 36, pt. 2, no. 16, pp. 1256-1261. ♂ holotype, ♀ allotype, 2 ♂, 9 ♀, 1 larval paratypes. 5420.

Steneotarsonemus kieferi Beer, 1958, Jour. N.Y. Ent. Soc., vol. 66, nos. 3-4, pp. 153-156. ♂ holotype, ♀ allotype, 2 ♂, 33 ♀ paratypes. 6264.

Tarsonemella beameri Beer, 1958, Jour. Kans. Ent. Soc., vol. 31, no. 2, pp. 189-192. ♀ holotype, 3 ♀ paratypes. 6265.

Tarsonemus dispar Beer, 1954, Univ. Kans. Sci. Bull., vol. 36, pt. 2, no. 16, pp. 1148-1155. ♂ holotype, ♀ allotype, 1 ♂, 9 ♀ paratypes. 5406.

Tarsonemus pritchardi Beer, 1954, Univ. Kans. Sci. Bull., vol. 36, pt. 2, no. 16, pp. 1202-1210. ♂ holotype, ♀ allotype, 3 ♂, 6 ♀, 1 larval paratypes. 5414.

Tarsonemus sulcatus Beer, 1954, Univ. Kans. Sci. Bull., vol. 36, pt. 2, no. 16, pp. 1155-1162. ♂ holotype, ♀ allotype. 5407.

Tarsonemus viridis Ewing, 1939, U.S. Dept. Agr. Tech. Bull. 653, pp. 35-37. 1 ♂ syntype. 5432.

Tarsonemus waitei Banks, 1913 (1912), Proc. Ent. Soc. Wash., vol. 14, no. 2, pp. 98-99. 2 ♀ syntypes. 5411.

Xenotarsonemus denmarki Beer, 1960, Florida Ent., vol. 43, no. 1, pp. 23-27. ♂ holotype, 2 ♂ paratypes. 6266.

Tarsonemidae—Paratypes

Pseudotarsonemoides cryptocephalus Ewing. 3 ♀. 5048.

Tarsonemus occidentalis Ewing. 3 ♂. 5430.

Tetranychidae

Aplonobia dyschima Beer & Lang, 1958, Univ. Kans. Sci. Bull., vol. 38, pt. 2, no. 15, pp. 1234-1235. ♀ holotype, 9 ♀ paratypes. 6267.

Aplonobia verrucosa Beer & Lang, 1958, Univ. Kans. Sci. Bull., vol. 38, pt. 2, no. 15, pp. 1233-1234. ♂ holotype, ♀ allotype, 14 ♂, 16 ♀ paratypes. 6268.

Eotetranychus oistus Beer & Lang, 1958, Univ. Kans. Sci. Bull., vol. 38, pt. 2, no. 15, p. 1241. ♂ holotype, ♀ allotype, 4 ♂, 1 ♀ paratypes. 6269.

Neotetranychus flabellosetus Beer & Lang, 1958, Univ. Kans. Sci. Bull., vol. 38, pt. 2, no. 15, p. 1239. ♂ holotype, ♀ allotype, 1 ♀ paratype. 6270.

Neotetranychus hamus Beer & Lang, 1958, Univ. Kans. Sci. Bull., vol. 38, pt. 2, no. 15, p. 1238. ♂ holotype, ♀ allotype, 7 ♂, 6 ♀ paratypes. 6271.

Neotetranychus hispidosetus Beer & Lang, 1958, Univ. Kans. Sci. Bull., vol. 38, pt. 2, no. 15, p. 1237. ♂ holotype, ♀ allotype, 6 ♂, 7 ♀ paratypes. 6272.

Neotetranychus undulatus Beer & Lang, 1958, Univ. Kans. Sci. Bull., vol. 38, pt. 2, no. 15, pp. 1239-1240. ♂ holotype, ♀ allotype, 1 ♂ paratype. 6273.

Oligonychus flexuosus Beer & Lang, 1958, Univ. Kans. Sci. Bull., vol. 38, pt. 2, no. 15, pp. 1243-1244. ♂ holotype, ♀ allotype, 2 ♂, 6 ♀ paratypes. 6274.

Schizonobiella aeola Beer & Lang, 1957, Pan-Pacific Ent., vol. 33, no. 2, pp. 87-89. ♀ holotype, ♂ allotype, 1 ♂, 9 ♀, 2 nymphal paratypes. 6275.

Trombiculidae

Acomatacarus angulatus Greenberg, 1952, Ann. Ent. Soc. Amer., vol. 45, no. 3, pp. 485-488. Larval holotype, 4 larval paratypes. 5369.

Acomatacarus micheneri Greenberg, 1952, Ann. Ent. Soc. Amer., vol. 45, no. 3, pp. 480-482. Larval holotype, 10 larval paratypes. 5366.

Acomatacarus (Xenacarus) plumosus Greenberg, 1951, Jour. Parasitol., vol. 37, no. 6, pp. 525-527. Larval holotype, 4 larval paratypes. 5367.

Acomatacarus polychaetus Greenberg, 1952, Ann. Ent. Soc. Amer., vol. 45, no. 3, pp. 488-489. Larval holotype. 5371.

Acomatacarus senase Greenberg, 1952, Ann. Ent. Soc. Amer., vol. 45, no. 3, pp. 484-485. Larval holotype, 2 larval paratypes. 5368.

Acomatacarus whartoni Greenberg, 1952, Ann. Ent. Soc. Amer., vol. 45, no. 3, pp. 489-491. Larval holotype. 5370.

Cheladonta crossi Lipovsky, Crossley & Loomis, 1955, Jour. Kans. Ent. Soc., vol. 28, no. 4, p. 139. Larval holotype, 5 larval paratypes. 5580.

Cheladonta micheneri Lipovsky, Crossley & Loomis, 1955, Jour. Kans. Ent. Soc., vol. 28, no. 4, pp. 137-139. Larval holotype, 12 larval paratypes. 5578.

Cheladonta ouachitensis Lipovsky, Crossley & Loomis, 1955, Jour. Kans. Ent. Soc., vol. 28, no. 4, p .139. Larval holotype, 13 larval paratypes. 5410.

Euschöngastia cynomyicola Crossley & Lipovsky, 1954, Proc. Ent. Soc. Wash., vol. 56, no. 5, pp. 240-243. Larval holotype. 5564.

Euschöngastia diversa Loomis, 1956, Univ. Kans. Sci. Bull., vol. 37, pt. 2, no. 19, pp. 1337-1340. Larval lectotype (Loomis, 1962, Jour. Parasitol., vol. 48, p. 154). 5571.

Euschoengastia eadsi Loomis & Crossley, 1963, Acarologia, vol. 5, no. 3, pp. 372-374. Larval holotype, 1 larval paratype. 6325.

Euschöngastia finleyi Crossley, 1955, Jour. Parasitol., vol. 41, no. 3, pp. 289-291. Larval holotype. 5566.

Euschöngastia jonesi Lipovsky & Loomis, 1954, Jour. Parasitol., vol. 40, no. 4, pp. 407-410. Larval holotype. 5558.

Euschöngastia loomisi Crossley & Lipovsky, 1954, Proc. Ent. Soc. Wash., vol. 56, no. 5, pp. 243-246. Larval holotype. 5565.

Euschöngastia trigenuala Loomis, 1956, Univ. Kans. Sci. Bull., vol. 37, pt. 2, no. 19, pp. 1343-1345. Larval lectotype (Loomis, 1962, Jour. Parasitol., vol. 48, p. 154). 5570.

Fonsecia palmella Brennan & Loomis, 1959, Jour. Parasitol., vol. 45, no. 1, p. 62. Larval holotype, 6 larval paratypes. 6323.

Hannemania multifemorala Loomis, 1956, Univ. Kans. Sci. Bull., vol. 37, pt. 2, no. 19, pp. 1247-1250. Larval holotype, 23 larval paratypes. 6324.

Neoschöngastia brennani Crossley & Loomis, 1955, Ent. News, vol. 66, pp. 114-117. Larval holotype. 5567.

Pseudoschöngastia farneri Lipovsky, 1951, Jour. Kans. Ent. Soc., vol. 24, no. 3, pp. 100-102. Larval holotype, 8 larval paratypes. 5363.

Pseudoschöngastia hungerfordi Lipovsky, 1951, Jour. Kans. Ent. Soc., vol. 24, no. 3, pp. 95-99. Larval holotype, 46 larval paratypes. 5362.

Speleocola tadaridae Lipovsky, 1952, Jour. Kans. Ent. Soc., vol. 25, no. 4, pp. 134-137. Larval holotype. 5559.

Trombicula arenicola Loomis, 1954, Univ. Kans. Sci. Bull., vol. 36, pt. 2, no. 13, pp. 930-933. Larval holotype, 29 larval paratypes. 5555.

Trombicula breviseta Loomis & Crossley, 1963, Acarologia, vol. 5, no. 3, pp. 374-376. Larval holotype, 1 larval paratype. 6326.

Trombicula crossleyi Loomis, 1954, Univ. Kans. Sci. Bull., vol. 36, pt. 2, no. 13, pp. 920-922. Larval holotype, 24 larval paratypes. 5551.

Trombicula (Neotrombicula) finleyi Kardos, 1954, Univ. Kans. Sci. Bull., vol. 36, pt. 1, no. 4, pp. 88-90. Larval holotype, 1 larval paratype. 5373.

Trombicula fitchi Loomis, 1954, Univ. Kans. Sci. Bull., vol. 36, pt. 2, no. 13, pp. 926-928. Larval holotype, 53 larval paratypes. 5553.

Trombicula gurneyi campestris Loomis, 1955, Univ. Kans. Sci. Bull., vol. 37, pt. 1, no. 9, pp. 258-260. Larval holotype, 22 larval paratypes. 5576.

Trombicula (Euschöngastoides) hoplai Loomis, 1954, Univ. Kans. Sci. Bull., vol. 36, pt. 2, no. 13, pp. 924-926. Larval holotype, 23 larval paratypes. 5552.

Trombicula kansasensis Loomis, 1955, Univ. Kans. Sci. Bull., vol. 37, pt. 1, no. 9, pp. 260-262. Larval holotype. 5577.

Trombicula kardosi Loomis, 1954, Univ. Kans. Sci. Bull., vol. 36, pt. 2, no. 13, pp. 929-930. Larval holotype, 25 larval paratypes. 5554.

Trombicula (Eutrombicula) lipovskyana Wolfenbarger, 1952, Ann. Ent. Soc. Amer., vol. 45, no. 4, pp. 660-666. Larval holotype, 10 larval paratypes. 5372.

Trombicula (Neotrombicula) loomisi Kardos, 1954, Univ. Kans. Sci. Bull., vol. 36, pt. 1, no. 4, pp. 85-87. Larval holotype, 3 larval paratypes. 5375.

Trombicula merrihewi Loomis & Lipovsky, 1954, Jour. Kans. Ent. Soc., vol. 27, no. 2, pp. 51-53. Larval holotype, 40 larval paratypes. 5557.

Trombicula ornata Loomis & Lipovsky, 1954, Jour. Kans. Ent. Soc., vol. 27, no. 2, pp. 47-51. Larval holotype, 39 larval paratypes. 5556.

Trombicula trisetica Loomis & Crossley, 1953, Jour. Kans. Ent. Soc., vol. 26, no. 1, pp. 32-34. Larval holotype, 13 larval paratypes. 5374.

Trombicula (Leptotrombidium) twentei Loomis, 1954, Univ. Kans. Sci. Bull., vol. 36, pt. 2, no. 13, pp. 922-924. Larval holotype, 8 larval paratypes. 5550.

Trombiculidae—Paratypes

Acomatacarus arabicus Radford. 1 larval. 5562.
Acomatacarus lawrencei Radford. 1 larval. 5561.
Acomatacarus thallomyia Radford. 1 larval. 5585.
Acomatacarus tubercularis Brennan. 1 larval. 5593.
Chatia setosa Brennan. 1 larval. 5594.
Euschöngastia africana Radford. 1 larval. 5575.
Euschöngastia campi Brown & Brennan. 2 larval. 5589.
Euschöngastia cordiremus Brennan. 1 larval. 5590.
Euschöngastia hamiltoni Brennan. 1 larval. 5588.

Euschöngastia luteodema Brennan. 1 larval. 5591.
Euschöngastia pipistrelli Brennan. 1 larval. 5599.
Eutrombicula lumsdeni Radford. 1 larval. 5584.
Hannemania hegeneri Hyland. 2 larval. 5681.
Neoschöngastia kohlsi Brennan. See *N. paenitens* Brennan.
Neoschöngastia moucheti Brennan. 1 larval. 6287.
Neoschöngastia paenitens Brennan, new name for *N. kohlsi* Brennan, preoccupied. 1 larval. 5592.
Neotrombicula saperoi Radford. 1 larval. 5582.
Pseudoschöngastia guatemalensis Brennan. 1 larval. 5587.
Pseudoschöngastia occidentalis Brennan. 1 larval. 5586.
Schöngastia guyanensis Floch & Abonnenc. 1 larval. 6288.
Schöngastia haddowi Radford. 1 larval. 5583.
Trombicula aplodontiae Brennan. 1 larval. 5598.
Trombicula brevitarsa Radford. 1 larval. 5563.
Trombicula canis Floch & Abonnenc. 1 larval. 5568.
Trombicula hoogstraali Radford. 1 larval. 5573.
Trombicula jamesoni Brennan. 1 larval. 5597.
Trombicula (Neotrombicula) jewetti Brennan & Wharton. 2 larval. 5596.
Trombicula (Trombiculindus) kansai Jameson & Sasa. 1 larval. 6328.
Trombicula knighti Radford. 1 larval. 5581.
Trombicula montanensis Brennan. 1 larval. 5600.
Trombicula mounti Radford. 1 larval. 5569.
Trombicula scottae Brennan. 3 larval. 5595.
Trombicula texana Loomis & Crossley. 1 larval. 6327.

Trombidiidae

Neotrombidium tricuspidum Borland, 1956, Jour. Kans. Ent. Soc., vol. 29, no. 1, pp. 30-35. Larval holotype. 5572.

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THE LIFE CYCLE AND SOCIAL ORGANIZATION OF BEES OF THE GENUS *Exoneura* AND THEIR PARASITE, *Inquilina* (Hymenoptera: Xylocopinae)

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Charles D. Michener

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The Life Cycle and Social Organization of Bees of the Genus *Exoneura* and their Parasite, *Inquilina* (Hymenoptera: Xylocopinae)[1]

By

Charles D. Michener[2]

This paper consists of an account of biological observations on several species of bees of the genus *Exoneura* and on their social parasite and close relative, *Inquilina*. These bees belong to the same section of the xylocopine tribe Ceratinini as the genera *Allodape, Allodapula, Exoneuridia,* etc. This group of genera is virtually restricted to Africa and the Indo-Australian region and is well known as the only group of bees other than *Apis* and *Bombus* which practices progressive feeding of the larvae.

GENERAL ACCOUNT OF THE LIFE HISTORY OF *EXONEURA*

Sakagami (1960) has given a review of the biology of this group of genera, most of which make their nests in hollow or pithy dry stems. The nests of most *Exoneura* are burrows through pith or rotting stems that are as soft as pith. Sometimes they clean the pithlike frass out of beetle burrows in wood (Rayment, 1935) or nest in cavities in galls (Rayment, 1951) but probably most species do not habitually occupy beetle burrows as does *Allodapula* in Australia (Michener, 1962). However, nests of three species have been recorded from beetle burrows in solid fence posts and spars (Rayment, 1954).

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Beetle burrows in branches and twigs are also used (e.g., Rayment, 1956) by some species. Data on the related genus or subgenus *Exoneurella* are presented elsewhere (Michener, 1964).

Exoneura makes no separate cells, all young being reared together in the burrow. Rayment's early (1935) references to cell partitions are in error. I never saw the threads on the walls of the nest tubes reported by Rayment (e.g., 1951).

Nest entrances are regularly constricted, either being excavated in that way or narrowed by a constructed collar made of bits of the material removed from the burrow. The narrow entrance is important in defense of the nest. At a small disturbance, a female in the nest may bite at an intruder or a fine fiber held at the nest entrance, but usually she quickly turns and blocks the hole firmly with the flattened dorso-apical part of the abdomen. The females also secrete from the mouth region, seemingly from the mandibular glands, a brown liquid having the odor of tenebrionid or carabid beetles. They emit this material either at the nest or, if captured or greatly disturbed, away from the nest. On one occasion I found females of *E. bicolor* so common (11 miles south of Uralla, New South Wales, on November 5, 1958) visiting the flowers of *Daviesia latifolia* that when the bushes bearing the flowers were beaten with a net, the odor could be perceived several feet away.

The effectiveness of adult females in defending their nests is shown by a series of nests of *E. variabilis* set up for observation in Brisbane. Within a day those containing no adults were robbed of all immature stages by ants. Those containing adults mostly survived for many days.

Eggs of most species are laid in a mass (usually criss-crossed) at the bottom of the burrow, not attached to the burrow walls. However, in some species the eggs are attached by their posterior ends to the wall of the burrow and project into the lumen of the nest (Rayment, 1948, 1951; Erickson and Rayment, 1951; and *E. aterrima* discussed below). In some cases such attached eggs are placed in a row; in other cases they are scattered about on the inner nest wall. The duration of the egg stage was not determined by me but is obviously long enough that numerous eggs (10 or more) may accumulate in a single nest, probably laid by a single female, before the first ones hatch. The ovaries mature only one egg at a time, as in most bees, although three or four may be nearly mature (Figs. 77, 78). Rayment (1948) showed that at the temperatures of late winter in Sydney the egg stage lasted between two and three weeks.

Larvae hatching from loose eggs remain in a cluster at the bottom of the nest until they grow large enough to maintain a position above the bottom. Larvae hatching from attached eggs may retain their positions on the nest walls for a time and may be fed pollen in this position.

The larvae are fed progressively with pollen mixed with a liquid (nectar?)

to form a rather sticky but firm mass. Sometimes more than one larva feeds from a single mass and this may be the usual way of feeding small larvae lying in groups. Larger and sometimes even the smallest larvae (e.g., in *E. aterrima,* see below) are fed by individual pollen masses placed on their venters. Even within a species the manner of feeding varies, as was noted for *E. variabilis* (see below) and for *E. roddiana* by Rayment (1948), who observed both communal and individual pollen stores, depending on the arrangement of the larvae in the nest.

At any one time the number of larvae having pollen supplies on which to feed is small. For example, in one group of nests of *E. variabilis* (see below) only eight larvae out of 74 had food available when the nests were opened. Rayment (1951) showed that in 17 nests of *E. richardsoni* containing 209 larvae, only six nests contained food and these had a total of only 23 pollen masses.

Rayment has repeatedly (1946c, 1951; Erickson and Rayment, 1951) described the feeding of larvae, especially young ones, by a liquid from the mouthparts of females which he stated was "pap" from the pharyngeal glands. The scarcity of larvae feeding on pollen supports this idea. However, the long larval life suggests sporadic feeding. Moreover, the finding of very young larvae feeding on pollen indicates the inaccuracy of the idea that young larvae must be fed only liquid. (For *E. aterrima,* see below; for *E. angophorae, asimillima, richardsoni,* etc., see Rayment, 1951, in which publication pollen is reported among the eggs and very small larvae lying in a cluster at the bottom of the nest.) Disturbed adults often move the larvae about in the nest with their jaws and mouth the larvae; such movements might simulate feeding and cause erroneous accounts of feeding. Feeding of larvae by glandular secretion (or by other liquid from the mouth of the adult) requires verification, although it seems probable in view of the detailed accounts of Rayment.

The young larvae lack ventrolateral lobes but have strong subspiracular ridges (Figs. 4, 53, and 57). Ventrolateral lobes appear on the mesothorax in the penultimate larval stage and exist on most segments in the ultimate larval stage. The mesothoracic arms are much the largest of such lobes (Syed, 1963). As described below for *E. variabilis,* these lobes (arms, or pseudopodia) are partially retractile in the last larval stage but shrivel in the prepupal part of the last stadium. Rayment (1948) appears to have been correct in regarding these lobes as non-secretory protuberances. His subsequent certainty (e.g., 1951) that they have secretory importance is not supported by my observations of their external and internal structure. As Rayment said, the mesothoracic arms are often mouthed and chewed by larvae but so are any other small soft objects which the larvae can reach. This activity therefore does not indicate any exudation. In contrast to *Allodapula* (Michener, 1962), larvae of *Exoneura* are constantly active, bending about as though reaching for something. Immature stages generally lie roughly in order of youngest at the bottom to oldest near the entrance of a nest. Food, therefore, has to be carried past a series of pupae and prepupae to the larvae which are being fed. Feces are produced while larvae are still feeding (Rayment, 1951) and must be carried out of the nest by adult bees.

The duration of the immature stages is not well known but is long, as Rayment clearly showed. Rayment (1951) thought that development from egg to adult of *E. rufitarsis* and *richardsoni* required from early July (midwinter) to early December (early summer). He also showed (1948) that both larvae and adults could survive up to 90 days closed in a container without food, and Erickson and Rayment (1951) showed survival of adults for over 100 days at 10°C. Thus survival of both larvae and adults during periods of drought when flowers are scarce and during the winter is not surprising. Overwintering of larvae certainly occurs (Rayment, 1946b, 1951). It is probable in some of the species discussed in detail below. However, the principal way of overwintering is by means of fertilized adult females. Often several females overwinter together. In the spring new colonies are commonly established by single females (*E. variabilis,* see below; *E. concinnula,* see Rayment, 1951). Sometimes, however, two or more adult females are present in nests in spring (*E. illustris,* see Erickson and Rayment, 1951; *E. richardsoni,* see Rayment, 1951). Whether or not supernumerary females later disperse from such nests, leaving monogynous colonies, is not known, but in *E. variabilis* such dispersal is suggested by the polygynous October (early spring) nests and the largely monogynous November nests. Some species maintain more nearly continuous reproductive activity than does *E. variabilis,* as is quite clearly the case for *E. roddiana, concinnula,* and *rufitarsis* which had many eggs in their nests in July (midwinter) (Rayment, 1951).

At least in summer many nests contain two ore more adult females. Large groups usually consist in part of young individuals which have not yet dispersed, but as many as three or four females may be long term inhabitants of a nest. Such groups, as will be shown in detail later, commonly consist of one or sometimes two egg layers[3] and one or more workers. The important role of workers in pollen collecting has been shown by Michener (1963). Further information on the division of labor and social organization is presented in the body of this paper and in brief form, in the summary.

Rayment (1951) described males as guarding nests, leaving and returning to them, and in short constituting a significant part of the society. His observations were probably made in winter and early spring when low temperatures presumably prolong all activities. Data obtained by me show that males

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[3] I have not used the word queens, because so many of the nests at least in the species I studied contained only one female, which was like the egg layer in nests containing more than one female.

are produced in rather large numbers but after reaching maturity stay in nests for much shorter periods of time than females, so that adult nest populations are predominantly female. Presumably under warm conditions males leave the nests and soon mate and die.

A swarm of males of *E. hamulata* was found about noon of April 5, 1959, on Noosa Hill in Noosa National Park, Queensland. A few hundred males were flying about in the sun between large bushes, sometimes only two or three in a place, sometimes 25 forming a loose flying swarm. The bees never seemed to alight but remained in flight continually. No females were seen, but I have little doubt about this being a mating swarm. Probably only those species with large eyed, hairy males indulge in such swarming.

METHODS

The principal method used was to collect nests, plug the entrances in the field, bring them to the laboratory, and preserve for study the entire contents of each nest. Nests were mostly taken in early morning, late afternoon, or on cool or rainy days when all the bees would presumably have been in their nests.

Each female bee was examined using the methods described by Michener, Cross, Daly, Rettenmeyer and Wille (1955). The wings of *E. variabilis* do not often become much worn. The number of nicks on the forewing margins was recorded in the belief that it provides some rough index of previous flight activity. For purposes of the present paper, these data are given as unworn (no nicks), slightly worn (1 to 5 nicks in total on both wing margins), well worn (6 to 10 nicks in total on both wing margins), and much worn (11 or more nicks in total). The last category was very rare. Mandibular wear was rather slight and recording of it was abandoned.

Spermathecae were never found partially empty and it seems probable that once mated, a female retains a supply of sperm for life.

For the ovaries, the maximum width of each was measured as well as the length of the longest developing egg. The average width of the two ovaries is correlated with the length of the longest developing egg (see figure 1), and the latter has been used in the following sections of this paper on the theory that it better represents the reproductive activity of the female concerned (see also figures 65 to 82).

For convenience in expression, ovaries with the longest oocyte 0.50 mm. long or longer are considered to be enlarged in the discussions which follow. As can be seen from figure 1, this means enlargement beyond the initial stages common among slender ovaries.

The whitish areas noted in the section on ovaries of *E. variabilis* were used as an aid in judging age and egg laying by bees in the latter part of the study, after their meaning was realized.

In the following discussions the words "adult" or "female" always mean adult female except when otherwise specified. Callow adults are those showing paler coloration than mature adults. The youngest callows have milky wings but the wings harden and become transparent long before full colora-

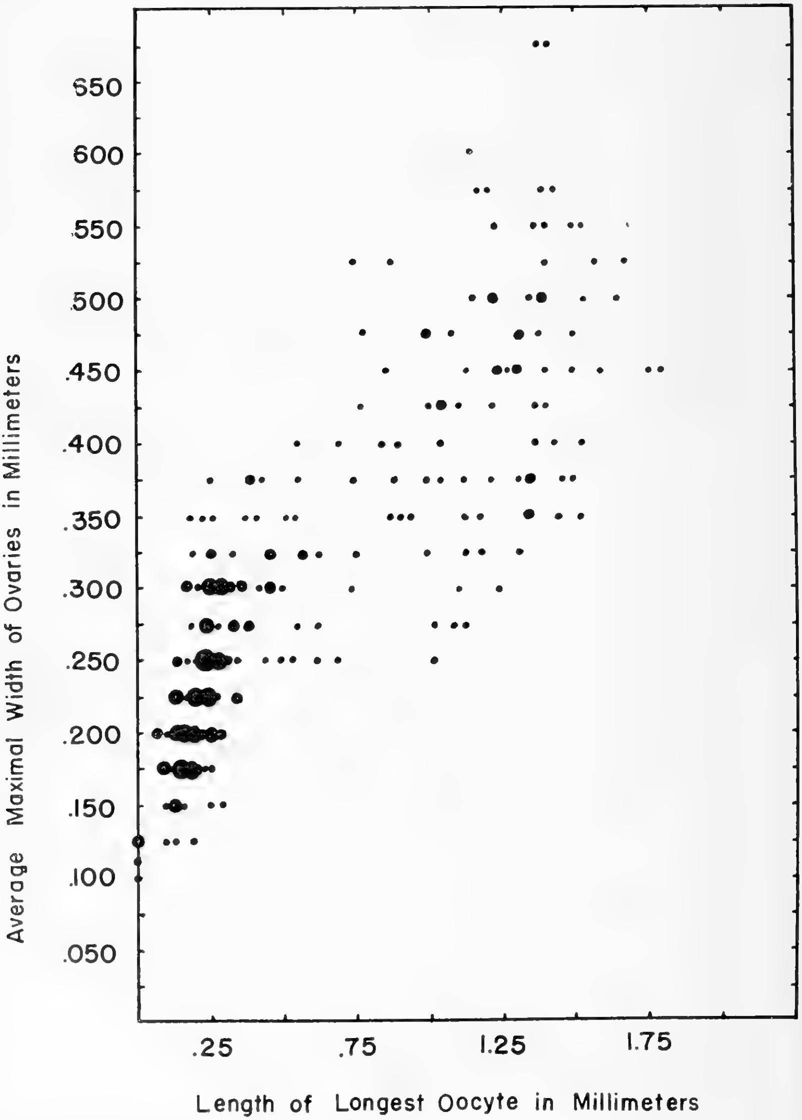

FIG. 1. Scatter diagram showing relations between ovarian width (maximum width of each ovary measured and averaged for each individual) and length of the longest oocyte in *Exoneura variabilis.* Small dots represent one individual; numbers of individuals represented by larger dots may be estimated by their diameters.

tion of the body is attained. Callows are unfertilized, with unworn wings, and with regularly formed, slender ovaries (longest oocyte less than 0.22 mm.) having no whitish areas in the bases or stalks. Fully colored but otherwise similar females are also considered as young but are not recorded as callows, being listed as mature adults.

EXONEURA VARIABILIS RAYMENT

Habitat: Observations were all made in southeastern Queensland. Nests were found in large numbers at the margins of the rain forest areas which occur on the higher mountains of this region. None was found in *Eucalyptus* savanna or in the depths of the rain forest, but breaks in the forest caused by roads as well as natural forest margins provided suitable habitats.

The localities where series of nests were taken for study are as follows: (1) roadside at summit of Cunningham's Gap, near Mount Edwards (October 3, November 9, December 27, February 25); (2) forest margins in Lamington Naional Park, near Binna Burra, in the McPherson Range (December 8, January 11-13); and (3) roadside and forest margins on Tamborine Mountain, on the side nearest to the town of Tamborine (December 18, February 15, March 22).

Nests: From the localities and dates listed above, 233 nests or at least burrows occupied by one or more *Exoneura variabilis* were opened for study. A few of these were merely burrows in which bees were resting, or were probably nests in the process of excavation, but 221 were nests in later stages of development.

The nests are simple burrows in broken or cut, standing, dry, pithy stems of bushes, brambles, or vines. Rarely, they are in stems that are soft because of rotting rather than because of pithyness. The holes are obviously made by the bees themselves, as in most other *Exoneura* and in contrast to species of *Allodapula* (see Michener, 1962). They enter the stems at the broken or cut ends. In slender stems the burrows are nearly straight while in thick stems with much pith the burrows are often sinuous. The stems are typically erect and the nests more or less vertical, but they often also occur in slanting, horizontal, or even hanging stems. In the last case, the entrance is the lowest part of the nest. Such orientation is especially common in roadside bushes of *Lantan*a whose dead stems have been cut or broken.

Plants utilized for nesting sites were the following: *Rubus rosaefolius* (most nests at Cunningham's Gap, many at Binna Burra, few at Tamborine Mountain), *Lantana camara* (most nests at Tamborine Mountain, few at Binna Burra), *Eupatorium adenophorum* and *Plectranthus graveolens* (many from each at Binna Burra), *Homalanthus populifolius* (some from Tamborine Mountain), *Erigeron* (few from Cunningham's Gap), *Deeringia baccata* (few from Binna Burra), cultivated *Hydrangia* (one from Binna Burra), dead stems of rain forest vines (few from Binna Burra), and rotten stems of various plants (few from Binna Burra). Rayment (1949b) recorded a nest from a dead stem of a "reedy grass or sedge."

A few nests in *Lantana* and *Deeringia* were excavated through the dry portions of the stems and terminated at the beginning of moist living material. The same phenomenon was common in nests of *Exoneurella lawsoni* (Rayment) (see Michener, 1964) and was shown to influence the length of the burrows. These few nests of *Exoneura variabilis* in such stems were excluded from consideration in the following paragraphs on nest size and growth although all of them are within the extremes noted for nests in dry stems. No significant correlation was noted between nest measurements and the kind of stem in which the nest was located.

The nests are burrows 2.0 to 3.0 mm. in diameter. The mean of 140 measurements of burrow diameters is 2.5 mm. At the entrances the burrows are narrowed to 1.5 to 1.6 mm. in diameter. The burrows are excavated with narrow entrances. However, if an entrance is artificially enlarged or if the apex of a stem, including the constricted part of a burrow, is broken off, the *Exoneura* narrows the entrance by means of small pieces of pith stuck to each other and to the wall of the burrow near the entrance. Often such pieces of pith can be noted at nest entrances not altered in any way by an experimenter.

Nests in dead, dry twigs or stems and containing immature stages were 24-295 mm. in depth. The nests are seemingly deepened during the time that the young are being reared and the nest reused, as shown by the following data: Nests containing a single adult female and eggs or small larvae but no older immature stages ranged from 24-190 mm. in depth, mean 70.6 ± 8.65 mm. ($n=32$). Older nests, containing a single adult female and immature stages up to pupae, but no young adults, were 25-260 mm. in depth, mean 83.2 ± 5.95 mm. ($n=71$). Still older nests containing more than one adult or containing a young egg layer and also older immatures apparently her sisters (i.e., nests whose use is continuing beyond the brood of the founding female) ranged from 38-290 mm. in depth, mean 118.4 ± 11.41 mm. ($n=33$). Differences in depth between the latter group of nests and each of the others are significant ($p < .01$) but the differences between the first two is not ($.50 < p > .10$).

A few nests were found which contained larvae or pupae and at the same time had loose bits of pith outside the entrances; this observation corroborates the statistical evidence that pith is sometimes and perhaps regularly removed from the bottom of a nest and pushed past the brood and out the nest entrance by adult bees with resulting lengthening of the burrow.

Seasonal variation in nest depth was suggested, but the differences between seasons were not significant. Nests in October and November were

24-143 mm. in depth, mean 79.5±9.84 mm. (n=13). In February and March depths were about the same, 25-295 mm., mean 78.0±9.58 mm. (n=28). In summer, however, nests seemed deeper, 25-260 mm. in December and January, mean 95.3±6.12 mm. (n=95).

Life History Data: Group 1. This species was first encountered by me at Cunningham's Gap in the spring, on October 3, 1958. Nine nests were found; in them were 17 adult females and no adult males. Three of the nests contained only one adult; all of these lacked immature stages and were presumably excavated for establishment of new nests. The remaining six nests contained two or three adults each and five of them contained larvae, four to six each, mostly small; middle sized and large larvae were present in only one nest. Since there were no eggs nor pupae, I thought at first that these larvae had passed the winter in the nests and did not hatch from eggs early in the spring.

At least 65 percent of the females taken from the nests in October, including all that were alone in their nests, contained no sperm cells in the spermathecae. In all but two the largest developing egg was less than 0.45 mm. long; one was 1.00 and another 1.38 mm. in length. Most of the females, therefore, were unfertilized with scarcely enlarged ovaries, and most did not show any wing or mandibular wear. These data are in various ways confusing. If they represent an overwintered population, there should be adult males to fertilize at least the isolated unfertilized females; also they do not correspond with data from the overwintering fall populations (groups 8 and 9) which were studied in much larger numbers and which included no young larvae, very few mature ones, and few unfertilized females. It is my tentative supposition that the high percentage of unfertilized females and the lack of eggs represent sampling errors (the sample size was small) and that the young larvae found in five of the nests hatched from eggs laid in September.

Group 2 consists of 11 nests from the same locality taken on November 9. Each contained only a single adult female, except for one with two. Immature stages were absent in three of the nests. In one nest, the only immature individual present was a single prepupa. In one nest there were seven small larvae and five eggs. In the remaining six nests there were two to 11 (average 5.5) eggs and no other young. The nest with two adult females was the one with 11 eggs.

All of the adults that were successfully dissected (9) were fertilized. Those with eggs in the nest had enlarged ovaries with the longest oocyte 1.00 mm. or longer. Those without eggs had more slender ovaries with the longest oocyte .035-0.50 mm. in length. Of the 12 females, eight had one or more nicks in the wings and two were much worn.

Clearly conditions had changed since the preceding month, most of the females being alone, fertilized, and in egg laying condition.

TABLE 1. *Exoneura variabilis.* Numbers of Young and Adults in Nests of Group 3, taken on December 8. (Each horizontal row represents a nest. Nests without immature stages or with only eggs were omitted. Under adults C=callows. "I" indicates the parasitic bee, *Inquilina.*)

Nest No.	Eggs	Small Larvae	Medium Larvae	Large Larvae	Prepupae	Pupae	Total Young	Adult ♀♀	Adult ♂♂
274	3	1	..	..	..	..	4	1	..
300B	2	2	..	..	..	..	4	1	..
287	2	1	1	2	..	..	6	1	..
276	..	..	..	..	..	7	7	1+1I	..
269	..	..	..	..	2	..	2	1	..
278	..	..	..	2	4	..	6	1	..
280	..	..	..	1I	2I?	2	5	1	..
285	..	..	..	2	..	..	2	1	..
294B	..	..	2	..	..	..	2	1	..
297B	..	..	..	1	..	..	1	1	..
303B	..	..	..	..	1I	11I	12	2	..
304B	..	..	2	..	..	..	2	1	..
310B	..	..	..	3	3	1	7	1	..
311B	..	..	..	2	..	1	3	1	..
312B	..	..	..	2	..	1	3	1	..
317B	..	..	2	2	..	..	4	2	..
321B	..	..	..	..	..	1	1	2+1C	1C
322B	..	..	2	..	..	..	2	2	..
318B	..	2	..	..	..	..	2	1	..
273	4	..	..	..	..	..	4	2	..
272	7	3	..	..	..	..	10	2	..
270	13	..	..	..	..	7	20	1	..
275	11	3	3	..	..	..	17	2	..
281	..	1	2	..	..	..	3	1	..
286	5	..	..	..	..	3	8	1	..
288	10	..	..	2	1	3	16	3	..
289	..	1	..	1	..	..	2	1	..
296B	3	..	..	..	..	1	4	1+2C	..
298B	6	4	..	2	..	..	12	3	..
301B	2	4	..	4	2	..	12	2+2C	..
302B	2	..	..	..	4I	16I	22	3+1I	..
306B	11	8	..	1	..	4	24	2C	4C
308B	1	1	..	7	1	14	24	5+1C	5C
314B	20	..	..	..	..	10	30	2+4C	3C
315B	11	6	6	8	3	6	40	3+10C	10C
316B	6	..	..	..	1	5	12	2	..
319B	1	2	2	..	..	..	5	1	..

Group 3 consists of 44 nests taken at Binna Burra on December 8. Of these, four were only burrows without immature stages, three of them only 10 to 18 mm. deep, apparently being excavated. Each contained a single fertilized adult female, two with slender and two with enlarged ovaries.

Three of these four bees showed some wear of the wing margins. Apparently new nests were being established at this season.

Three other nests had progressed somewhat farther and contained one to four eggs each but no other young. A single adult female was in each of these nests; all three were fertilized, one had enlarged ovaries while two had slender ovaries, one showed some wing wear.

The contents of the remaining 38 nests in Group 3 are indicated in Table 1. Nests 274, 300B, and 287 were like those discussed in the preceding paragraph except that some of the eggs had hatched. The majority of the nests were older and their interpretations more complex, as indicated below.

Several nests (269-322B) contained only older larvae or pupae. Except for 303B, 317B, 321B, and 322B, these contained only one adult, which had been fertilized. About half of these females were unworn; the remainder showed wing wear. The ovaries were slender (longest oocyte 0.18-0.28 mm.) except for 276 and 310B which had swollen ovaries (longest oocyte 1.23 and 1.00 mm.). Presumably at least some of these adult females were of the same generation as the immature stages; others may have been mothers of the immatures in their nests. Those with enlarged ovaries would presumably soon have laid eggs, so that their nests would have been similar to those discussed below with young as well as old immature stages. Nest 322B contained two adults, both fertilized and with worn wings, one with slender ovaries, one with rather enlarged ovaries (longest oocyte 0.78 mm). Nest 303B contained two adults, both unfertilized, with very slender ovaries, and worn wings. Nest 317B also contained two adults, one fertilized and unworn, one unfertilized with worn wing margins (worker). Both had slender ovaries. Nest 275 contained two adults; their spermathecae were lost in dissection; both had worn wings; one had slender, the other enlarged ovaries.

The remaining nests contained immatures of various ages, often young ones (eggs or small larvae) and older ones (prepupae, pupae, or callow or young adults) with few intermediates. For example, nests 272 and 273 contained eggs and young larvae as well as unworn adults with very slender ovaries without whitish areas; in addition 273 contained a fertilized, well worn adult with more robust ovaries (longest oocyte 0.55 mm.) with whitish areas in the stalks. The latter individual must have laid the eggs and could have been also the mother of the young adult. As shown in Table 1, most of the nests (numbers 272-319B) had a larger number of immature stages than did 273. One of these nests (306B) contained only callow adults and another (272) only young adults with slender ovaries. In spite of the eggs, no old adults were in these nests. Presumably they had died by the time I opened the nests. Nests 273, 281, 286, 288, 289, 296B, 315B, and 319B contained only one mature adult each. (In nests 288 and 315B, two of the three adults shown in Table 1 were probably young, perhaps only slightly older than those recognized as callows. Perhaps they were workers.) These mature adults were fertilized; those in nests 273, 286, 288, and 315B had worn wing margins and swollen ovaries (longest oocyte 0.55-1.42 mm.) while those in nests 281, 289, 296B, and 319B had unworn wings and slender or slightly enlarged ovaries (longest oocyte 0.17-0.87 mm.). Those having the longest oocytes, 0.87 mm. or longer, had eggs in the nests; the others (except for 273 in which the longest oocyte was 0.55 mm.) did not. Probably only the worn individuals, and perhaps not all of them, were mothers of the older immatures in the nests. The other nests (298B, 301B, 302B, 308B, 314B, and 316B) contained two or three seemingly mature adults each. In 298B and 301B, the mature females were all fertilized; one in each nest had somewhat enlarged ovaries (longest oocyte 0.55 and 1.08 mm.) and worn wing margins, the others had slender ovaries and unworn wings. Nests 302B, 314B and 316B had ovaries of all mature females enlarged (longest oocytes 1.03 to 1.70 mm.). All were fertilized except one in 302B. Most showed wing wear but one each in 314B and 316B did not. The five mature females in 308B included two with swollen ovaries (longest oocytes 0.70 and 1.35 mm.) and worn wing margins which were probably fertilized. The other three had slender ovaries. One was unfertilized with worn wings, one fertilized with worn wings, and one fertilized with unworn wings.

Group 4 consists of 35 nests taken at Tamborine Mountain on December 18. Of these, one was only 11 mm. deep and contained only an unfertilized, unworn adult with slender ovaries. One lacked immature stages but contained an unworn adult with large ovaries, probably ready to start laying. Another contained a similar but somewhat worn adult. Three nests contained two, four, and five eggs respectively but no other young, and a single fertilized adult with large ovaries (longest oocytes 1.13 and 1.3 mm.) was in each; one had unworn wings, another slightly worn wings, and the third had much worn wings as though she had had some other activity before laying the few eggs observed. Such a bee might come from a nest that had been destroyed, or might be a worker that later became a reproductive.

Two nests lacked immature stages entirely but contained two and four adults respectively. Each contained one fertilized adult with somewhat enlarged ovaries (longest oocyte 0.75-1.20 mm.); the others were unfertilized with slender or slightly enlarged ovaries (longest oocytes 0.23-0.63 mm.). The wings were unworn or nearly so. Presumably these were adults of the same brood, reared in these nests. In each nest the fertilized bee would presumably soon have started laying; the others might have dispersed or remained as workers.

The contents of the remaining nests in Group 4 are indicated in Table 2. Nest 311T seems to have passed just beyond the stage of those discussed in the preceding paragraph in that eggs had been laid. One adult, the egg layer, was fertilized with enlarged ovaries (longest oocyte 1.23 mm.) while the other was unfertilized with slender ovaries and must have been a worker. Both had worn wings.

The nests listed as 297T to 326 in Table 2 contained only older larvae and pupae. In those containing only one female (297T, 308T, 324, 326), she was fertilized, and except for 324, had much enlarged ovaries (longest oocyte 1.13-1.50 mm.), suggesting that egg laying was about to begin. Nests with two adult females (302T, 318T) contained one adult each that was fertilized with enlarged ovaries (longest oocyte 0.63 mm.) and one each that was unfertilized with slender ovaries. The first would presumably have soon started egg laying while the second, probably a sister in each case, would have remained as a worker or perhaps left to start a new nest.

Table 2. *Exoneura variabilis.* Numbers of Young and Adults in Nests of Group 3, taken on December 18. (Each horizontal row represents a nest. Nests without immature stages or with only eggs were omitted. Under adult females, C=callows. "I" indicates the parasitic bee *Inquilina*.)

Nest No.	Eggs	Small Larvae	Medium Larvae	Large Larvae	Prepupae	Pupae	Total Young	Adult ♀♀	Adult ♂♂
311T	6	..	..	..	..	..	6	2	..
297T	..	..	..	..	..	3	3	1	..
302T	..	..	..	4	..	..	4	2	..
308T	..	..	..	1	..	6	7	1	..
318T	.	..	..	..	..	3	3	2	1
324	..	..	..	1	1	..	2	1	.
326	..	..	..	..	..	3	3	1	..
305T	..	..	1	2	..	..	3	1	.
313T	5	2	..	..	..	4	11	1	..
321T	5	..	..	..	..	2	7	1	..
322T	4	..	..	..	..	1	5	1	..
323	3	..	..	..	..	2	5	1	..
293T	2	7	1	..	..	..	10	6	..
294T	1	..	3	3	..	..	7	3	..
298T	8	3	..	..	3	7	21	4	..
301T	2	1	..	6	..	..	9	4	..
303T	8	..	..	2	..	3	13	2+1I	.
307T	3	1	..	..	..	4	8	2	..
310T	6	2	1	6	..	..	15	5+1C	1
314T	8	..	1	1	..	1	11	2	..
317T	2	..	..	1	..	1	4	2	..
319T	3	2	3	..	..	..	8	2	..
320T	6	3	2	..	..	..	11	5	..
325	8	4	2	..	1	..	15	3	..
316T	10	2	..	2	2	5	21	2	..
304T	1	..	..	8I	..	..	1+8I	3+1I	.
328	9	2	..	2	1	5	19	2	..

Nests 305T, 313T, 321T, 322T, and 323 contained only one adult each. All were fertilized except the one in 313T which was unfertilized, unworn, with slender ovaries, and could not have laid the eggs in the nest. The adult in 305T had slender ovaries and worn wings; the adults in 321T, 322T, and 323 had enlarged ovaries and those in the first two had unworn wings. It is very likely that such unworn individuals and perhaps the others as well are not mothers of the older immature stages in their nests; probably they are their sisters. They are, however, mothers of the eggs, and presumably care for and protect the older larvae and pupae present as well as their own offspring.

Nests 293T to 325 on Table 2 all contained more than one adult. In each case one was fertilized, with large ovaries, and in a few cases with worn wings, while the other individuals were unfertilized, with slender ovaries and usually unworn wings. The unfertilized individuals may function as workers; presumably they are sisters of the egg layer in each nest and also of the pupae and prepupae when present. Nest 316T was similar except that the individual with slender ovaries was fertilized. Nests 304T and 328 contained only unfertilized individuals with slender ovaries which could not have produced the eggs found in those nests.

Group 5 consists of 23 nests. Some were taken from Tamborine Mountain on December 18, established in Brisbane for observation, and opened on December 26; the others were taken at Cunningham's Gap on December 27. Two lacked immature stages and contained one adult each. One of these adults was fertilized, unworn, with enlarged ovaries (longest oocyte 1.18 mm.). The other had slender ovaries but its other characteristics were not ascertained.

Three nests contained one, two, and seven eggs each and no other immature stages. The first two contained one adult each, fertilized, one with worn wing margins, the other unworn, both with enlarged ovaries (longest oocyte 0.90 and 1.35 mm.). The third nest contained two females, both fertilized with well worn wing margins, one with enlarged ovaries (longest oocyte 1.48 mm.), the other with long slender ovaries except for one large oocyte 1.45 mm. in length. The latter, although fertilized, may have been more or less workerlike in function.

The contents of the remaining 18 nests of Group 5 are indicated in Table 3. Nests 331 to 379 in Table 3 contained only older larvae and pupae. Of the two adults in 331, one was fertilized with enlarged ovaries (longest oocyte 1.18 mm.) and the other was unfertilized, unworn, with slender ovaries (longest oocyte 0.15 mm.), probably a worker. Nests 376, 377, and 379 each contained a fertilized, unworn adult with somewhat enlarged ovaries. Probably eggs would soon have been laid; also it seems very probable that these adults were sisters rather than mothers of the pupae and prepupae in their nests.

TABLE 3. *Exoneura variabilis.* Numbers of Young and Adults in Nests of Group 3, taken on December 26. (Each horizontal row represents a nest. Nests without immature stages or with only eggs were omitted. Under adults, C=callows. "I" indicates the parasitic bee *Inquilina.*)

Nest No.	Eggs	Small Larvae	Medium Larvae	Large Larvae	Prepupae	Pupae	Total Young	Adult ♀♀	Adult ♂♂
331	..	..	..	6I	..	..	6I	2	..
376	..	..	..	..	3	..	3	1	..
377	..	..	..	..	2	..	2	1	..
379	..	..	..	..	..	2	2	1	..
374	1	..	..	..	..	2	3	1	..
382	9	1	2	10	..	2	24	1+4C	4C
386	10	5	..	..	1	5	21	1	..
388	2	..	..	..	2	2	6	1	..
329	2	..	1	4	3	..	10	2+2C	..
330	4	3	2	5	1	4	19	2+1I	..
332	5	1	4	2	..	1	13	4	1
373	..	2	2	2	..	..	6	3	..
375	8	5	1	5	..	..	19	6+2C	..
381	7	1	..	..	..	4	12	3+1I	..
385	11	5	..	..	..	4	20	2+1C	..
389	8	..	..	..	..	4	12	2	..
390	8	..	..	..	..	2	10	2	..
391	6	..	..	..	3	1	10	2	..

The remaining nests contained a variety of immature stages. Nests 374, 382, 386, and 388 contained only one adult each (if callows are ignored); in every case this adult was fertilized, with worn wings, and with much enlarged ovaries (longest oocyte 1.50 to 1.68 mm.). Nests 329, 331, 332, 373, 375, and 381 had one fertilized individual with swollen ovaries (longest oocyte 1.18-1.58 mm.) in each. Two had worn wing margins, three did not. The other adults in each of these nests were unfertilized, unworn, with slender ovaries, and in some cases were known to function as workers. Nest 390 was similar except that the probable worker was fertilized, although with slender ovaries. Nests 385, 389, and 391 had two mature adults each, both fertilized; most were worn and all had enlarged ovaries (longest oocyte 0.85-1.52 mm.). Nest 330 contained two unfertilized adults with slender ovaries, one with worn wing margins. Probably both functioned as workers.

Group 6 consists of seven nests taken at Binna Burra, January 11-13. They show no differences from those of Group 5 except that the small number of eggs may be significant. Five of the nests contained eggs, but three contained only one each, the others two each. Only two of the nests contained small larvae, one five, the other one. Correlated with the small number of eggs was the few adults with enlarged ovaries; there were only two. One was in a nest without other adults and with one pupa; presumably the adult would soon have laid eggs. The other was in a nest containing young from the egg to pupal stages and two other adults, unfertilized, with slender ovaries, probably functioning as workers.

Group 7 consists of 31 nests taken at Tamborine Mountain on February 15. The approach of autumn was already obvious. Fourteen of the nests contained no immature stages. Of the 17 remaining nests, only three contained eggs. Two others contained small larvae, so that five or about one sixth of the nests contained eggs or small larvae. Ten contained prepupae or pupae. The number of immature stages, even in nests containing some, was small (1-4) with the exception of three nests. These three contained eggs, small larvae, medium sized larvae, large larvae, prepupae, and pupae respectively, in the following numbers: (nest 421) 0, 0, 0, 3, 4, 15; (nest 443) 5, 5, 3, 3, 1, 0; and (nest 445) 7, 4, 4, 4, 0, 1.

The 31 nests of group 7 contained a total of 50 adults, one to seven per nest. Twenty-two, or nearly half, were unfertilized, the rest fertilized; 14 showed some damage to the wing margins, the others showed no wear. Only five had enlarged ovaries; all five were fertilized but their distribution among the nests was not intelligible. Of the three nests containing eggs only one also contained a bee with enlarged ovaries. Probably the egg layers in the other two had died. The other four adults with enlarged ovaries were in nests with no young or only older larvae or pupae. Two were the only adults in their nests and two were in nests with another adult each.

Apparently fertilized and unfertilized adults with slender ovaries were functioning as workers to feed larvae in most of the nests containing larvae.

Group 8 consists of 13 nests taken at Cunningham's Gap on February 25. One large larva, two dead prepupae, and one pupa were the only immature stages; these were distributed among three nests. Callow adults were present in another nest. Of the 17 adults, about 50 percent were fertilized, six showed worn wings, and none had enlarged ovaries (longest oocyte .25 mm.).

Group 9 consists of 48 nests from Tamborine Mountain taken on March 22. Immature stages were present in only five of these and callow adults in a sixth. Dead parasitized[4] prepupae were present in three others. The youngest immatures were large larvae, of which there was one each in three different nests. The total number of living immatures per nest was one in each of three nests and seven in each of two other nests.

The 70 adults in the 48 nests were from one to six per nest. Twenty two were unfertilized; the rest fertilized; 28 showed worn wing margins, eight of them well worn or much worn; all had slender ovaries (longest oocyte 0.13-.35 mm.).

Summary of Discussion of Life History: The data for groups 8 and 9

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[4] Parasitization was by chalcidoid wasps similar to those recorded by Rayment (1949b).

above show that this species goes into winter primarily as fertilized adult females with slender ovaries. Young immature stages had disappeared by February 25 (late summer) and only a few older larvae and pupae remained. As shown in Table 4, about half of the adult females were worn, showing that many females that had been active earlier were now preparing for overwintering. Most of the nests contained one or two adult females. Those with more than two often contained callows, showing that the larger number was usually due to a recently matured brood; probably such individuals would not remain together throughout the winter.

In the spring, ovarian enlargement of some individuals occurs and eggs are laid in some nests in September and October. The presence of a few large immature stages suggests that a small number pass the winter in such stages rather than as adults. Reproduction goes on in September and October while several individuals are still in some nests, but group 2 (early November) indicates that by that time nearly all females have dispersed from overwintered groups and each has her own nest. Presumably each overwintered female ultimately develops enlarged ovaries and rears her offspring.

Production of eggs and of young adults goes on throughout the summer as shown in the preceding section and in Table 4. New nests seem to be established throughout the summer by single females. Old nests often contain several females but the large groups are usually mostly young individuals, often partly callows.

As shown in Table 4, production of immature stages is reduced by February 15 and many nests already lack immatures completely (see paragraphs above on group 7). Only 16 percent of the nests contained a female with enlarged ovaries (nearly all fertilized). However, the two nests containing several eggs and young larvae (443, 445) lacked egg layers; care of the young was by bees with slender ovaries, mostly unfertilized. Thus well before the end of summer the bees are progressing toward the overwintering condition.

The Reproductive Cycle Within Nests: In order to better understand the summer part of the life cycle, the social interactions and reproductive cycle must be examined. Many nests, especially as summer advances, are difficult to interpret, but others, with greater or lesser certainty, can be placed in one or another of the groups discussed in the following paragraphs. Those that cannot be so placed are often difficult to interpret because of lack of knowledge of the age of the egg-laying female; one may not be able to decide whether she is a sister or the mother of her associates. Examples of nests of various types are given below; further details on the same nests can be obtained from Tables 1-3 or the commentary in preceding sections.

Nest establishment and the egg layer with her first brood are exemplified as follows: Burrows without immature stages, usually containing only one adult and presumed to be young nests, were found throughout the summer.

TABLE 4. *Exoneura variabilis.* Average Number of Individuals per Nest in Various Developmental Stages on Different Dates. (In parentheses are percentages of nests taken on each date that contained each stage.)

Group No. Date No. of Nests	1 X-3 9	2 XI-9 11	3 XII-8 44	4 XII-18 35	5 XII-27 23	6 I-11 7	7 II-15 31	8 II-25 13	9 III-22 48
Eggs	....	3.5(64)	2.9(50)	3.2(66)	4.0(70)	1.0(71)	.5(10)	....	....
Small larvae	1.2(56)	.6 (9)	.9(32)	.8(31)	1.0(35)	.9(29)	.4(13)	....	....
Medium larvae	.2(11)	....	.5(20)	.3(23)	.5(30)	.1(14)	.4(20)	....	....
Large larvae	.1(11)	....	1.0(41)	1.1(37)	1.5(30)	2.1(43)	.7(32)	.1 (8)	.1 (6)
Prepupae	....	.1 (9)	.5(23)	.2(14)	.7(30)	.1(14)	.6(23)	....	.1 (4)
Pupae	....	....	2.0(32)	1.4(43)	1.4(52)	1.7(43)	.7(20)	.1 (8)	.2 (6)
Total immatures	1.5(56)	4.2(73)	7.8(93)	7.1(86)	9.0(78)	6.0(100)	3.2(55)	.2(15)	.4(10)
Adult ♀♀ (total)	1.9(100)	1.1(100)	2.0(100)	2.1(100)	2.3(100)	1.9(100)	1.6(100)	1.3(100)	1.5(100)
Callows	....	....	.5(16)	.0 (3)	.4(17)	.4(29)	.1 (3)	.2 (8)	.1 (4)
Fertilized	.4(33)	1.0(100)	1.2(84)	.9(86)	1.2(91)	.6(57)	.9(81)	.6(62)	1.0(83)
Worn	1.0(67)	.7(73)	.8(57)	.7(50)	1.0(61)	.3(29)	.5(35)	.5(46)	.6(54)
With enlarged ovaries	.2(22)	.7(64)	.7(52)	.9(83)	1.1(91)	.3(29)	.2(16)	....	....
Workerlike	.8(67)	....	.3(20)	1.1(51)	.6(30)	.7(43)	.7(35)	.5(46)	.4(31)
Adult ♂♂	....	....	.5(11)	.1 (6)	.2 (9)	.1(14)	.2 (7)	.1 (8)	.2 (8)

Similar beginning nests, but with eggs already laid, were also found in each sample of nests studied. Other nests contained only eggs and young larvae; examples are nests 274 and 319B. Such nests usually contain a single fertilized adult female each; if she is continuing to lay eggs, her ovaries are enlarged. Usually several eggs are laid over a relatively short period, after which egg-laying by the mother ceases at least for a time, as shown by nests such as 276, 278, 310B, and 297T in which the several young are large larvae or pupae but younger immatures are lacking. The mothers in such nests are fertilized, often with some wing wear as one would expect, and the ovaries usually somewhat enlarged. In other cases, however, the egg production seems to have been more protracted. Nest 287, for example, had young throughout the range from eggs to large larvae. The mother, as would be expected, was fertilized, with some wing wear, and with enlarged ovaries. The number of young in nests such as those described in this paragraph does not usually exceed seven or eight.

Most egg layers probable survive to lay a second batch of eggs. Nests are rather common in which a group of older, immature individuals is present, and in which, in addition, there is a group of eggs or small larvae, young of intermediate ages being absent. When the egg-laying adult in such a nest shows considerable wing wear, I have interpreted the evidence as indicating resumption of egg laying by the same mother that produced the older offspring. An example is nest 270, in which the adult bee was much worn, fertilized, with much enlarged ovaries. The fact that, in addition to the seven pupae in the nest, there were 13 eggs may suggest that in addition to the old mother, another individual, possibly a sister of the pupal individuals, had contributed to the egg cluster. This seems unlikely because of the lack of callows or other young adults; this nest was taken at 5:00 a.m. when almost certainly all individuals living in it would have been present. Nests 286 and 323 are other examples showing probable resumption of egg laying by a worn, fertilized female with large ovaries.

Such nests can sometimes also be recognized at a later stage when some or all of the individuals of the first brood have reached adulthood. For example, in nest 273, in addition to eggs, there was an old, fertilized adult with well worn wings and enlarged ovaries and an unfertilized, unworn female with slender ovaries. The latter presumably represented the first brood of young; males and any other females of that brood must already have dispersed. The eggs represented the second brood of young. The unworn female would probably have remained and functioned as a worker or might have mated and become reproductive. Nest 311T was the same except that the unmated individual with slender ovaries already had three nicks in one wing margin. Nest 288 presents a similar picture, six large immatures and two presumably young adults[5] (unworn, unfertilized, with slender ovaries)

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[5] One of the young adults was teritological, lacking one front leg and one side of the prothorax. The mesonotum was so shaped that the bee probably could not fly.

apparently representing the first brood and ten eggs representing the second brood of a worn, fertilized female with enlarged ovaries.

Nests 314B and 316B are similar to those described above in having only young and old immature stages, without intermediate ages. Each also had a worn, fertilized female with enlarged ovaries. In addition, each contained an unworn, fertilized female with enlarged ovaries. No doubt both individuals contributed to the clusters of eggs, as indicated by the large number of eggs (20) in nest 314B. The 17 pupae and callow adults in the same nest suggest a double source for the earlier brood also. The sources of the unworn egg layers cannot be established but probably they are older sisters of the pupae and callow adults in these nests.

Nest 315B also may contain one of its founders; at least there was a well-worn, fertilized female with large ovaries in the nest. The other adults in the nest were unworn, unfertilized, with slender ovaries, and no doubt were sisters of the callow adults and pupae. The large number of immature stages suggests that more than one egg layer was involved in their production.

Nests such as 270 and 288 suggest that the second brood of a female may be larger than the first. This may be reasonable since there is often more than one female to care for young of the second brood, while the first brood ordinarily must be cared for by the mother alone.

There is evidence that the founder of a nest does not generally survive long after laying the eggs for her second bood. Only 24 well and much worn females were found in the course of the study; they become no more common as the season advances and are no more common in large colonies than in small ones. These facts argue against long survival of a colony-founding mother such as occurs in *Lasioglossum malachurum* (Noll, 1931) or *L. inconspicuum* (Michener and Wille, 1961). Further support of this interpretation is provided by Skaife's (1953) observations on *Allodape* and by the many nests containing immature stages, obviously being fed, yet lacking any individual that could have been their mother. Obviously care of young is taken over by other individuals, probably usually older sisters of the young concerned. The nests discussed below illustrate such phenomena.

Nest 272, containing eggs and young larvae, was inhabited by two adult females, both unworn, one fertilized, one unknown because the spermatheca was lost in dissection, both with slender ovaries lacking white areas. Such ovaries could not have produced the eggs found in the nest. Presumably these adults were from the first brood of a female; her second brood consisted of the eggs and young larvae being cared for by the individuals of the first brood. This nest was taken at about 5:00 a.m., long before the bees become active. Hence it is unlikely that any surviving inhabitants were away from the nest. Nest 313T was similar in that it contained young immatures. It also contained pupae and one unworn, unfertilized adult with slender ovaries; these must represent the first brood of a female no longer present, whose second brood was the eggs and young larvae. The young adult was obviously caring for the eggs and young in the nest.

Nest 421 contained large larvae as well as prepupae and pupae. Of the seven adult females in the nest, only one was fertilized, three showed slight wing wear, and all had slender ovaries with no white areas. Obviously these adults were caring for the larvae although no one of them could have been their mother.

Nests 443 and 445 both contained numerous immature individuals and several adults. One adult in each nest was fertilized, that in 443 slightly worn, but none of the adults had enlarged ovaries. Obviously one or more older bees, presumably dead by the date when the nest was taken, must have been the mothers of the immatures in each nest. Young bees were clearly caring for the eggs and larvae.

Not only are young commonly cared for by their older, workerlike sisters, but some of the sisters also replace their mothers as egg layers, as indicated in the following paragraphs. Nest 295T is interesting in that it contained no immatures. The original egg layer must have failed to produce a second brood. The four bees in the nest were all unworn, only one was fertilized and she had enlarged ovaries. Presumably she would soon have laid a group of eggs. One of the unfertilized females had slightly enlarged ovaries (longest oocyte 0.55 mm.).

It is my unverified suspicion that nests such as 275 (both adults with slightly worn wings, only one fertilized with enlarged ovaries) and 301B (one of the noncallow adults unworn, unfertilized, with slender ovaries; the other only slightly worn, fertilized, with enlarged ovaries) had lost their original founders and that each contained another egg layer which was presumably one of the offspring of the founder. The principal reason for this surmise is the slight amount of wear of the wings of the individuals with enlarged ovaries.

In other cases it seems clearer that the founder of a nest has died and been replaced by another egg layer. Nest 296B contained eggs, a pupa, callow adults, and one mature, unworn, fertilized adult with enlarged ovaries. It seems most likely that this individual is a sister of the pupa and callows but the mother of the eggs. Nest 293T was similar in that it contained young immature stages and young adults. Five of the adults were unworn, unfertilized, with slender ovaries. The remaining adult differed in being fertilized, with enlarged ovaries. Presumably she was a sister of the other five adults and mother of the eggs and young larvae. Nest 463 can be interpreted along similar lines; the three adults were unworn, only one was fertilized with enlarged ovaries.

Division of labor: From the above paragraphs it is evident that the typical nest population contains only one fertilized adult female with enlarged ovaries. During the main reproductive period in summer (December), over half of the nests contain only one mature (i.e., not callow) female and at other seasons the percentage of monogynous nests is even higher. However, in some nests, additional mature females are present. Thus of 102 nests taken during December (groups 3-5), 48 contained more than one mature female. As shown in Table 5, 30 of these 48 nests contained two mature females and only small numbers had three or more. Table 5 also shows, as was suggested from less specific data at the beginning of this paragraph, that in most nests (28 or 29 out of 48) containing two or more mature females, only one is fertilized and only one has enlarged ovaries. In the great majority of cases the same individual shows both of these features and is obviously the only reproductive individual in the nest. However, among the 131 mature females in the 48 nests, 13 were fertilized but had slender ovaries. The 54 monogynous December nests contained 16 fertilized females with slender ovaries. This 27 to 30 percent fertilized individuals with slender ovaries consists of (1) individuals, probably relatively young, in their parental nests, sometimes associated with fully reproductive individuals, (2) individuals starting new nests (among the monogynous nests only), and (3) individuals that have laid their first brood of eggs and whose ovaries have regressed. There may be other conditions under which such individuals appear; from available data it is often difficult to place specific individuals in one or another of these classes. My impression is that classes (1) and (3) are about equally numerous and (2) less so.

TABLE 5. *Exoneura variabilis.* Frequencies of December Nests with Two or More Mature Females (out of total of 102 nests) and, among these, Frequencies of Nests with Varying Numbers of Reproductive Females.

No. of mature ♀♀	0	1	2	3	4	5	6
Frequencies of nests with 2 or more mature ♀♀.	..	..	30	8	5	3	2
Frequencies of such nests having varying nos. of ♀♀ with enlarged ovaries.	4	29	12	3	..	..	..
Frequencies of such nests having varying nos. of fertilized ♀♀.	2	28	15	3	..	..	..

In addition to fertilized individuals with slender ovaries, there were among the 48 nests containing more than one female, three females with enlarged ovaries but no sperm cells in the spermathecae. One of these actually had only one oocyte enlarged (0.55 mm. long), so that its ovaries barely qualified as "enlarged"; it was in a nest (295T) containing two other young mature adults (unfertilized with slender ovaries) in addition to a fully reproductive female, and was undoubtedly only a young female which for some reason had an unusually enlarged oocyte. The other two unfertilized females with enlarged ovaries both had worn wings and the longest oocytes of each were 1.03 and 1.10 mm. long. Both had ovaries smaller than average for such large oocytes (0.25-0.30 mm. wide), as shown in Fig. 1, a fact which suggests that the ovarian enlargement may have been incomplete. One was in a nest (385) with a fully reproductive female, a callow female, and brood; the other was in a nest (302B) with two fully reproductive females and a female of the parasite *Inquilina*. Apparently such individuals are more or less in the nature of abnormalities.

Among the December nests there were eight in which two of the females were fully reproductive. In several nests these were the only adults present while in other cases other mature adults were also present.

Among the 131 mature females in the 48 December nests containing more than one mature female, 53 had enlarged ovaries and were fertilized. Such individuals are the principal reproductives and, as shown above, are usually distributed one per nest. At least many of the remaining individuals function as workers. This was established by capturing pollen collectors returning to their nests and dissecting them along with the other females in the nests. The pollen collectors were, in all cases studied, unfertilized bees with slender ovaries, and can be called workers. As examples, nest 332 contained a well worn reproductive, a worker, and two other individuals which seemed workerlike and probably also served as workers. Probably the reproductive was the mother of the workers which were therefore functioning in the presence of a queen mother just as in many halictids and other social bees. Nest 329 contained a reproductive, a worker, and two callows. Since all were unworn, they were probably all sisters. Nest 331 contained a reproductive and a worker. Because the reproductive's wings were damaged in capture, it is not known whether she was an old bee or not. All the larvae in the nest were *Inquilina;* the reproductive evidently had not yet started to lay and was most likely a sister of the worker. Finally, in nest 330 there was no reproductive, the two females being unfertilized, with slender ovaries. At least one of them, however, was bringing pollen into the nest, presumably to feed larvae which probably were her sisters. Nests such as 330 substantiate the view already presented that young adults take over the work of caring for any young in the nest when the old adults die.

The importance of workers in foraging in this and other species of *Exoneura* has been shown elsewhere (Michener, 1963) by dissections of pollen collecting individuals taken on flowers. At least at some seasons more than 80 percent of the pollen collectors were shown to be unfertilized and an even higher percentage have slender ovaries. The high percentage of workers collecting pollen indicates the inactivity of egg layers in such work, for less than 50 percent of the mature females from nearby nests were workers.

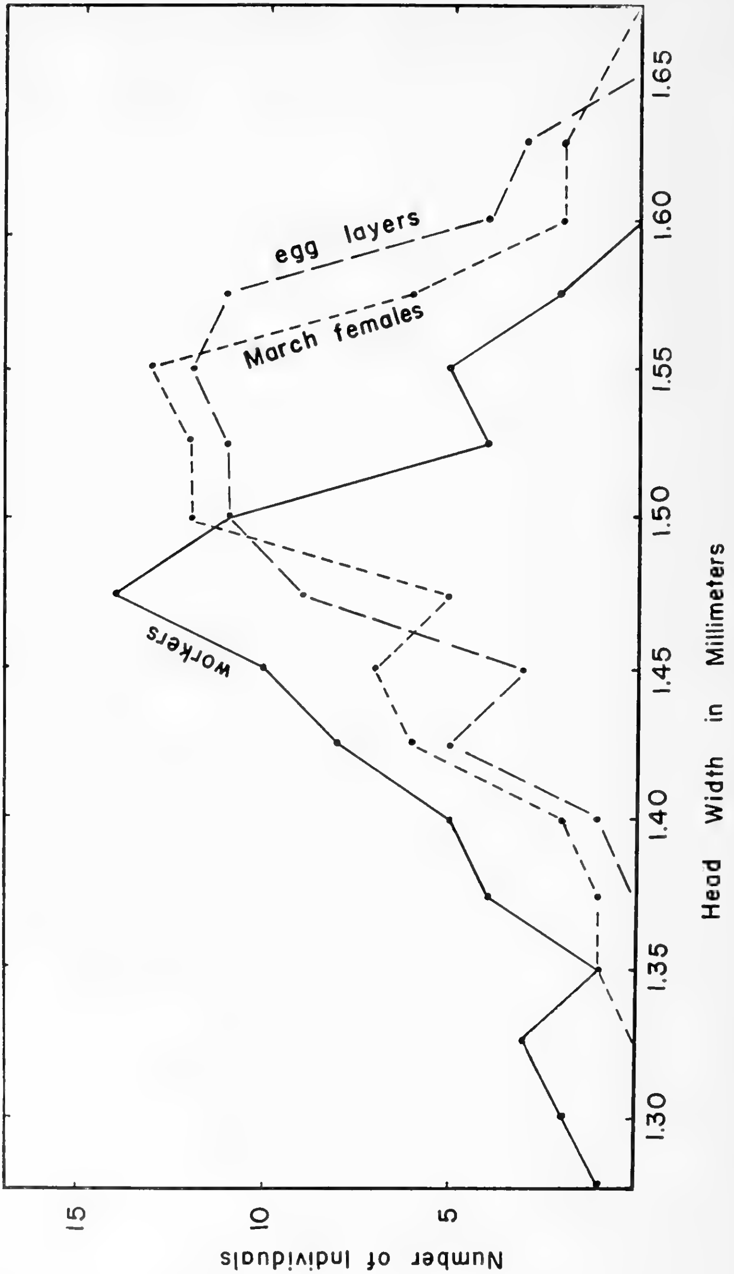


FIG. 2. Frequency distribution of head widths of females of *Exoneura variabilis*, based on 70 egg layers taken in December, 70 workers and presumed workers taken in December, and 70 females taken in March.

Since most workers are unworn, the problem arises as to whether workers die off as such or ultimately mate and disperse to establish new nests. The abundance of immature stages compared to the small number of adults (Table 1 to 3) suggests that the workers are short lived in this capacity—they either die after a short adult life or they disperse and cease to be workers. The number of new nests found in each group during the summer was small, as indicated in the discussion of nest groups 3 to 5. It is therefore my belief that most workers are relatively short lived, as in other social bees, and that they die before their wings become very worn. On the other hand the seemingly new nests sometimes found being established by worn bees may suggest that some workers do become reproductives later (see first paragraph in discussion of Group 4 above). The idea that the workers, or at least many of them, represent a caste rather than a stage in the adult life of females is further supported by the average size difference between workers and egg layers. Seventy fertilized individuals with large ovaries taken in December were compared with 70 unfertilized mature adults with slender ovaries taken in the same month and presumed to be workers (including 19 known to be workers from behavioral observations). Head width was used as a measure of size. The mean head width of the 70 egg layers was $60.9 \pm .257$ micrometer divisions, that of the 70 presumed workers was $58.1 \pm .101$. These means are significantly different as shown by a t-test ($p < .01$). These data are shown in millimeters in Fig. 2. There was no significant or even suggestive size difference between lone egg layers and those in company with workers or other females. In the same figure is presented comparable data for 70 females taken on March 22. There was no significant difference between these females, prepared to overwinter, and the summer egg laying females.

The difference in size between egg layers and workers is more clearly shown by comparing sizes in various nests separately. Among 33 nests taken in December and January in which egg layers and workers could be distinguished with some degree of assurance, 24 had the egg layer larger than any worker in the same nest (Table 6). Moreover, 61 of the 71 workerlike individuals from these nests were smaller than the accompanying egg layers.

Adults produced in December, as judged by callows, included a few individuals of maximum size but most were the size of workers; 21 of the 24 callows taken in December with accompanying egg layers were smaller than those egg layers. In February, however, of six callows in three nests that contained egg layers, two were larger, two smaller, and two equal in size to those egg layers. These data, although few, suggest that at that time callows become overwintering egg layers rather than workers.

Sex Ratio: The sex ratio may support the idea of a worker caste somewhat similar to that of social halictines for there is an excess of females produced. December and January pupae, callow adults, plus a few prepupae

TABLE 6. Relation of Size of Workers (W) to Egg Layers in Various Nests of *Exoneura variabilis* taken in December and January.

Relation	No. of nests	No. of workers
W < egg layer	24	54
W = egg layer	4	4
W > egg layer	2	2
W <>* egg layer	1	2
W <=* egg layer	1	6†
W >=<*egg layer	1	3
Totals	33	71

* Multiple symbols indicate that some workers are smaller than, others larger than or equal to the egg layer.

† These six consisted of 5 smaller than and one equal to the egg layer.

reared to the pupal stage for determination of sex, numbered 207. Of these only 40.1 percent were males.

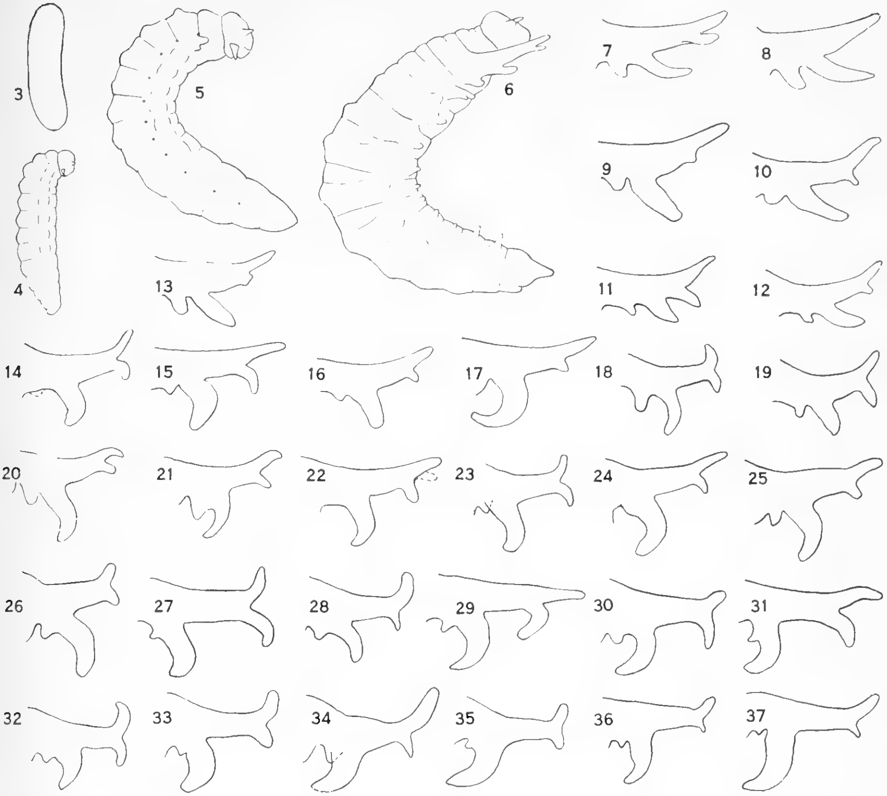
Males are generally short lived or leave the nests when young, for the number of noncallow males found in the nests is small (see Tables 1 to 3).

Ovarian Development: The various stages of ovarian development among adults, from young callows to mature egg layers and workers and overwintering individuals, are shown in Figures 65 to 82. The explanations of the illustrations are given in some detail and make an extended account here unnecessary. Drawings are based on specimens fixed in Kahle's (Dietrich's) solution. There are four ovarioles per ovary, and in each several oocytes enlarge simultaneously, thus permitting the laying of several eggs at about the same time. This is in sharp contrast to *Allodapula* and *Exoneurella* (see Michener, 1962 and 1965).

The white areas found in the posterior parts of some ovaries presumably result from resorption of eggs or from the laying of eggs or both and are therefore of value in giving some idea of previous ovarian activity.

Immature Stages: The occurrence of immature stages in nests is given in detail in the section on Life History Data, including Tables 1 to 3. The details of larval form and structure are given by Syed (1963), who showed that there are probably four larval stages. His drawings were from fixed specimens; Figures 3-13 were made from living material.

The mesothoracic arms of the last stage larvae vary more than Syed indicated, as shown by Figures 7-37. These arms are sticky and soft in life. Branches may stick together or even to the body wall and then practically disappear. There is thus a good probability of observational errors in studies based on living material. Moreover, the arms are partially retractile; in inactive individuals they are not fully exerted. Tactile stimulation, for example with a needle, especially in the head region, results in full extension of the arms, as though by blood pressure; after a short time they retract.



FIGS. 3-37. *Exoneura variabilis.* 3, egg (length 1.75 mm.); 4, small, probably second stage, larva (maximum diam. 0.58 mm.); 5, half grown (third stage) larva (maximum diam. 0.75 mm.); 6, mature larva. Figures 7-37 represent maximally exerted mesothoracic arms of mature larvae before the prepupal stage. Figures 7-13 were drawn from live or freshly dead specimens. Figures 14-37, which tend to have the branches recurved, were drawn from specimens that had been fixed for weeks in Kahle's (Dietrich's) solution. Broken lines in some locations represent projections present on one side of the body, absent on other side of the same larva. Figures based on larvae from the same nests are 7 and 8, 9 and 10, 11 and 12, 17 to 19, 20 to 22, 23 and 24, 25 and 26, 27 to 31, and 32 to 37.

Adult bees passing through the nest must cause this reaction which must be related to providing the pollen mass by the adults and its handling by the larger larvae.

In the prepupal stage the larval appendages shrivel.

The small projections on the mesothorax of third (?) stage larvae are not retractile.

Specimens dropped alive into Kahle's (Dietrich's) solution have fully extended appendages which after a time tend to have recurved branches as shown in Figures 14-37.

In the nests the immature stages are usually arranged from oldest above to youngest below. Perhaps because there are larger numbers of young of about the same age than in *Allodapula* (see Michener, 1962), the sequence is not so precisely kept as in that genus. For example, pupae of various degrees of pigmentation are usually mixed. The following lists illustrate selected cases in which marked irregularities in the usual sequence occurred. (In each list the nest number is given first and then the immature stages from top to bottom. Groups of immatures in clumps rather than in linear order are indicated in parentheses.)

288: 2 large larvae, 1 prepupa, 1 white pupa, 2 black pupae (10 eggs).
306B: 1 large larva, 4 pupae (11 eggs, 8 very small larvae).
308B: 6 large larvae, 1 prepupa, 14 pupae, 1 large larva (1 egg, 1 small larva).
310B: 3 large larvae, 3 prepupae, 1 white pupa.
289T: 2 black pupae, 5 white pupae, 3 prepupae (1 small larva, 2 very small larvae, 8 eggs).
316T: 2 large larvae, 2 prepupae, 3 pupae, 1 small larva, 1 pupa, 1 small larva, 1 pupa (10 eggs).
382: 10 large larvae (8 eggs, 1 small larva), 1 dead pupa, 1 pupa; 2 medium sized larvae, 1 egg.

Feeding of the larvae is progressive, as in other members of the genus. At any one time relatively few larvae have food. For example, on December 18 a series of nests was collected during the cloudy afternoon after a fine morning during which the *Exoneura* were common on flowers. The nests were opened in the evening. At that time only eight of the 74 larvae in these nests had pollen masses on them. These eight included larvae of all sizes.

I have two records of two small larvae curled around a single pollen mass but in general there is one mass per larva. The mass is on the ventral surface of the larva; the larva lies on its dorsal side and curls around the pollen as in the sketches reproduced in Figures 38-41.

Figs. 38-41. *Exoneura variabilis* larvae feeding on pollen masses. 38, very small larvae feeding on pollen mass which has been largely consumed (maximum dimension of pollen mass 1 mm.); 39, third stage (?) larva; 40 and 41, last stage larvae.

Eggs and small larvae are somewhat sticky and cling together in irregular clumps. The eggs are not attached in any way to the walls of the nest burrows.

Larvae removed from nests produce feces from middle size onward. Feces are never found in the nests, however; they must be removed by the adults.

Variation among adults: Rayment's name for this species is appropriate for there is more variability in coloration in this species than in any other *Exoneura* known to me. The face of the female is rarely wholly black. Commonly there is a small cream colored mark on the lower part of each paraocular area and sometimes these marks are rather large, nearly attaining the level of the summit of the clypeus. Commonly there is a longitudinal median clypeal mark, sometimes broadened at the summit to the full upper width of the clypeus. The clypeal mark may be present without the paraocular marks, or vice versa, or both may be present.

The females in any one nest *tend* to resemble one another in the markings but there is enough variation within nests to show that all the variation described is intraspecific.

There is also geographical variation. The abdomen, in specimens from Cunningham's Gap, is orange. In specimens from the other localities it is considerably darker because of broad basal blackish bands on the segments, and sometimes it is almost wholly black.

INQUILINA EXCAVATA (COCKERELL)

This bee is similar in size and appearance to *Exoneura variabilis* and inhabits the nests of that *Exoneura*. As was pointed out by Michener (1961), the females of *Inquilina* do not possess a fully formed scopa. They have not been seen to collect pollen and appear to be social parasites in the nests of *E. variabilis*. This habit explains some of the "heterospecific companionship" discussed by Sakagami (1960). The details of the larval structure of *I. excavata* have been described and figured by Syed (1963). Variation in the mesothoracic arms of mature larvae is illustrated in Figures 42-49.

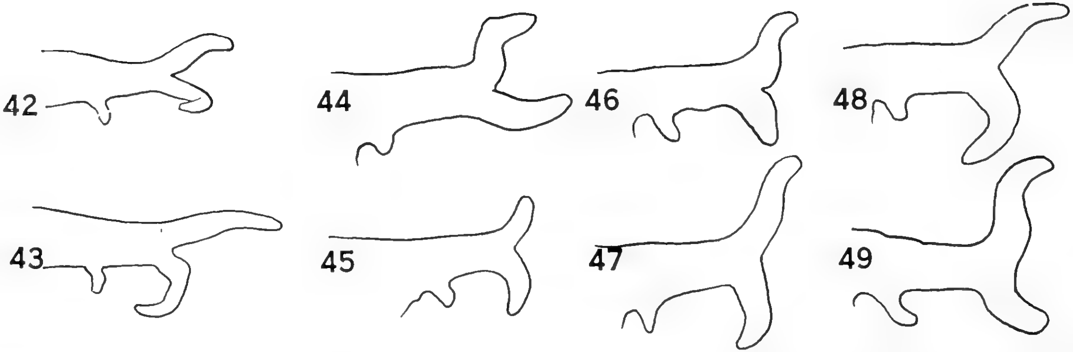
No specimens of *Inquilina* were found with nest groups 1 and 2 of *E. variabilis*. Occurrence in December (groups 3 to 5) is shown in Tables 1 to 3. In January (group 6) three nests (not included in previously presented statistics on *E. variabilis*) were found to contain only *Inquilina*. The contents were as follows (nest number at first of each line):

460: seven adult females.
461: two adult females, six large larvae.
464: five adult females, two adult males, one black pupa, one prepupa, seven large larvae.

In another nest one female of *Inquilina* was associated with a female, two small larvae, and seven large larvae of *E. variabilis*.

In February and March (groups 7 and 8) a total of eight *Inquilina*, all adult females, was taken, one in each of eight nests, and in every case in the company of one or more adult *E. variabilis* and sometimes with *variabilis* larvae.

The relation of *Inquilina* to the *Exoneura* cannot be learned in detail from



FIGS. 42-49. Sketches of mesothoracic arms of mature larvae of *Inquilina excavata*, based on fixed specimens. Figures 42 and 43 are based on larvae from one nest, the others, on larvae from another nest.

FIGS. 50-51. *Exoneura aterrima*. 50, lower end of nest, showing positions of eggs; 51, newly hatched larva, with posterior part of body still in chorion attached to wall of burrow, and with pollen mass already on venter of larva.

available data. It is obvious that the parasite must invade nests of *Exoneura* and lay eggs there. From the fact that whole groups of larvae and pupae in certain nests (302B, 303B, 304T, 331) were *Inquilina,* and from the frequency of adults in the nests, it seems clear that the *Inquilina* take up residence in association with *Exoneura,* rather than merely entering to lay an egg and then leaving.

The larvae of *Inquilina* must obviously be fed by the *Exoneura,* since the parasite cannot collect pollen. The *Inquilina* probably prevents the production of brood of the host in some way or destroys *Exoneura* eggs, in view of the seven nests (302B, 303B, 304T, 331, 460, 461, and 464) in which the whole broods seem to have been *Inquilina.* In some cases, e.g., 460, 461, and 464, the *Exoneura* appear to have reared their parasites and died, leaving the nest entirely to the parasite. In other cases, it seems that the *Exoneura* survive. For example, nest 331 was inhabited by two adult *Exoneura,* one of which was apparently about to start laying eggs. Perhaps such *Exoneura* resulted from larvae somewhat older than those of the parasites reared in the same nest; perhaps in the absence of *Exoneura* larvae of that age, the destruction of the *Exoneura* colony by the parasite is complete.

The individual females of *Inquilina* isolated in nests of *Exoneura* were nearly all fertilized, not or slightly worn, with slender ovaries. Only two with enlarged ovaries were found; these were the adult females in nests 302B and 381. Both were in nests with females of *Exoneura* which were also fertilized and with enlarged ovaries. From this it seems likely that egg-laying *Inquilina* live in nests where female *Exoneura* are actively laying eggs. The species of the eggs and young larvae in nests 302B and 381 is unknown, but it is reasonable to suppose that they were those of the *Inquilina* which probably destroyed host eggs.

EXONEURA HAMULATA COCKERELL

Habitat: This species was studied at the nearby localities of Beerwah and Tibrogargen, in southeastern Queensland. The area is *Eucalyptus* savanna.

Nests: Nests of this species have been recorded previously by Rayment (1946c, 1948). Twenty five nests of *E. hamulata* were found by me. All were burrows in standing dead, dry, flowering stems of *Xanthorrhoea.* Usually there was only one burrow in such a stem, but in one case two and in another case four burrows were parallel to one another in the pith, so close together as to be separated by only one half to one fourth of a millimeter of pith for considerable distances, yet never connecting. *E. hamulata,* like *E. variabilis,* makes its own burrows; it enters stems cut off by an insect which leaves a smoothly cut end. Stems broken or cut by man have rough ends and were not utilized.

Nest burrows sufficiently advanced to contain young are 30-310 mm. deep (mean of 21 measurements, 164 mm.). The entrances of the burrows are narrowed to 2.0-2.5 mm. (mean of six measurements, 2.4 mm.).

The entrance may be narrowed by means of bits of pith forming a neat collar or the burrow may be excavated with a narrow entrance; perhaps all are first constructed in the latter way and a collar built only if the original entrance is damaged. The diameter of the burrow below the entrance is 2.5-4 mm., usually being 3 mm. or more (mean of 39 measurements, 3.4 mm.).

Life History and Reproductive Data: Information on the nest contents of the 21 nests that contained young is given in Table 7. These data suggest that nests are active more nearly continuously than in *E. variabilis* for nests full of immature stages were found both in October and February. October and February nests of *variabilis* do not contain such a variety of immature stages. A longer season for *hamulata* is not surprising in view of its warmer habitat, not far above sea level. Perhaps immature stages are numerous throughout the winter in these nests but adults were not taken on flowers in spring until mid-September nor in fall after April. Two lone females were

TABLE 7. Numbers of Young and Adults in Nests of *Exoneura hamulata.* (Each horizontal row represents a nest. Nests without immature stages or callows and containing only a single adult were omitted from this table. Under adults, C=callows.)

Nest No.	Date	Eggs	Small Larvae	Medium Larvae	Large Larvae	Prepupae	Pupae	Total Young	Adult ♀♀	Adult ♂♂
88	X-17	..	..	2	2	..	..	4	2	..
89	X-17	..	..	..	..	3	12	15	2	..
90	X-17	7	..	7	..	..	10	24	4	..
92	X-17	..	..	4	4	..	..	8	3	..
245	XI-24	4	..	..	..	..	1	5	2+5C	..
253	XI-24	6	..	..	..	..	1	7	3+17C	6C
400	I-6	3	2	..	..	..	..	5	1+1C	..
401	I-6	1	..	..	..	..	1	2	2C	..
402	I-6	9	4	..	3	..	..	16	3	..
403	I-6	10	2	..	..	..	..	12	1+3C	..
404	I-6	9	..	..	..	..	10	19	1+8C	2C
405	I-6	4	1	2	6	..	2	15	5	..
406	I-6	1	..	..	4	..	..	5	2	..
407	I-6	4	..	..	..	..	..	4	2	..
408	I-6	..	..	..	4	1	..	5	3	..
409	I-6	15	..	..	..	..	4	19	3+6C	1C
410	I-6	..	..	..	..	..	..	0	2+1C	..
416	I-6	..	..	..	4	..	..	4	2	..
419	I-6	..	..	..	..	..	1	1	1	.
420	I-6	1	..	..	..	..	..	1	1+1C	..
465	II-19	4	..	..	2	1	..	7	2	..

found making new nest burrows on November 24, two others on January 6. It is likely that new nests may be established at various seasons, as in *E. variabilis.* None of the nests containing immature stages was recently established by a lone female, however; all contained older young and most contained more than one mature female.

Obviously, as in *E. variabilis,* females lay considerable numbers of eggs over a short period and then rest, probably laying a second group of eggs later. The result is the normal occurrence of young of two very different ages (e.g., eggs and pupae, as in nest 404) in the nests. Occasionally (nest 405) a more or less continuous sequence of young exists in a nest, perhaps because of the presence of more than one egg laying female.

The rather numerous callow adults in the nests (see Table 7) no doubt originated from the same groups of eggs as the pupae usually found in the same nests.

Division of Labor: Consideration of mature adults in the nests suggests the existence of the same sort of colony organization at least from October through January or February as exists during December for *E. variabilis.* Nests with a single mature female exist (e.g., 400, 403, 404). All show a major gap between young and older immature stages. The adult females in nests 400, 403, and 404 were well worn, fertilized, with enlarged ovaries, as might be expected of females laying their second groups of eggs.

Nests with several mature females are more common than in *E. variabilis,* as shown in Table 7; 15 of the nests contained two to five mature females each. The features of the mature females in these 15 nests are shown in Table 8. One or more fertilized bees were present in each nest. One fully reproductive individual (fertilized and with large ovaries) was found in each of six polygynous nests (90, 406, 408, 409, 416, and 465) and two in five nests (245, 253, 402, 407, and 410). Most of the remaining bees were (1) unworn, fertilized individuals, not yet laying eggs (no white areas in ovaries), but caring for larvae which could not have been their progeny (e.g., all females in nests 88 and 92); or (2) unfertilized individuals, either worn or not, almost all of which had slender ovaries. These are presumably workers, except perhaps for a few which would later mate and become egg layers. The presence of worn workers (e.g., the last bee listed in nest 90, Table 8) supports the view of workers as a distinct caste rather than as a phase in the life cycle, as elaborated in the discussion of *E. variabilis.* Wing wear is much more evident in larger bees than in smaller; it is therefore not surprising to find it more useful in studies of the large species, *hamulata,* than in *variabilis.* Workers are relatively abundant in *E. hamulata.*

The size of workers in *E. hamulata* probably averages smaller than that of egg layers. Workers in four nests were smaller than the associated egg layers, in a fifth, the reverse was true. Most of the callows were also smaller than associated egg layers.

TABLE 8. Data on Mature Females in Nests of *Exoneura hamulata* Containing Two or More Such Females. (Degrees of wing wear are from unworn, —, to very much worn, ++++.)

Nest No.	Fertilized	Worn Wings	Enlarged Ovaries	Nest No.	Fertilized	Worn Wings	Enlarged Ovaries
88	+	—	—	405	—	—	—
	+	—	—		+	++++	+
89	—	—	—		—	—	—
	+	—	—		?	—	—
90	—	—	—		—	—	—
	+	++++	+	406	+	—	—
	—	—	—		+	—	+
	—	++	—	407	+	+	+
92	+	—	—		+	++	+
	+	—	—	408	—	—	—
	+	—	—		+	++++	+
245	+	—	+		—	—	—
	+	+++	+	409	—	+	—
253	+	—	+		—	+	+
	+	++++	+		+	+	+
	+	+	—	410	+	++	+
402	+	—	—		+	—	+
	+	—	+	416	—	—	—
	+	—	+		+	—	+
				465	?	—	—
					+	—	+

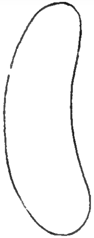
Sex Ratio: Of 93 pupae and callow adults, only 42 percent were males. This is in almost exact agreement with *variabilis.*

Ovarian Development: No differences in ovarian development were noted between *E. hamulata* and *E. variabilis.*

Immature Stages: The details of larval structure were given by Syed (1963). The figures presented in the present paper (Figures 52-56) were based on living specimens. The arrangement of the stages in the nests is similar to that of *E. variabilis,* perhaps less regular.

EXONEURA OBSCURIPES MICHENER

Six nests of this species were found, all in Lamington National Park near Binna Burra in the McPherson Range, Southeastern Queensland. They were in rotting, broken stems of vines in the rainforest, three of the six in a single broken stem. Nests containing immature stages ranged from 55 to 125 mm. in depth; diameters were 3 to 3.5 mm., with entrances narrowed to 2 mm. Eggs, small larvae, and large larvae were found both on December 8 and January 11. A new nest was being excavated by a lone, fertilized, unworn female on December 8.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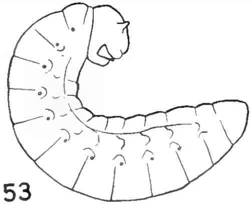
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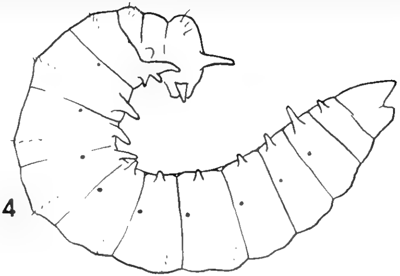
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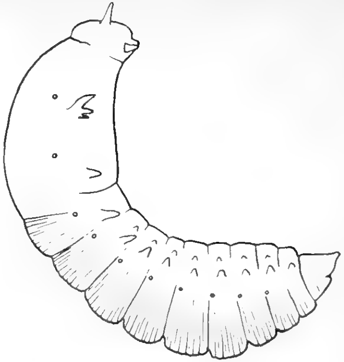
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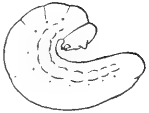
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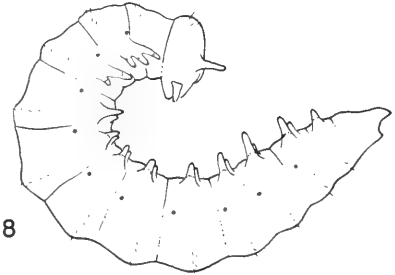
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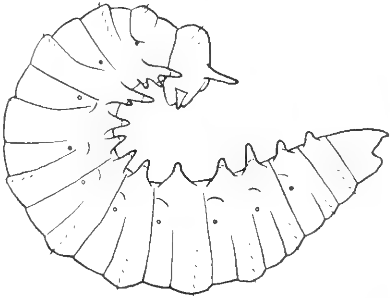
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FIGS. 52-56. *Exoneura hamulata.* 52, egg (length 2.15 mm.); 53, small larva (rear part of body was still in egg shell before it was pulled out for sketching); 54, mature larva; 55, prepupa, hairs omitted; 56, mesothoracic arm of mature larva.

FIGS. 57-59. *Exoneura obscuripes.* 57, small larva (rear portion of body was still in egg shell before it was pulled out for sketching); 58 and 59, larvae in last stadium, 59 older. In these drawings dotted lines show lengths of appendages when not exserted.

In Figures 54 and 59 the inner small row of abdominal tubercles does not show.

Nests with one, two, and three mature adults were found. The one with three contained an egg layer and two unfertilized, unworn probable workers. In each of the two nests with two adults, one was an egg layer, the other a fertilized, worn bee with slender ovaries.

Larval structure was described by Syed (1963). The illustrations included herein (Figures 57-59) are based on sketches made from living specimens.

EXONEURA ANGOPHORAE COCKERELL

Only two nests of this species were found, both at Tibrogargen, in dead flowering stems of *Xanthorrhoea*, like those occupied by *E. hamulata*. One was taken on November 24, the other on February 19. These nests were 62 and 94 mm. deep with diameters varying from 3.5 to 5 mm., the entrance of one (for other not recorded) narrowed to 1.5 mm. Each nest contained eggs and small larvae but no other immature stages. Each contained more than one adult, however, suggesting that a previous brood of young had been reared in the nest.

The nest taken on November 24 contained (1) a fertilized, worn female with enlarged ovaries, obviously the egg layer; (2) two unworn bees with slender ovaries, one fertilized, the other not, probably both acting as workers; and (3) three mature males. The nest taken on February 19 contained an unworn egg layer (fertilized, enlarged ovaries) and a worn individual with slender ovaries probably acting as a worker although fertilized.

EXONEURA HACKERI COCKERELL

Two nests of this species (which is apparently the same as *insularis* Cockerell) were found, both in stems in the rainforest margin in Lamington National Park near Binna Burra, southeastern Queensland. One entered the stem through a beetle hole in the side of the stem instead of through a broken end. Lengths of the nests were 63 and 210 mm., diameters were 2.5 to 3 mm.

One of the nests contained 12 eggs, one pupa, and two worn, fertilized females, neither with greatly enlarged ovaries. The other contained ten large larvae and six mature females, four fertilized, one unfertilized, and one doubtful. Two of the fertilized individuals were worn, the other adults were unworn. One worn and one unworn fertilized female had enlarged ovaries.

EXONEURA ATERRIMA COCKERELL

A single nest of this species was found at Tibrogargen on November 24, 1958 in a dead flowering stem of *Xanthorrhoea*. The entrance was through a hole (made by a beetle?) in the side of the stem rather than through a broken end. The burrow was only 19 mm. long, 3 mm. in diameter, narrowed to 1.5 mm. at the entrance. It contained four eggs and one very young larva with the rear half still in the egg shell but with a pollen mass on its under surface (Figure 51).

An unusual feature, differing from all other *Exoneura* studied by me but resembling certain species studied by Rayment (1948, 1951) and Erickson and Rayment (1951), was the attachment of the eggs, usually by their posterior ends, to the burrow wall near the end of the burrow (Figure 50). The eggs therefore do not lie loose and form a clump as in other species dealt with in this paper. The chorion of the one egg that had hatched kept this position and held the young larva in the position shown in Figure 51.

EXONEURA SUBBACULIFERA RAYMENT

Five nests were found in dead, cut stubs of *Rubus* stems at Cunningham's Gap on November 9. The nests ranged from 60-148 mm. in depth and from 2.5-3 mm. in diameter. Some of them were being deepened (as shown by pith fragments thrown out of the entrances) in spite of the presence of brood.

Like nests of *E. variabilis* found on the same date, those of *subbaculifera* contained eggs, one of them also with small and medium sized larvae. The nests contained two to four females each, all but one fertilized, mostly worn, and one or two in each nest with enlarged oocytes. The one unfertilized individual is of interest because it was well worn with slender ovaries; it was probably a worker or workerlike individual that had survived the winter.

The larvae were described and figured by Syed (1963) and are noteworthy for the large frontal projection, also shown in Figures 62 and 63 based upon fresh material. Like the ventrolateral projections of this and other *Exoneura,* the frontal projection can be exserted; all are shown in the exserted position in the figures but when withdrawn the apical part of the frontal projection is reduced in size and less turgid and the abdominal appendages are all mere convexities, like those shown on the eighth and ninth abdominal segments in Figure 62.

EXONEURA BACULIFERA COCKERELL

Two nests were found in broken stems at the edge of the rainforest in Lamington National Park near Binna Burra.

The nests were 30 and 260 mm. deep, 2.75 to 4 mm. in diameter, the constriction at the entrance of one of them had a diameter of 1.75 mm.

The shallow nest was apparently new, containing a single fertilized female with enlarged ovaries and four eggs. The deep nest contained six mature females, five callow females, 13 males, six pupae, and three eggs. Two of the mature females were fertilized, worn, with enlarged ovaries. The other four were unfertilized, unworn (except for one nick in one wing), three


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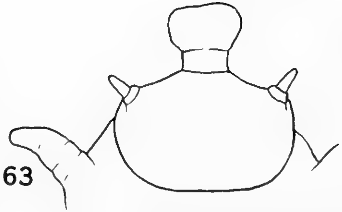
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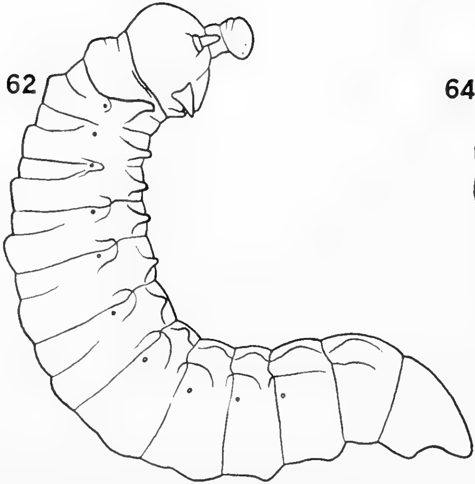
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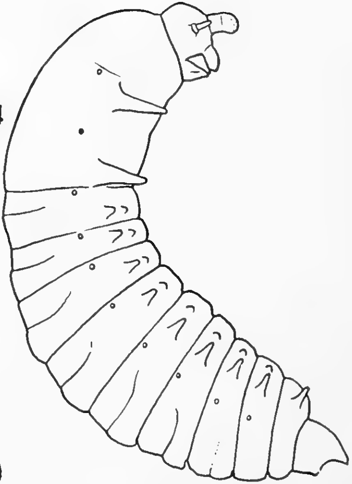
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FIGS. 60-63. *Exoneura subbaculifera.* 60, egg (length 1.78 mm.); 61, head of third stage (?) larva (head width 0.60 mm.); 62, mature larva (head width 0.80 mm.); 63, dorsal view of head and front of thorax of same.

FIG. 64. Prepupa of *Exoneura baculifera* (maximum diameter 1.70 mm.).

with slender ovaries, the fourth, surprisingly, with enlarged ovaries.

The prepupa of this species is shown in Figure 64. The frontal projection is similar to that of *E. subbaculifera.*

SUMMARY

This paper consists mainly of an account of the life cycle and social organization of *Exoneura variabilis,* with less complete data on several other species of *Exoneura* and on the socially parasitic bee, *Inquilina excavata.* The bulk of the information was derived from statistical examinations of nest populations, spermathecal content, wing wear, number and stages of the immature forms, and the like, rather than from direct observation of behavior in the nests.

E. variabilis nests in simple burrows, not divided into cells, in dry pithy stems in rainforest boarder regions. It overwinters in such burrows, primarily as fertilized adult females of varying ages (or amounts of wing wear). One to three females inhabit a single nest. A few larvae apparently also overwinter.

In spring the bees disperse so that most nests contain one female. Egg laying occurs throughout spring and summer and adults of both sexes are produced. New nests are established throughout the active season by lone females. However, apparently the majority of the young adult females do not leave the parental nest but remain there. Some replace the original egg laying female who dies soon after laying two, sometimes incompletely separated, batches of eggs. Since the larvae are fed progressively, those hatching from the second batch are usually reared by one or more of their adult sisters from the first batch of eggs. Such an individual may coexist for a time with the worn mother, but in many nests larvae are cared for in the absence of any individual that could be their mother. Commonly such sisters are workerlike, having slender ovaries and being unmated, but others mate and replace their mothers as egg layers.

At all seasons over half the nests opened contained only one mature female (recently emerged adult females are not counted). However, especially in summer, some nests (e.g., 48 out of 102 in December, the first summer month) contained more than one mature female, usually two but rarely as many as five or six. Usually only one but sometimes more are egg layers; the rest have slender ovaries and are often unfertilized workers; they were seen to be active in collecting pollen for nests containing egg layers which did not leave during the period of observation. (Rarely unfertilized individuals have enlarged ovaries.) Workers average smaller in size than egg layers and are probably short lived compared to egg layers.

A worker can be either daughter or (usually) sister of an egg layer in her nest. Female bees care for their younger sisters, their own progeny, and progeny of their sisters. Both workers and egg layers care for whatever young are in the nest, although egg layers in nests that also contain workers do little or no foraging.

About 40 percent of the young produced are males. Adult males do not remain long in the nests, and are probably short lived.

Ovarian development was studied and illustrated. In contrast to halictids, conspicuous white masses are formed, presumably indicating both resorption of eggs and prior laying.

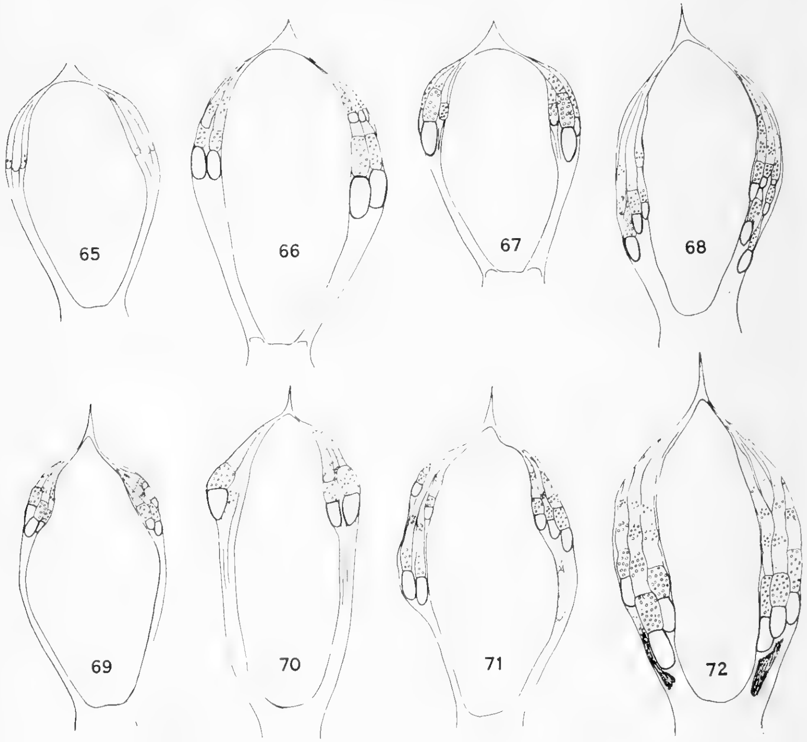
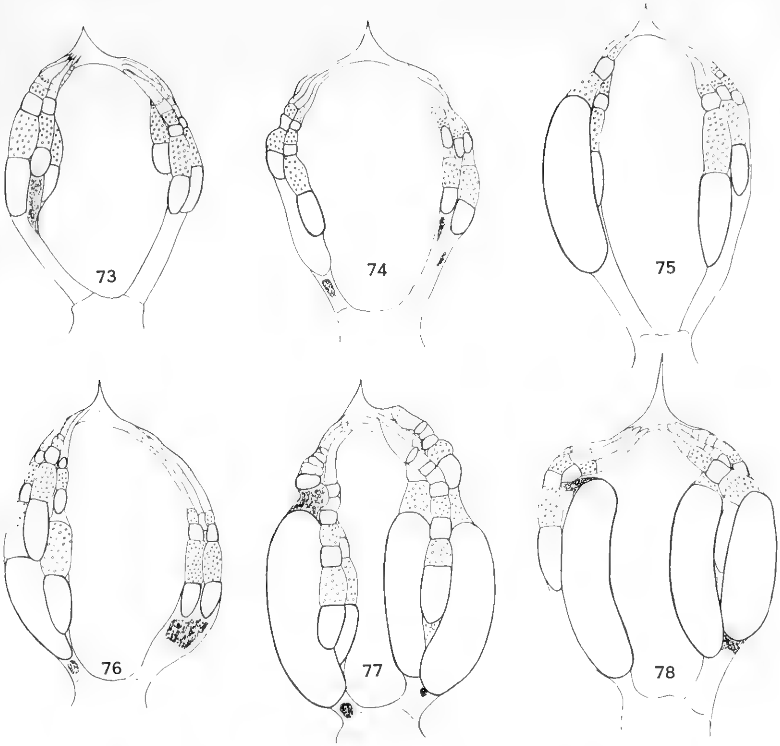
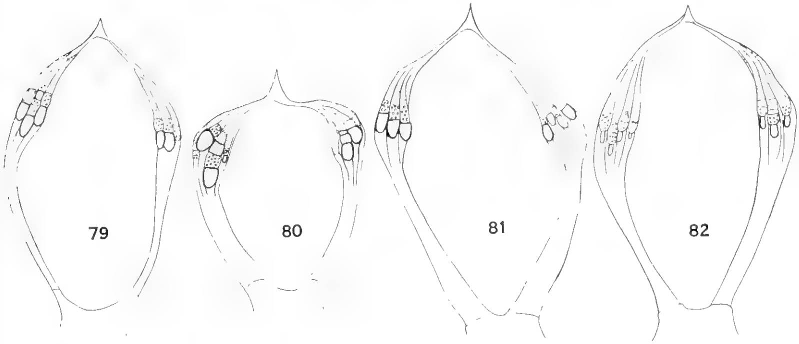


FIG. 65. Ovaries of soft, pale, young callow. Note that oocytes at the lower ends of the ovarioles are scarcely enlarged.

FIGS. 66 AND 67. Ovaries of callows. Note enlarged oocytes and well formed groups of nurse cells; in the right ovary of figure 66 each of the ovarioles has a second enlarging oocyte. There are no white bodies indicating oosorption or remains of nurse cells.

FIGS. 68-72. Ovaries of overwintering bees taken from nests and fixed on March 22, 1959. Figures 68 and 69 were from unfertilized bees with unworn wings, 70 and 71 from fertilized bees with unworn wings, and 72 from a fertilized bee with worn wing margins. Figures 68, 71, and 72 show white areas (dark in figures) in one or both of the lateral oviducts indicating oosorption. Figures 69 and 70 seem to show an anterior retreat of the ovarioles as compared to the callows. This is common in overwintering bees. There is commonly only one distinct enlarged oocyte per ovariole but there may be none (some ovarioles, figs. 67 and 68) or as many as three (right side, fig. 68). The bee that had worn wings and was therefore presumably older than the others had larger ovaries, but none of the oocytes was very large (Fig. 72). Apparently at this season oocytes of only moderate size are resorbed.





Figs. 73-78. Ovaries of some adults taken on December 26, 1959. Figures 73 (fertilized) and 74 (unfertilized) are based on bees with worn wings. They might have been either workers, or egg layers for some reason not at the moment laying eggs, and therefore with rather slender ovaries. The left hand ovary in figure 74 evidently produced a large oocyte, now being resorbed (lightly stippled). White areas (dark in figures) below the ovarioles indicate oosorption or remains of nurse cells. Figures 75 to 78 represent bees apparently in or approaching egg laying condition. Figure 75 shows no white areas below the ovarioles; this bee probably never laid an egg. Figures 77 and 78 (left side of each) show the break down of groups of nurse cells above fully formed eggs. Similar white masses (dark in figures) below the eggs probably are of this origin and indicate prior egg laying.

Figs. 79-82. Ovaries of unfertilized workers taken on December 26, 1959. Often such ovaries are flattened against the wall of the crop so that all four ovarioles are in a single plane and visible from one view, as shown on one or both sides of figures 80 to 82. The lack of white areas suggests that these bees never laid eggs. Narrow apical oocytes such as are shown in figure 82 are very rare.

Immature stages are kept more or less in age groups in the nest. Food masses are placed on the ventral surfaces of the larvae. Occasionally two small larvae may curl around a single food mass.

Life cycles and social organization of other *Exoneura* species seem similar to those of *E. variabilis.* In *E. hamulata* the colonies average larger and the active season longer. In *E. aterrima* the eggs, instead of being placed together in a batch at the bottom of the nest, are stuck by their posterior ends to the walls of the nest and the young larvae retain this position and are fed there.

Inquilina excavata is a social parasite in the nests of *Exoneura variabilis* and is closely related to *Exoneura. Inquilina* cannot collect pollen. Its females invade nests of *E. variabilis* and take up residence there in association with the *Exoneura.* Apparently the *Inquilina* prevent the laying or survival of *Exoneura* eggs in some way, for production seems to go wholly to *Inquilina,* but adult *Exoneura* (workers) must be present to bring food for the parasite. The only two *Inquilina* found with enlarged ovaries, ready to lay eggs, were in *Exoneura* nests containing a female *Exoneura* having similar ovaries. Perhaps the *Inquilina* synchronize their laying with that of the *Exoneura* in order to fit into the social system of the latter. Ultimately the *Exoneura* die off, leaving the nest to the by now maturing *Inquilina,* or some *Exoneura* survive and probably may reestablish the *Exoneura* colony.

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THE LIFE CYCLE AND BEHAVIOR OF THE PRIMITIVELY SOCIAL BEE, *LASIOGLOSSUM ZEPHYRUM* (HALICTIDAE)

By

Suzanne W. T. Batra

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The Life Cycle and Behavior of the Primitively Social Bee, *Lasioglossum Zephyrum* (Halictidae)[1]

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SUZANNE W. T. BATRA

ABSTRACT

Lasioglossum zephyrum is a small halictine bee, widely distributed in the United States. In Douglas County, Kansas, aggregations of nests were found in exposed, south-facing banks of streams or in horizontal ground near such banks. Males and females from a population on Tauy Creek had relatively larger heads than those a few miles away along the Wakarusa River. Factors influencing nest distribution in suitable habitats may include visual and chemical attraction to areas where nests have been established. The high rate of mortality of colonies throughout the season apparently was not due to any of the obvious parasites common at the nesting sites.

Males and females produced in fall were larger than those emerging in summer, perhaps because the oviposition rate declines in late summer, permitting each cell to be amply provisioned before egg laying. Castes are not distinct. The overwintered nest-founding egg-layers are often replaced by their daughters during summer. There is a continuum from queenlike to workerlike females in each nest and there are no discontinuous morphological or behavioral differences between egg-layers and females that lay few or no eggs. Unfertilized females with enlarged ovaries are common during summer and probably lay male-producing eggs. Foragers usually have somewhat enlarged ovaries and are polylectic. They were induced to collect pollen from a petri dish. Guards defend the nests against some parasites. Burrows are often tortuous with many branches. The subhorizontal cells are arranged along main burrow and branches, each cell being provided with one pollen ball and one egg before being plugged with soil. Inseminated females are the only bees that overwinter. They hibernate in short branch burrows of the previous summer's nest. In April most of them begin new nests. Each female makes, provisions, and oviposits in about 4 cells, then rests in the nest until her progeny emerge. The young females stay in the nest and deepen it

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[1] Contribution number 1245 from the Department of Entomology, The University of Kansas, Lawrence.

as reproduction continues throughout the summer. By August, nests may reach depths as great as 57 cm, with as many as 38 branch burrows, 85 occupied cells and 45 females. The number of males gradually increases during summer. They leave the nests and swarm over the nesting areas, where they mate with females of various ages.

INTRODUCTION

Halictine bees or sweat bees are of interest to many biologists because various levels of social organization occur within the subfamily. Even within *Dialictus*, a subgenus of *Lasioglossum* (to which *L. zephyrum* belongs), are found bees with solitary life cycles, such as *L. herbstiellum* (Claude-Joseph, 1926) and *L. opacum* (Michener and Lange, 1958); social bees with poorly defined castes, such as *L. rhytidophorum* (Michener and Lange, 1958); and bees with fairly distinct castes, such as *L. imitatum*[2] (Michener and Wille, 1961). A comprehensive review of the literature on life cycles of halictine bees was given by Plateaux-Quénu (1959), and nest structures and some aspects of the social behavior of many halictines were discussed in detail by Sakagami and Michener (1962), with an extensive bibliography.

In this paper, the life cycle and behavior of a primitively social, small (5-7 mm), greenish-black sweat bee are discussed. This study is part of an investigation by C. D. Michener and his associates on comparative halictine behavior, intended to elucidate the origin and evolution of social behavior.

Lasioglossum zephyrum (Smith) is widely distributed in the United States (Michener, *in* Muesebeck, *et al.*, 1951). A description of this species, as *Dialictus zephyrus*, is in Mitchell's (1960) monograph on bees of the eastern United States.

Rau (1922, 1926), Robertson (1926), Krombein (1938), Sakagami and Michener (1962), Knerer and Atwood (1962), LaBerge and Isakson (1963), and Lin (1964) all noted nests of this species, mostly in aggregations in banks of streams or lakes; but sometimes in flat ground adjacent to such banks. The nests recorded by Krombein and by Lin were seemingly in flat ground not associated with any bank. The authors listed above recorded the general structure of nests and also the swarming of males ("sun-dances" of Rau) near the nesting places. They also recorded several females in some nests; Rau (1926) found 14 in one nest.

The flight period has been shown to extend from March 21 to November in southern Illinois (Robertson, 1926) and from April to September in southern Ontario (Knerer and Atwood, 1962).

Pearson (1933) found that *L. zephyrum* was a widespread and common bee, relatively abundant in moist dune groups and on flood plains near Chicago. *Lasioglossum zephyrum* was relatively more sensitive to dryness than

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[2] Referred to as *L. inconspicuum* by Michener and Wille (1961). The synonymy was established by Knerer and Atwood (1962).

most bees experimentally tested. He thought that a function of the nest guard may be to keep moisture in the nest on warm, dry days.

Robertson (1928) recorded *L. zephyrum* on the following plants (m= male, f=female, c=female collecting pollen):

- Anacardiaceae
  - *Rhus canadensis*
  - *Rhus copallina* (f)
  - *Rhus glabra* (m, f, c)
- Apocynaceae
  - *Apocynum androsaemifolium* (f)
- Asclepiadaceae
  - *Gonolobus laevis*
- Bignoniaceae
  - *Tecoma radicans* (f, c; also f, m, on extra-floral nectaries)
- Caprifoliaceae
  - *Sambucus canadensis* (c)
  - *Symphoricarpus orbiculatus* (m, f)
- Celastraceae
  - *Euonymus atropurpureus*
- Compositae
  - *Antennaria plantaginifolia* (f)
  - *Aster ericoides* (m, f)
  - *Aster paniculatus* (f)
  - *Cacalia reniformis* (f)
  - *Erigeron ramosus* (m)
  - *Eupatorium altissimum* (m)
  - *Eupatorium serotinum* (m)
  - *Helianthus tuberosus* (c)
  - *Rudbeckia subtomentosa* (f)
  - *Rudbeckia triloba* (f, m)
- Cornaceae
  - *Cornus florida*
- Cruciferae
  - *Arabis dentata*
  - *Arabis virginica*
  - *Capsella bursa-pastoris* (f, c)
  - *Radicula obtusa*
  - *Radicula palustris*
- Ebenaceae
  - *Diospyros virginiana* (f, c)
- Hydrophyllaceae
  - *Ellisia nyctelea*
- Labiateae
  - *Blephilia ciliata*
  - *Pycnanthmum pilosum* (f)
- Lauraceae
  - *Sassafras variifolium* (f, c)
- Leguminosae
  - *Cercis canadensis*
- Liliaceae
  - *Asparagus officinalis* (f, c)
  - *Smilacina racemosa*
  - *Smilacina hispida* (c)
- Malvaceae
  - *Malva rotundifolia* (m)
- Onagraceae
  - *Ludvigia polycarpa* (f)
- Papaveraceae
  - *Sanguinaria canadensis*
- Phytolaccaceae
  - *Phytolacca decandra* (f)
- Portulacaceae
  - *Claytonia virginica*
- Ranunculaceae
  - *Actea alba* (c)
  - *Clematis virginiana* (m, f, c)
  - *Isopyrum biternatum*
  - *Myosurus minimus* (f)
  - *Ranunculus abortivus*
  - *Ranunculus septentrionalis*
- Rhamnaceae
  - *Rhamnus lanceolata* (f, c)
- Rosaceae
  - *Amelanchier canadensis*
  - *Crataegus mollis* (f, c)
  - *Prunus americana* (f, c)
  - *Prunus serotina* (f, c)
- Rutacaceae
  - *Zanthoxylum americanum*
- Salicaceae
  - *Salix amygdaloides* (f, c)
  - *Salix cordata* (f)
  - *Salix humilis* (f)
  - *Salix longifolia* (m, f, c)
  - *Salix nigra* (f, c)
- Polygonaceae
  - *Polygonum persicaria* (f)
  - *Polygonum scandens* (m)
- Saxifragaceae
  - *Philadelphus grandifloris* cult.
  - *Ribes gracile*
- Scrophulariaceae
  - *Scrophularia marilandica* (m, f)
  - *Veronica perigrina*
- Thymeleaceae

  - *Dirca palustris*
  - *Tilia americana* (f, c)
- Umbelliferae
  - *Cryptotaenia canadensis* (m, f)
  - *Sium cicutaefolium* (m, f)
  - *Taenidia integerrima*
  - *Zizia aurea*
- Verbenaceae
  - *Verbena hastata*

Mitchell (1960) and Knerer and Atwood (1962) recorded *L. zephyrum* from flowers of the following additional genera:

- Caprifoliaceae
  - *Virburnum*
- Compositae
  - *Baccharis*
  - *Cirsium*
  - *Helenium*
  - *Leucanthemum*
  - *Solidago*
  - *Taraxacum*
- Cruciferae
  - *Barbarea*
- Cucurbitaceae
  - *Cucurbita*
- Leguminosae
  - *Lotus*
  - *Medicago*
  - *Melilotus*
  - *Vicia*
- Liliaceae
  - *Scilla*
- Malvaceae
  - *Althaea*
- Nymphaeaceae
  - *Castalia*
- Polygonaceae
  - *Fagopyrum*
- Pontederiaceae
  - *Pontederia*
- Rhamnaceae
  - *Ceanothus*
- Rosaceae
  - *Aronia*
  - *Malus*
  - *Rubus*
- Saxifragaceae
  - *Hydrangea*
- Symplocaceae
  - *Symplocos*

Obviously this is a polylectic bee, as are most other species of *Lasioglossum*.

MATERIALS AND METHODS

Observations were made during 1957, 1959, 1961, 1962, and 1963 in Douglas County, eastern Kansas. Data obtained in 1957 and 1959 were kindly supplied by Dr. C. D. Michener. The techniques described by Linsley, MacSwain and Smith (1952) and by Michener, *et al.* (1955) were used in the field, with a few modifications to be described in appropriate places below. Methods for rearing *L. zephyrum* in insectary rooms were described by Batra (1964).

A total of 255 nests was excavated; 1,075 females were measured, dissected to determine reproductive condition, and examined for wear of wings and mandibles, and 741 males were examined for wear and measured. Many observations on living bees in the field and in four insectary rooms were made. A total of 152 days were spent in the field (107 of these days were during 1962 and 1963).

GENERAL LIFE HISTORY

A brief account is given here to provide background for subsequent sections of the paper.

Relatively unworn, inseminated females with slender ovaries are the only bees that overwinter. They stay at the ends of short branch burrows diverging from the main burrows of the previous summer. In early spring, at about the time *Ulmus americana* is in bloom (March 24, 25 and April 1),[3] females appear at the entrances of the nests, and begin flying during warm hours of the day. Some of these females stay in the old nests, but most begin to excavate new nests. They feed on nectar and pollen as their ovaries enlarge. New nests were first seen on April 2, 13, and 14, and the bees were first seen carrying pollen to nests on April 17 and 21. Three or four cells per bee are made and mass-provisioned with a mixture of pollen and honey. An egg is laid on the provisions in each cell, which is then plugged with a little soil. The females then cease activity and wait in the nests while their brood matures. Bees had ceased collecting pollen on May 7, 12, and 13, although a few were still flying about after these dates.

The new generation of males and females emerged from the nests on May 22 and 25. A few young pollen collectors were seen on these dates. These young females stay in the nests started by the overwintered females, enlarge them and make and provision cells. Some mate and many of them, whether inseminated or not, develop large oocytes. They probably lay eggs and apparently replace the overwintered females (no marked overwintered females were found after June 14). The nests remain continuously open and the bees active through the rest of the summer. Castes are not clearly defined in this species and all intergradations from queen to worker are found in nearly every nest. During summer, the relative proportion of males produced gradually increases, and by August they form large swarms over the nesting areas.

The last females collecting pollen were seen on September 13, 20, 27, and October 2. The last males were seen October 2, 12, and 10. Overwintering females were guarding nests as late as October 19, 23, and 29.

Nests are usually excavated in banks of streams at about a 90° angle to the soil surface. The circular entrance is about 2 mm in diameter; the burrow, usually branched, is 4 mm in diameter and lined with a thin layer of compressed soil. Cells are 9 to 11 mm in total length, 4 mm in maximum width, and except for the neck, which is about 2 mm long, are lined inside with a shiny waterproof film. Constructed serially along the main burrows, they are bilaterally symmetrical (*sensu* Malyshev, 1935) and subhorizontal. As in other halictines, each cell contains one ball of moistened pollen and one egg. After oviposition, the neck of each cell is filled with loose soil.

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[3] Dates in series such as these refer to different years in which meaningful data pertaining to initiation or cessation of specific activities were available. In some years, observations concerning these activities were not frequent enough and are therefore omitted.

Usually cells deepest in the nest contain the youngest stages of the brood. Nests are in groups known as aggregations and the several females in each nest constitute a colony.

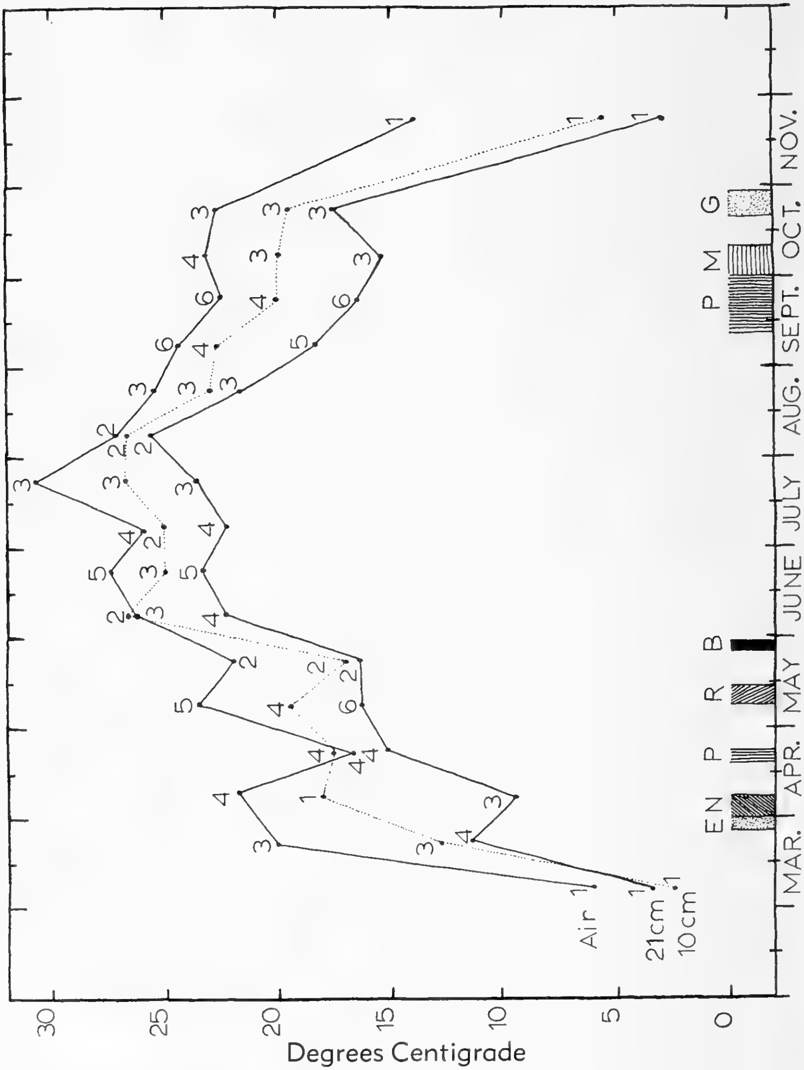


FIG. 1. Mean air temperatures (measured at a height of 1 m, in shade, upper line), and mean soil temperatures [at depths of 10 cm (dotted line) and 21 cm (lower line)] taken at the County Line and Wakarusa nesting areas between 10 a.m. and 4 p.m. over a period of 3 years. The number of measurements for each mean is indicated at each point. Below the temperature graph is a chart indicating the first dates when bees were seen emerging from hibernacula (E), excavating nests (N), collecting pollen (P), resting in closed nests (R), and when the first brood emerged (B). The last dates for pollen collectors (P), males (M) and guards (G) are also indicated.

NESTING AREAS

The Environment and the Aggregations

Douglas County, where my observations were made, is in central eastern Kansas. Altitudes are 236 to 366 m above sea level. The climate is continental. Nearly three-fourths of the annual precipitation falls during the growing season (196 days). The average date of the last killing frost in spring is April 10 and the average date of the first killing frost in fall is October 23 (Fig. 1). The mean annual precipitation at Lawrence is 88 cm and the mean annual temperature is 14°C (O'Connor, 1960). Non-cultivated areas are now covered with trees and brush, although before the arrival of European man, most of the area was prairie.

Lasioglossum zephyrum, in this area, usually nests in the bare, steep, periodically eroded silty-clay banks of permanent or semipermanent streams. Compact soil, exposed to the sun much of the day (at least in spring, when nests are founded), seems to be preferred.

Most observations were made at two locations where nests were numerous, described below:

1. *County Line.*—This area, on the farm of Mr. Roy Stecher, at the Douglas-Franklin County line, is near Tauy Creek, a semipermanent tributary of the Marais des Cygnes River. When this location was discovered in 1957, the bees were nesting in a south-facing, bare bank of clayey sand about 15 m from the creek. A few nests were found in sloping or horizontal ground (a cowpath) at the base of the bank and some nests were in the temporarily dry creek bed. In 1959, nests were confined to the almost vertical bank (1.5 x 2 m), with very few in the horizontal ground nearby. By 1961, bees had deserted the bank, which was crumbling, over 90 per cent of the nests being located on nearby flat ground in the cowpath; maximum density was 30 nests per square meter (maximum internest distance 44 cm; minimum internest distance 2.5 cm). This flat area of 16 sq. m in front of the bank was partly covered with clumps of short grass and weeds. Nests were in bare patches of ground as well as in the vegetation and *Lasioglossum imitatum* was also nesting here. The bank and flat area, partly shaded by trees, were in sun during most of the afternoon and were subject to occasional flooding. In March, 1962, the owner widened the path with a bulldozer, cutting into the compact clay soil of a southeast-facing slope about 20 m away, and clearing all vegetation from the cowpath. In 1962, the bees colonized this new vertical bank (Fig. 2), digging 49 nests in its surface of roughly 1.4 x 4 meters. An additional 23 nests were made in a horizontal area of 3 x 4 meters in front of this second bank (maximum internest distance 2 m; minimum internest distance 3 cm). These areas were in sun all day during spring but the bank was shaded by a small tree most of the day in summer. Twenty-five nests were started that year in the original bank, and 5 nests in the cowpath in front of it, but all of them had died out by the end of the summer. In 1963, the horizontal areas in front of both banks had no nests, and were partly covered with grass and weeds. No bees were nesting in the crumbling original bank, which was riddled with old abandoned burrows of past years. The new bank had only seven nests.

2. *Wakarusa River.*—In June, 1962, a large aggregation of *L. zephyrum* was found in a steep alluvial bank of this tributary of the Kansas River, 7.5 miles southwest of Lawrence. The nearly vertical bank, facing southwest, extended from the water level to a height of about six meters (Fig. 3). It was composed of compact silty light brown clay previously deposited by the river. No vegetation was on its surface, but brush and a black walnut tree (*Juglans nigra*)

FIG. 2. The nesting area in a bank at County Line (1962). Nests were in the bank and the flat ground near the equipment.

grew above it. The overhanging tree shaded the bank until 4:30 p.m. during the summer. Bees' nests were in the topmost 1.5 meters of the bank, under loose hanging roots of the tree, reaching a maximum density of 320 nests per square meter (maximum internest distance 16 cm; minimum internest distance 6 mm in this square meter). No nests were in a zone of heavy dark gray clay that was in the nesting area. The entire bank was occasionally eroded by flood water. Few bees remained in this bank in 1963 after a flood had eroded much of the bank (maximum density was two nests per square meter) and by August, no nests were there. A new nesting site was found in April, 1963, about 50 meters upstream. This bank, composed of similar soil, was about three meters high and faced south. It was exposed to sun all day and had no vegetation on its face, although grass and weeds grew above it. The nests were in the upper one to two meters of the bank among hanging roots and stems of *Vitis*. There were 5 to 10 nests per 0.09 sq. m over most of the nesting area (maximum density 36 nests per 0.09 sq. m; maximum internest distance 14 cm; minimum internest distance 6 mm). Nests in this bank all appeared to be new; there was no evidence of a previous year's burrows or cells.

The disappearance of aggregations at the County Line and Wakarusa nesting sites may have been in part due to my removal of colonies for study. Many nests were destroyed by floods but most of the colony mortality was due to unknown causes.

Small aggregations of *L. zephyrum* were found also (1957, 1959, 1961, 1962) in a south-facing sandy bank of the Kansas River, in North Lawrence, and in a southwest-facing vertical clay bank near a small stream at Hole-in-the-rock (1959), 12 miles south of Lawrence. The latter aggregation reached a density of 20 nests per square meter; *Anthophora abrupta* was also nesting there. Twelve nests were found on the gently sloping bare clay banks of a small semi-permanent tributary of the Wakarusa River, but the bees died out during the summer (1962). *Lasioglossum zephyrum* may occasionally make isolated, scattered nests but no search was made for them. Two females were collected on the campus of The University of Kansas in April, 1963, at a footpath on a north-facing partly shaded slope. They apparently were looking for nesting sites although far from water or known aggregations. No nests were established there.

Factors Influencing Nest Distribution

Although in Douglas County, *L. zephyrum* usually nests in bare, south-facing banks of compact silty alluvium and in horizontal surfaces of similar soil near inhabited banks, many apparently favorable habitats did not contain nests. The aggregations that were found were limited in extent and did not fully occupy apparently suitable areas, but nests were somewhat clustered together.

When about to start nests, females often appear to be attracted to sites where others already have begun nesting. They may be attracted by the odor of existing nests or bees, as seems to be the case in *Amegilla salteri* (Michener, 1961). When vials were opened in which living females of *L. zephyrum* had been kept for several weeks, a sweet pungent odor could be often detected. The pollen balls and wet, newly-made waterproof linings of empty new cells had a similar, rather stronger odor.

Females are attracted by visual stimuli such as entrances of nests and other irregularities in the soil surface. In the insectary rooms, nests and shallow "sleeping places" were frequently started where a clod of soil rested on the soil surface, or around the edges of small stones. Females readily

FIG. 3. The nesting area on the Wakarusa River (1962). Nests were in the bank below tree marked 'X.'

entered holes 4 mm in diameter punched in the soil and some began nests in these.

In the field, females about to begin nest construction in spring fly back and forth in front of banks, often alighting to investigate nest entrances, crevices, holes, or protuberances. Ten holes, 4 mm in diameter and about 6 cm deep, were made by me in a bank, and one week later five of them were occupied (April 21, 1962). Females also appear to be attracted by concavities in the bank surface and by overhangs, in this respect resembling *Thygater* and *Lonchopria* (Michener, *et al.*, 1958). Nests were often started during spring in cavities where I had previously excavated, and the greatest concentrations of nests were found below the overhanging tops of banks.

SURVIVAL OF COLONIES AND AGGREGATIONS

In studying survivorship, numerous nests were marked by pushing a wire bearing a numbered aluminum tag into the soil 2 cm to the right of each nest. The number of such nests having a guard was counted at intervals. Because new nests are not normally founded during summer, counts of the number of active nests in designated areas, made at intervals, indicated colony mortality rates in large aggregations. When a sample of apparently vacant nests was excavated, no bees of any age were found.

Most nests founded in spring were abandoned after a few months. The reasons for this mortality of colonies were not clear. Survivorship curves for colonies of *L. zephyrum* (Fig. 4) resembled those for *L. imitatum* (Michener and Wille, 1961). The survivorship curve for eight colonies in an insectary room was similar to curves for 510 colonies in seven aggregations at three locations in the field.

This seasonal mortality does not seem to be due to any of the natural enemies discussed by Batra (1965) but a few observations of sudden extinction of colonies in the insectary rooms suggested that disease may be a factor. In these instances, the adults ceased activity and died within a few days either staying in the nest or crawling out. Larvae and pupae (visible through the glass walls of the nest boxes) apparently were unaffected. When they emerged from cells as adults they probably died or left, for the nests were not repopulated. Dissections of dead and dying bees revealed no obvious parasites or lesions. It is possible that death of the egg-layer, and failure to replace her, may have been a factor in colony mortality. However, in this species there are usually some "workers" with enlarged ovaries in each nest and males were available all summer for insemination; it is probable that egg-layers are normally replaced.

In 1957 a heavy infestation by the mermithid nematode, *Hexamermis* sp., apparently was responsible for the mortality of many colonies in an aggregation. However, this nematode is usually not very common.

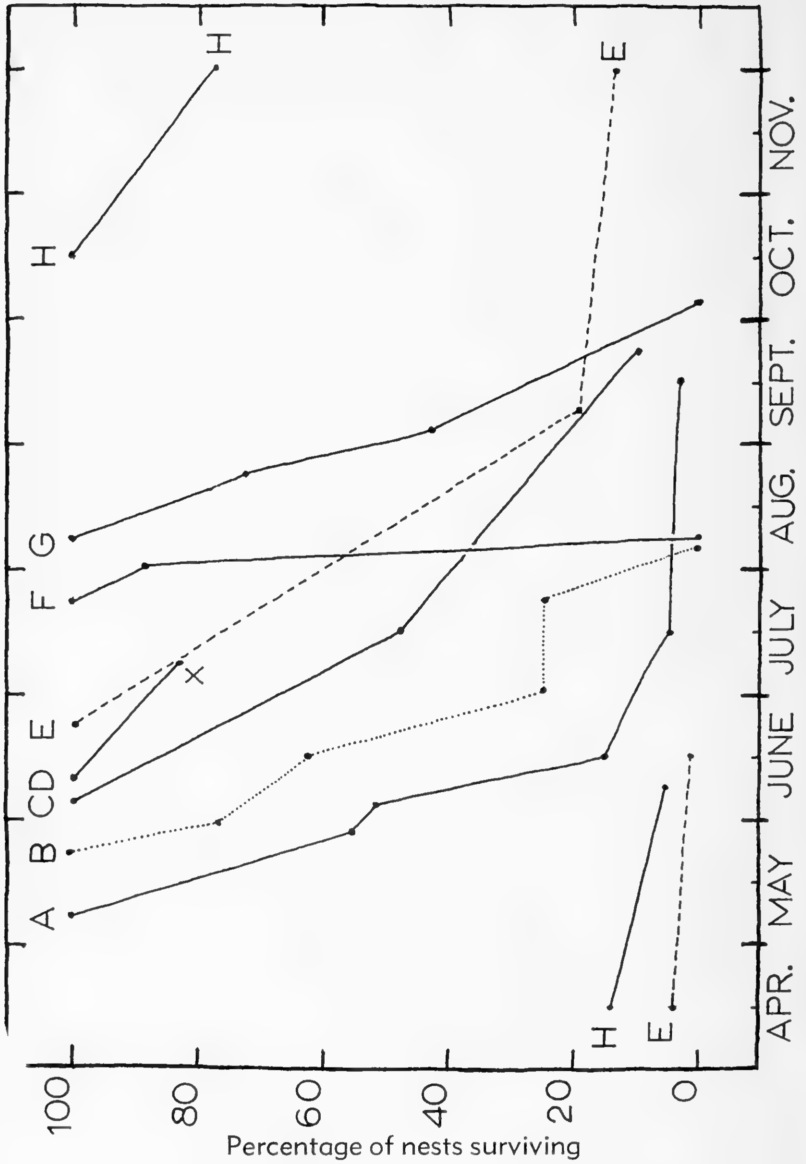


FIG. 4. Survivorship curves for colonies in 8 aggregations. A, 34 nests at County Line, 1962; B, 8 nests in the insectary room, 1963; C, 28 nests at County Line, 1962; D, 36 nests at Wakarusa, 1963 (observations terminated (X) when a flood destroyed the aggregation); E, 320 nests at Wakarusa 1962 to 1963; F, 49 new nests begun in summer after a flood at Wakarusa, 1963; G, 7 nests at Wakarusa, 1963; H, 36 nests at Wakarusa, 1962 to 1963.

Lasioglossum zephyrum, as mentioned above, usually nests in locations subject to flooding. All aggregations regularly observed were covered by water at least once annually. In one nest, excavated soon after it had been covered for several hours by about 1.5 m of water (July, 1963), living pupae were found in cells 4 cm or more below the surface of the bank. All pupae less than 4 cm from the surface of the flooded bank were dead. Several living adults of various ages were in this nest, as well as in others excavated at the same time. Twenty-four hours after water one meter deep had covered a nest site for six hours (September, 1961), guards were at the repaired entrances of three of seven marked nests (the tags of many more were washed away). Apparently the nest entrances are plugged by mud, which traps sufficient air in nests for survival. Nests excavated after flooding did not appear to have had water flowing into them.

Flooding causes great mortality when parts of banks containing nests are washed away. This happened to portions of two aggregations (July, 1963, September, 1962). Two days after the flood of July, 1963, in which hundreds of nests were completely washed away, many inseminated, somewhat worn females with enlarged ovaries excavated at least 50 new nests in the freshly eroded area. These nests, similar in structure (Table 5) to the early spring nests made by overwintered bees, rapidly died out (Fig. 4), perhaps due to the dryness that followed the flood. Apparently none of the brood reached adulthood.

LOCAL AND SEASONAL VARIATIONS IN SIZE

Local Size Difference

Females and males from the County Line aggregations had relatively larger heads (mean head widths) and mandibles than individuals from the Wakarusa aggregations. Mean wing lengths of large samples of each sex from both locations were similar and will therefore be used in the discussion of seasonal sizes and castes. Although there was a conspicuous difference in the relative proportion of head size to body size (measured as wing length) between the County Line and Wakarusa populations, no significant differences (except those rather obviously due to environmental factors) were found in the behavior or life cycles of bees in these populations. Mr. George Eickwort (personal communication) has found similar morphological differences between populations of *L. zephyrum* in Oregon and size variation in Ontario (Knerer and Atwood, 1962) may be of the same sort. Possibly populations of this bee are genetically more isolated than those of other halictines because it nests along streams and mates at the nesting site. The County Line population on the Marais des Cygnes watershed is about 16 miles south of the Wakarusa population, on the Kansas River watershed. An extensive sampling of *L. zephyrum* from many areas should be made to clarify this situation.

Head capsule widths of 22 preserved last instar larvae from the Wakarusa population averaged 1.07 mm (S.E.=.007). Head capsule widths of 17 last instar larvae collected in June at the County Line nest site averaged 1.12 mm (S.E.=.010) and 27 last instar larvae from that population in August averaged 1.14 mm (S.E.=.007) in head capsule width. Larvae, as well as adults, from the Wakarusa population had relatively smaller head widths than those from County Line.

SEASONAL DIFFERENCES IN SIZE

Seasonal size differences in both males and females have been recorded for *L. imitatum* (Michener and Wille, 1961), and seasonal size differences in females are known for *L. duplex* (Sakagami and Hayashida, 1958), *L.*

TABLE 1. Seasonal variations in mean wing lengths of females in Groups A, C and E. Standard errors (S.E.) and sample sizes (N) are indicated. Young females (Group E, wear < 3) significantly differ in mean size at the 5% level when May and June, June and July-Aug., July-Aug. and Sept.-Oct. samples are compared. Mean sizes of Group A females did not differ significantly during the year, and little-worn Group A females are not significantly smaller than Group A females in general. (All comparisons made with "Student's "t" test.)

		Group A total "queens"	Group A wear <3 new "queens"	Group C total	Group E wear <3 young bees	Group E wear >5 old "workers"
April	$\overline{X}$ S.E. N	4.565 .087 11	0	0	0	0
May	$\overline{X}$ S.E. N	4.626 .054 31	0	4.616 .114 3	4.371 .03 27	0
June	$\overline{X}$ S.E. N	4.524 .057 30	4.395 .111 6	4.354 .04 39	4.227 .03 39	4.180 .162 3
July	$\overline{X}$ S.E. N	4.555 .051 17	4.200 2	4.289 .019 64	4.149 .018 188	4.164 .044 22
Aug.	$\overline{X}$	4.469 .072 21	4.270 1	4.184 .022 48		
Sept. and Oct.	S.E. N		0	5.310 1	4.526 .046 96	4.513 .369 14

rhytidophorum (Michener and Lange, 1958), *Halictus ligatus* (Knerer and Atwood, 1962) and *L. malachurum* (Stockhert, 1923; Bonelli, 1948), all of which show social tendencies and production of young in both summer and fall. In these species, females emerging in summer are smaller than those which emerge in the fall, overwinter, and start new nests in spring (queens). *Lasioglossum zephyrum* also shows this pattern of seasonal size variation in males and females. This trend is most clearly seen if only the youngest of the females are considered (Table 1, unworn group E females), probably because older bees are of variable and unknown ages, so that they confuse the relation between size and season.

Observations made in the insectary room (Batra, 1964) suggested that seasonal size variation may be caused by fluctuations in the relative number of pollen collectors and egg-layers in each nest. Mean numbers of eggs and pollen balls without eggs per nest in the field (Fig. 21) show peaks in egg production in early June and early August. In contrast to the situation in preceding months, the mean number of eggs in late July and August was clearly greater than the mean number of pollen balls without eggs, possibly indicating some competition for available provisions among egg-layers. If, under such circumstances, pollen balls are completed and eggs laid on them before they reach maximum size, production of relatively small bees in late summer could occur (Table 1, unworn group E females). The larger, overwintering bees seen in October and spring may arise from the few eggs laid in late August and early September in more amply provisioned cells, when pollen collectors are more active than egg-layers according to Fig. 21. Too few pollen balls were measured, due to difficulty in handling them, to determine whether there are significant seasonal differences in their sizes.

FEMALES

Caste Differences

In studying castes, methods recommended by Michener, *et al.* (1955) were used, with minor alterations. Before nests were excavated, their entire populations were aspirated and immediately preserved in Carnoy's fixative. (The material was less brittle than when preserved in Dietrich's solution and could be used for later histological work.) Often the activities of marked individuals were observed for a day or longer before their nests were opened. The wing lengths and head widths of preserved bees were measured, and the number of nicks in both forewings was counted. Mandibles were grouped in seven classes of wear (Michener and Wille, 1961), ranging from unworn (class 1), to very worn, with the subapical tooth and notch gone (class 7). Index of total wear was a sum of number of wing nicks and mandibular class. This index ranges from 1 (unworn) to a maximum of 30. Abdominal terga of the preserved females were removed, the spermathecae examined for sperm cells, contents of the gut noted, amount of fat estimated, degree of enlargement of the poison glands of the sting apparatus noted, and development of oocytes in the ovaries recorded.

Lasioglossum zephyrum resembles *L. rhytidophorum* (Michener and Lange, 1958) in the weak differentiation of castes. There are no discontinuous morphological or behavioral differences between probable egg-layers and females that lay few or no eggs. Rather, there is a continuum from queen-like to worker-like individuals. Young (unworn) inseminated or non-inseminated females commonly develop enlarged ovaries as they become older (more worn), although one or more bees with enlarged ovaries may be living in the nest at the same time. Most workers are moderately worn females with somewhat enlarged ovaries and they probably occasionally lay eggs. Relatively few much-worn females with undeveloped ovaries, comparable to the females that constitute the worker caste in social bees, including *L. imitatum, L. malachurum,* and others, are found.

For this study, five groups of females were recognized, based on degree of ovarian development and presence or absence of spermatozoa in the spermatheca. As in *L. imitatum* (Michener and Wille, 1961), "group A" females were fertilized, with several large oocytes, the anterior portions (terminal filaments) of the ovaries sometimes being pressed into folds and containing somewhat swollen oocytes. Usually such bees had one or more eggs large enough to lay (1 mm or more in length).

Group B females were fertilized, with somewhat enlarged oocytes, and may or may not have had an egg ready to lay (largest oocyte 0.25 mm or more in length).

Group D females were fertilized but oocytes were not enlarged (largest oocyte less than 0.25 mm long).

Group C females were unfertilized, their degree of ovarian development like that of group B. They probably laid some male-producing (haploid) eggs.

Group E females were unfertilized with small oocytes less than 0.25 mm long, or rarely without oocytes visible with the dissecting microscope.

The percentage of females belonging to each of these groups varies during the year (Table 2). In spring, all bees are large, fertilized, overwintered females (groups A, B, D). A given female could have been classified in any of these three groups, depending on the amount of ovarian enlargement after she emerged from hibernation (as a group D female) and whether she had recently oviposited (possibly reducing her from group A to group B).

In May, the first young, on the average smaller, unfertilized females appear (group E). Many of them develop enlarged ovaries within about 15 days after emergence, thus joining group C.

Group C females (Fig. 5) comprise about 35 per cent of the population during midsummer. They may lay many haploid eggs, resulting in the

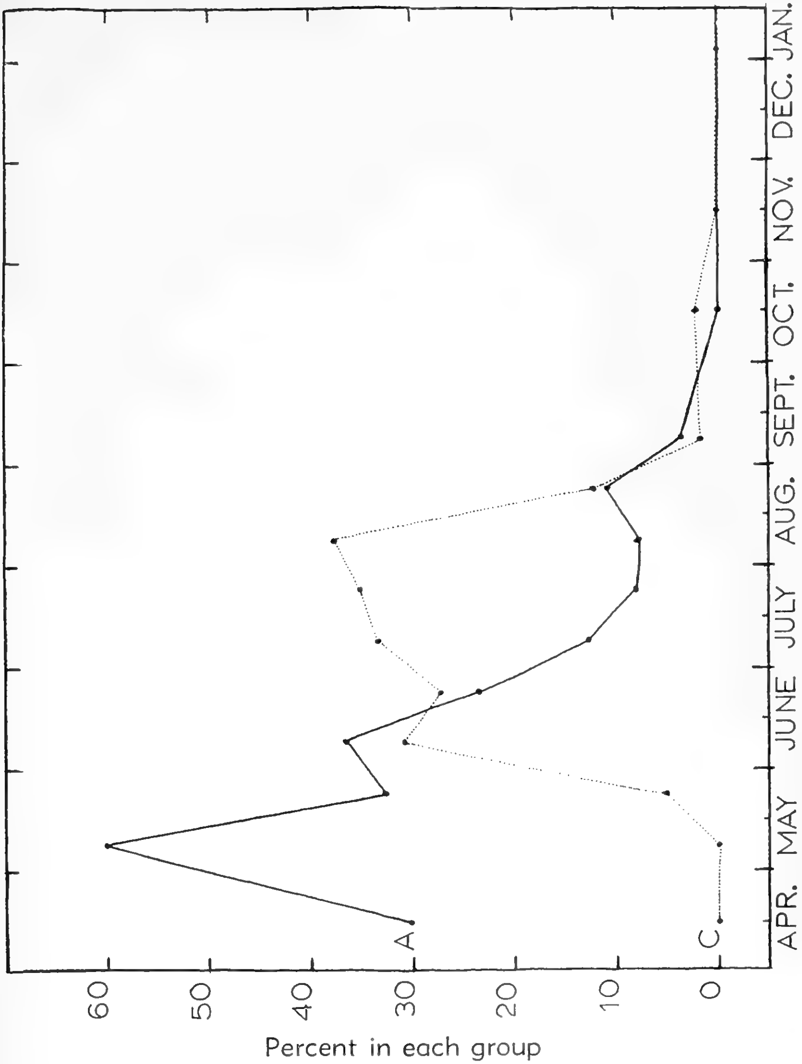


FIG. 5. Seasonal fluctuations in proportions of females belonging to groups A and C from nest populations. See Table 2 for information concerning other groups.

August and September peaks in production of males (Fig. 22). Unfertilized bees probably produce many of the males in *L. malachurum* also (Noll, 1931). In early August, as the number of males increases, many group C females probably become inseminated, thus joining group B, which increases at this time.

During summer, the proportion of females in group A decreases as the total number of females per nest (in other groups) increases. The number

TABLE 2. Seasonal fluctuations in the percentages of 831 females from nest populations that belong to each ovarian group.

	Inseminated			Not Inseminated		Number of bees
	A	B	D	C	E	
April	30.6	18.3	51.0	0.0	0.0	49
May 1-15	60.0	6.6	33.3	0.0	0.0	30
May 16-30	32.7	20.0	5.4	5.4	36.3	55
June 1-15	36.7	4.5	4.5	31.0	22.9	87
June 16-30	23.7	15.2	3.3	27.1	30.5	59
July 1-15	12.6	5.7	3.4	33.3	44.8	87
July 16-30	8.2	12.4	5.5	35.1	38.6	145
August 1-15	7.8	12.5	4.7	37.7	37.0	127
August 16-30	11.1	20.8	18.0	12.5	37.5	72
September 1-15	3.5	26.7	44.6	1.7	23.2	56
October	0.0	8.5	57.4	2.1	31.9	47
November	0.0	9.0	91.0	0.0	0.0	11
January	0.0	0.0	100.0	0.0	0.0	6

in group B remains fairly constant, perhaps because inseminated group C females and group D females whose ovaries had enlarged join this group.

In August and September, the total percentage of females with enlarged ovaries (groups A, B, and C) declined from about 58 to about 13 per cent, as the total percentage of females with slender ovaries increased from about 42 to about 87 per cent (Table 2). It is not clear why the ovaries of females do not enlarge in late summer, but perhaps environmental influences such as declining average temperatures (Fig. 1) or shortened day length have some effect. By October most bees with slender ovaries are inseminated (group D), and only these and a few little-worn group B females with slightly developed ovaries enter hibernation.

"QUEENS"

Because there is, during summer, a continuum between queenlike and workerlike individuals, only females belonging to group A will be classified as queens in the discussion below. Females in groups B and C probably lay some eggs, but many of them act as foragers (workers). All females in spring before the summer bees emerge are, of course, "queens," although they first appear as group D and later pass through group B to group A.

An effort was made to determine whether the large, overwintered egg-layers (group A) live longer than "workers" (groups B, D, E, and C in summer). Marking bees with "dope" and enamels was unsuccessful, for the spots of paint did not adhere well and often peeled away within a few days. Many overwintered females were marked in April and May by clipping off the tarsus of one middle leg, and replacing the bees in their marked nests. Five of them lived until the second week of June, but no marked spring egg-layer was recovered after June 14. These old egg-layers had an index of wear of five to eight, no pollen in the crop, and belonged to groups A and B.

The index of total wear may be used to indicate the relative age of bees, assuming that all bees are active or work equally and fairly constantly. The index of wear of group A bees showed a steady increase until the end of May after which it declined (Table 3). In June, an increase in wear in all groups was seen, probably related to a sharp increase in production of brood at that time (Fig. 21). During the rest of the summer, the mean index of wear of group A females fluctuated but showed no overall increase, probably indicating that as egg-layers became older (more worn) some of them were re-

Table 3. Indices of total wear of females belonging to groups A to E during the year. All specimens were taken from nests. Mean (X), range (R) and number of bees examined (N) are indicated. CL and W refer to females from County Line and Wakarusa, respectively. The usually lower indices of wear of County Line females may be due to the relatively lesser wear of their larger mandibles.

		Inseminated			Not Inseminated	
		A $\bar{X}$,(R),N	B $\bar{X}$,(R),N	D $\bar{X}$,(R),N	C $\bar{X}$,(R),N	E $\bar{X}$,(R),N
April	C.L.	0	2.29(1-4)7	2.58(1-6)24	0	0
	W.	5.40(3-8)15	2.50(2-3)2	3.00(3)1	0	0
May 1-15	C.L.	4.50(4-5)4	0	0	0	0
	W.	8.07(4-25)14	4.50(4-5)2	5.80(3-9)10	0	0
May 16-30	C.L.	6.00(5-8)8	3.50(3-4)2	0	0	3.25(1-8)4
	W.	8.23(4-25)13	6.50(3-11)6	4.33(1-10)3	2.33(2-3)3	1.56(1-3)16
June 1-15	C.L.	4.29(1-12)18	4.00(4)1	2.33(1-4)3	3.89(1-7)19	5.77(1-15)13
	W.	7.07(3-12)15	2.00(2)2	1.00(1)1	3.00(1-5)8	3.14(2-4)7
June 16-30	C.L.	6.92(3-14)12	4.00(4)4	9.00(9)1	4.73(1-13)15	2.40(1-9)15
	W.	10.33(8-13)6	10.00(10)1	6.00(6)1	6.00(6)1	3.30(3-4)3
July 1-15	C.L.	4.88(2-11)8	2.50(1-4)2	1.00(1)2	1.55(1-3)18	2.42(1-16)26
	W.	6.60(4-11)5	3.00(3)1	1.00(1)1	3.27(1-8)11	2.31(1-5)13
July 16-30	C.L.	5.38(1-13)13	6.00(1-9)5	2.00(1-4)7	4.34(1-15)32	1.97(1-6)30
	W.	9.55(2-19)11	3.00(1-8)8	1.00(1)1	2.68(1-4)19	2.00(1-6)26
August 1-15	C.L.	5.38(3-10)13	3.86(2-6)7	2.50(1-6)6	3.48(1-8)42	2.47(1-10)45
	W.	4.00(4)2	3.50(3-4)4	0	4.33(3-6)6	4.00(4)2
August 16-30	C.L.	7.05(1-30)21	9.00(3-15)2	4.62(1-10)13	4.89(2-12)9	3.37(1-18)27
	W.	0	0	0	0	0
September	C.L.	11.33(7-17)3	7.71(3-19)14	4.80(1-12)25	1.00(1)1	2.00(1-12)13
	W.	0	0	0	0	0
October	C.L.	5.50(2-9)2	9.00(6-12)2	1.48(1-4)27	1.00(1)1	2.53(1-7)15
	W.	0	0	0	0	0
November	C.L.	0	6.00(1)1	3.70(1-10)10	0	0
	W.	0	0	0	0	0
January	C.L.	0	0	0	0	0
	W.	0	0	2.30(1-5)6	0	0

placed by relatively unworn younger bees. However, observations in the insectary room (Batra, 1964) suggested that the egg-layers do little work in or outside the nest and it is possible that the index of wear of such bees does not significantly increase as they become older. But some group A females (indices of wear 1 to 3) which were not worn enough to have begun the nests in spring were found from early June to October, which strongly suggests that replacement of worn egg-layers by at least some unworn (young) ones is likely (Table 3).

The large mean size of group A females even in late summer may indicate either that few were replaced, or that only the largest summer bees joined group A. A sample of 6 little-worn group A females in June was not significantly smaller than 30 group A females in June, suggesting that large summer bees join group A (Table 1), but it is also possible that these little-worn group A females had overwintered and for some reason had done little work. Replacement of egg-layers may be common, since males are present all summer and ovaries of many females appear to enlarge spontaneously (i.e., without mating), as in *L. rhytidophorum* (Michener and Lange, 1958).

Females in group A are not always the largest individuals in each nest. Thirty-five nests containing at least one group A female each were examined from May to August, before production of the large overwintering bees began. In 21 of these nests, a group A female was the largest, but in 14 of them, a bee belonging to another group was largest (group E in 6 nests, group D in 2 nests, group C in 3 nests and group B in 3 nests). This also may indicate that the original large overwintered group A female is sometimes replaced by one of her smaller daughters.

Nests having no inseminated female with enlarged ovaries are common (Fig. 6). In April, many of the overwintered bees were just beginning nests and their ovaries had not yet developed mature oocytes. Before the first young females emerged from their cells at the end of May, many of the overwintered egg-layers that were resting in closed nests again had slender or only moderately enlarged ovaries. During mid-summer, death of egg-layers with no immediate replacement probably occurred. After August, development of eggs appeared to be inhibited.

"WORKERS"

Females with various degrees of ovarian development act as workers during summer. Dissections of 113 females that were collecting pollen in July, 1962, when nests were not being provisioned by solitary egg-layers, showed that 63 per cent of them belonged in group C, 20 per cent in group E, 11 per cent in group B, 4 per cent in group A, and 2 per cent in group D. At that time of year (Table 2) about 33 per cent of females in nests belonged in

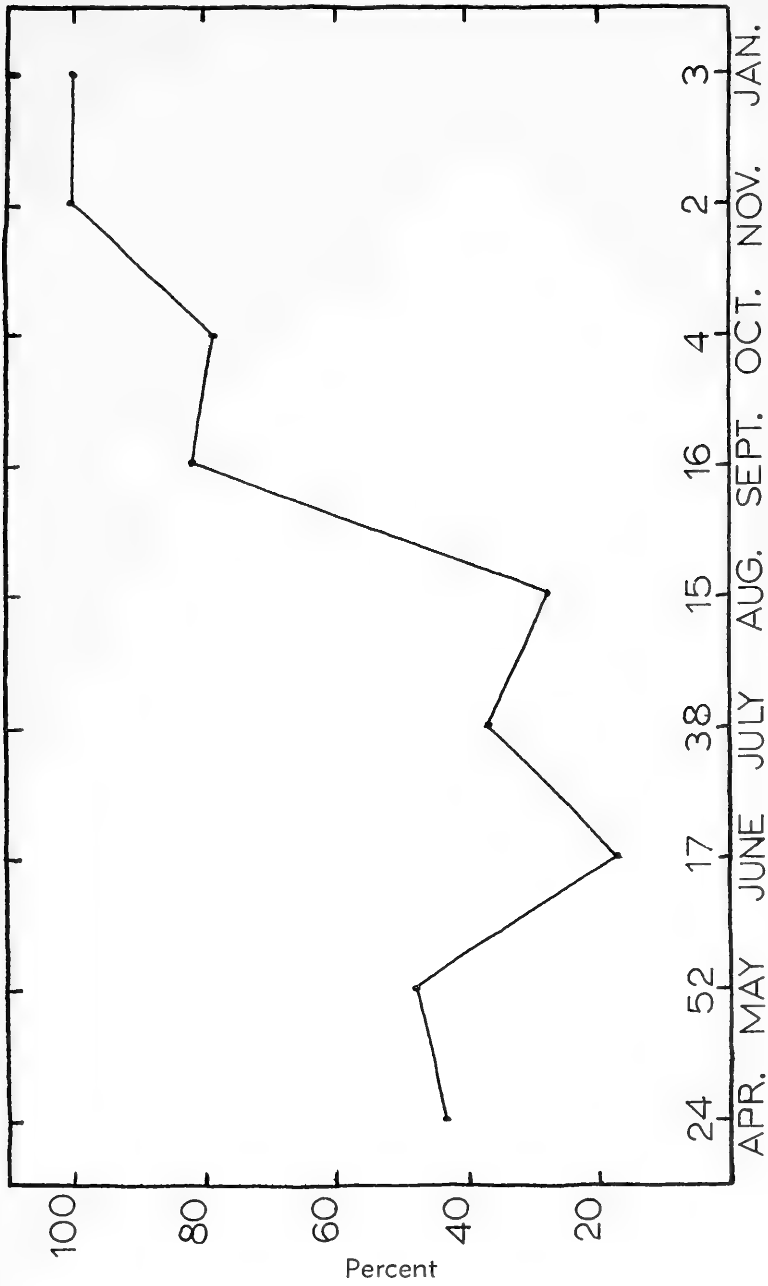


Fig. 6. Percentages of nests having no female ("queen") belonging to groups A or B. Numbers across bottom refer to numbers of nests examined each month.

group C, 45 per cent in group E, 6 per cent in group B, 13 per cent in A and 3 per cent in group D. Relatively more group C and fewer group E females acted as foragers than would be expected, if foraging were randomly distributed among the groups. Fewer females belonging to groups A, E, and D were collecting pollen than were present in the general population, probably because the group A females ("queens") mainly laid eggs and group D and E females were immature.

From the end of May to July, most foragers belong to group C, but in August most of them were in group E, perhaps reflecting the inhibition of oocyte development seen in late summer (Table 2).

The mean mandibular wear of pollen collectors during most of the summer was about three but wing wear fluctuated, maximum wing wear occurring in June and August, when peaks in production of brood were seen Figs. 7, 21). The increase in mean mandibular wear of foragers in fall probably occurred because younger, less worn bees emerging at that time did not also collect pollen.

The moderately worn mandibles and enlarged ovaries of most pollen-collectors suggest that, in this species, foragers are bees that have done or are doing some excavation in the nest while their ovaries enlarge. Observations in the insectary rooms showed that the youngest bees (probably group E) excavate the burrows, and only after a week or more do they usually begin to collect pollen and make cells (Batra, 1964). The relatively few group E females active as pollen collectors in the field also suggested this, although such bees leave their nests for other purposes.

Group C females appeared in nests 15 to 20 days after the emergence of group E females in May, indicating that females belonging to group C (most foragers) were individuals that had previously belonged to group E, as was expected.

Unlike *L. imitatum* (Michener and Wille, 1961), group E females with an index of total wear of five or more (typical "workers"), were rare, comprising only 3.4 per cent of summer females. *Lasioglossum zephyrum* does not have a large distinct worker caste, to which the older (more worn) females can be assigned. Worn group E females were of approximately the same sizes as unworn (total wear 3 or less) group E females (Table 1).

Apparently *L. zephyrum* is a bee in which castes are indistinct. Development of large oocytes occurs in most fertilized or unfertilized females during summer as they become older. Insemination is probably not related to age or to the degree of enlargement of the ovaries and occurs all summer, permitting replacement of group B females and of at least some females in group A. Many workers in groups C and B probably lay eggs and oviposition by a forager was actually observed (Batra, 1964).

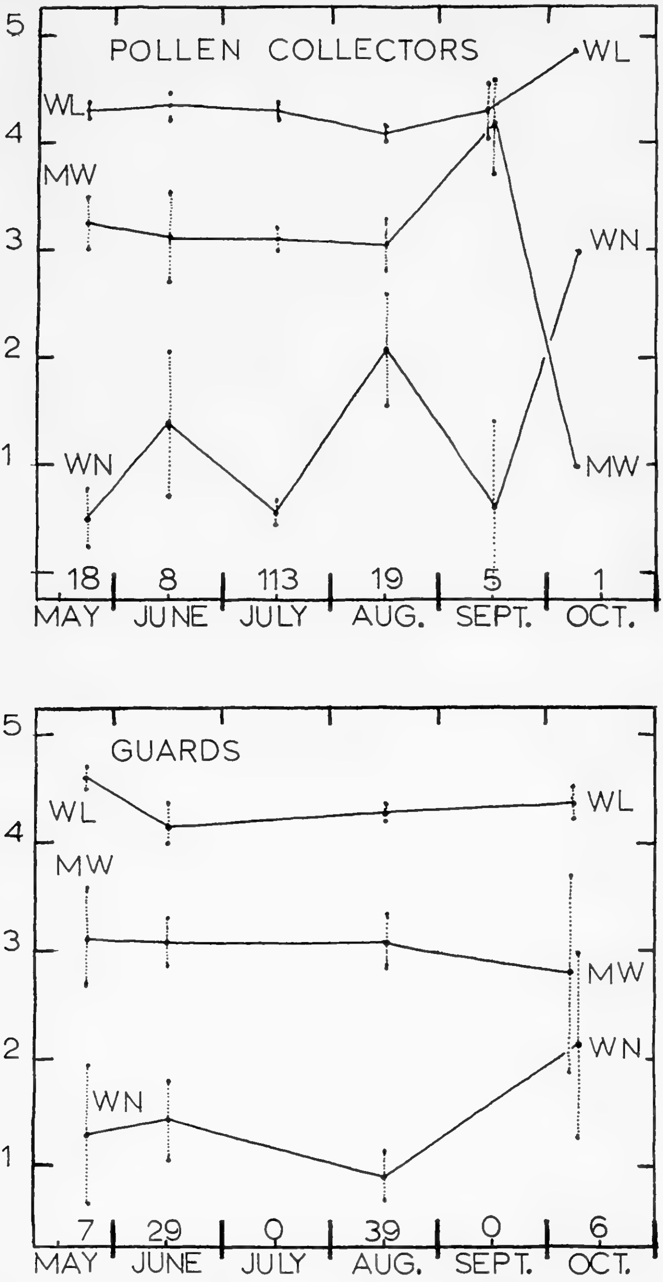


Fig. 7. Mean wing lengths in mm (WL), mean mandibular wear (MW) and mean number of wing nicks (WN) of pollen collectors and guards during various months. Standard errors are indicated for each point, and across the bottom of each graph, sample sizes are indicated.

ACTIVITIES VISIBLE OUTSIDE THE NEST

Conditions for Activity

Most aspects of the seasonal cycle are probably regulated by climate and are not obligatory. Colonies in the insectary rooms maintained continuous activity during fall and winter if suitable foods were available and other environmental conditions adequate. The resting period that follows provisioning by nest-founding females is, however, not dependent on environmental conditions and females that had started nests at any time of year in the insectary rooms always ceased activity until their progeny emerged.

Temperature was an important factor that influenced behavior in spring and fall. In March, guards appeared at the nest entrances when the soil at a depth of 21 cm was at least 7° C. New nests were excavated when the temperature of the soil (at a depth of 21 cm) was about 11° C (Fig. 1). Females removed from their nests at the end of April, when air and soil temperatures were 14° C, could not fly, although some of them had already been excavating. At air temperatures of 15° to 18° C (as measured in shade, 1 m above the ground on sunny days), females flew slowly, often alighting to "sun" themselves on the soil surface. At 16° C, bees were able to fly when the sun was out but when it became cloudy they apparently could not fly and crawled about or clung to vegetation. If it was windy at this temperature, they did not leave their nests but did fly on warmer windy days. During summer, flights occurred at air temperatures as high as 40° C, activity of this species not being inhibited by high temperatures. In fall, at air temperatures of 14° to 17° C, both males and females were active. Males were somewhat more active than females, this difference in activity perhaps facilitating copulation. The hibernating females are resistant to freezing. When nests in frozen soil were excavated, the bees (at 0° C) moved their legs and antennae feebly and when brought to 20° C, they began walking about. Males were not resistant, none being found after the first killing frost of autumn.

Changes in light intensity may influence activity. Normal flights occur on clear and slightly overcast days. One morning in July at the height of pollen collecting activity, as dark storm clouds rapidly approached, the maximum light intensity quickly dropped to 350 ft-c. Females no longer left their nests, and many, none carrying pollen, entered nests. Honeybees also return to the hive if dense clouds appear (Percival, 1947). Males continued their usual swarming activity, until I was forced to leave by sudden rain and tornadic winds. Both males and females maintained normal levels of activity during a partial solar eclipse in July, 1963.

Females continued to collect pollen during light rain (drizzle), but if rain became heavier (shower), they ceased collecting and returned to their nests. Males seemed to be somewhat more active in rain than females, but rested in vegetation or entered abandoned burrows during heavy rain.

Females are most active outside their nests during the morning hours (Fig. 8). *Lasioglossum imitatum* and other halictines show the same pattern of behavior (Michener and Wille, 1961). Unlike *L. imitatum*, females of *Lasioglossum zephyrum* return from most trips without pollen throughout the day. The morning peak in foraging activity may be related to other activities inside the nests. Usually, cells are made during the night and are ready for provisioning in the morning. By afternoon many of them have been provisioned and the foragers are engaged in making pollen balls or the cells have been closed after oviposition (Batra, 1964).

Few males or females were flying as early as 8:00 a.m., even on warm days, and in the insectary rooms they did not begin activity until the lights had been on for at least one half hour. By sunset (about 7:30 p.m. in summer), most females had returned to their nests and few males were still flying. Nests were guarded as late as 9:30 p.m. (with full moon) although the guards were timid. Some nests were guarded on dark nights, but others were not.

Foraging Behavior

Foragers are usually females that have done some work in the nest before beginning to collect pollen. Marked individuals lived as long as 31 days in the insectary room and some collected pollen at intervals for as long as 19 days. Observations in the insectary rooms showed that pollen collectors also excavate the burrow, guard, make cells, make pollen-balls, provide nectar for the provisions, and occasionally oviposit. For example, one bee collected pollen and nectar, made a pollen ball, and made a cell in one day; another collected pollen, made a ball and worked in the burrow in one day (Batra, 1964).

Increases in mean wing wear occurred at the same times that increased brood production was seen (Figs. 7, 21). This suggests that individual foragers make more flights when more cells are available for provisioning, and spend more time in the nests when there are fewer cells to provision. Seventeen marked foragers made one to eight pollen collecting trips per day (mean=3 trips) in the field. There is considerable variation in the amount of pollen collecting activity of different foragers in a nest and of the same forager on different days. This is probably related to the number of cells available for provisioning and to the physiological condition of the foragers.

Lasioglossum zephyrum visits many species of angiosperms for provisions. Other authors (see Introduction) have listed a large number of flowering plants visited by this bee; for this reason, little time was spent col-

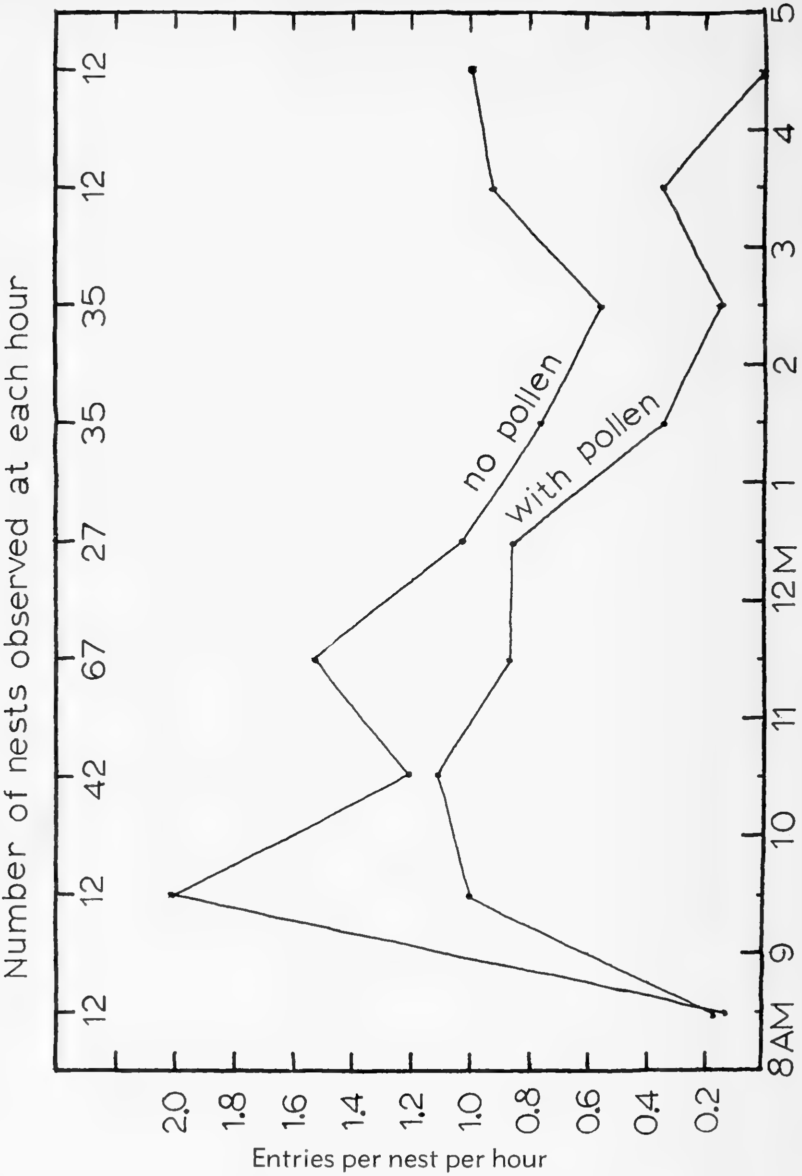


FIG. 8. Average number of times per hour that females entered their nests with and without pollen loads. The number of nests observed for each hour is indicated at the top of the graph. Observations of 67 nests were made in June and July during fair weather. Several adjacent colonies, having various degrees of activity, were observed on each day. Some nests were watched for as many as 3 days, others for only half a day.

lecting *L. zephyrum* on flowers. A list of plants on which it was observed during this study is given in Table 4. Most observations on foraging behavior were made in the insectary rooms, where the bees appeared to behave normally.

Foragers do not always exhibit flower constancy. Although females usually returned to the same species of plant, sometimes a female collected pollen from as many as three genera of plants in a single collecting trip. Bees frequently go back and forth between two different genera, finally

Table 4. List of flowers visited by *L. zephyrum*. P indicates that females were collecting pollen, N that they were taking nectar. M indicates that males were taking nectar. -BR indicates that observations were made in the bee-room.

- Liliaceae
  - *Allium mutabile* N-BR
- Iridaceae
  - *Iris* cult. var. N-BR
- Commelinaceae
  - *Tradescantia canaliculata* P-BR
- Ranunculaceae
  - *Thalictrum dasycarpum* P-BR
- Leguminosae
  - *Melilotus alba* M, N, P, M-BR, N-BR, P-BR
  - *Amorpha canescens* P-BR
  - *Petalostemon candidum* P-BR
  - *Petalostemon purpureum* P-BR
  - *Petalostemon multiflorum* P-BR
- Asclepiadaceae
  - *Asclepias* sp. N-BR
  - *Asclepias sullivanti* N, M, N-BR, M-BR
  - *Asclepias syriaca* N-BR
- Rosaceae
  - *Rosa setigera* P, P-BR
  - *Rosa suffulta* P, P-BR
  - *Rubus ostryifolius* P-BR
  - *Fragaria virginiana* N
  - *Spiraea* cult. var. P-BR
- Solanaceae
  - *Solanum rostratum* P, P-BR
- Oxalidaceae
  - *Oxalis stricta* N, M, M-BR
- Verbenaceae
  - *Verbena hastata* N
- Cruciferae
  - *Rorippa sinuata* N
  - *Brassica campestris* P-BR, N-BR
  - *Capsella bursa-pastoris* P-BR
  - *Draba reptans* N
- Onagraceae
  - *Oenothera speciosa* N-BR
- Scrophulariaceae
  - *Verbascum blattaria* N-BR, P-BR
- Campanulaceae
  - *Campanula americana* P-BR
- Labiatae
  - *Monarda fistulosa* N-BR
  - *Salvia azurea* M-BR
- Compositae
  - *Cacalia tuberosa* N-BR
  - *Cirsium lanceolatum* P-BR
  - *Chrysanthemum leucanthemum* P-BR
  - *Chrysanthemum* cult. var. P-BR, N-BR
  - *Amphiachyris dracunculoides* P-BR
  - *Echinacea pallida* P-BR
  - *Aster* sp. P-BR, N-BR, M
  - *Aster oblongifolius* M-BR
  - *Aster ericoides* M-BR, P-BR
  - *Erigeron* sp. N, P, N-BR, P-BR
  - *Erigeron ramosus* N-BR
  - *Rudbeckia hirta* M-BR, N-BR
  - *Rudbeckia* sp. M-BR
  - *Ratibida pinnata* N-BR
  - *Helianthus annuus* M-BR, P-BR
  - *Helianthus grosseserratus* M-BR, N-BR
  - *Silphium integrifolium* N-BR, P-BR
  - *Silphium laciniatum* N-BR, P-BR
  - *Taraxacum vulgare* N
  - *Vernonia fasciculata* N-BR, P-BR
  - *Solidago* sp. M-BR, N-BR, P-BR
  - *Solidago altissima* M
  - *Solidago glaberrima* M-BR, N-BR, P-BR
  - *Solidago rigida* M-BR, N-BR, P-BR

carrying a mixed pollen load to the nest. They sometimes obtained nectar from the pollen source but more often visited another kind of plant for this, or took the honey and water mixture provided on feeding stands and on various artificial flowers. Although this species is polylectic, foragers show strong preferences for certain flowers, and the flowers of many species of plants provided for them in the insectary rooms were completely ignored or visited much less frequently than those of other plants. Pollen collecting trips to flowers were 3 to 32 minutes in duration, most of them lasting about 10 minutes.

Foragers collecting pollen usually first loosen the pollen grains from the anthers by biting them. They rapidly brush back the pollen with the front tarsi, transferring it briefly to the middle tibiae. The middle legs immediately press it into the scopa on the hind legs and abdomen. As in *L. imitatum* (Michener and Wille, 1961), there is no regular alternation of movements, the forelegs and midlegs on one side of the body sometimes transferring pollen two or three times in succession before those on the other side are used. As the load of pollen becomes larger, foragers begin packing it into the scopa by pressing the hind legs together and against the abdomen. About one-third of the pollen load is carried on the abdominal scopa. Females that were collecting pollen of *Vernonia* sometimes used the mandibles to hold onto the anthers while the legs brushed up pollen.

The apices of the antennae of pollen-collectors are almost constantly in contact with the pollen. Bees, attracted to flowers of *Helianthus* having few pollen-bearing anthers, wandered across the disc and did not begin pollen-collecting motions until their antennae contacted the pollen. Foragers drink nectar before, after, or during the collection of pollen and sometimes eat pollen also. Sometimes females take no nectar, but only pollen, to the nest; others take both or only nectar. An individual often collected pollen on some trips and nectar on others. The kind of provisions collected depends on the consistency of the provisions deposited previously in the cells (Batra, 1964). Bees collecting nectar sometimes pause for five or ten minutes, while they extend and retract the glossa with a drop of nectar, about twice per second. Several other halictines show similar behavior (Plateaux-Quénu, 1959), probably evaporating water from the nectar.

Foragers and males were collected on flowers about 230 meters from the nearest known nesting area, and marked females readily returned to their nests when released about 170 meters away. Only one of nine marked females returned to her nest from a distance of 0.5 mile (809 meters). Few flowers are available near the Wakarusa nesting site, and foragers probably visit flowers in pastures that are at least 150 meters away.

Foragers apparently are able to learn what are suitable pollen or nectar sources, and ability to collect pollen seemed to improve with time. Two days after the first young bees were seen in insectary nests (May 20, 1963), three foragers on flowers of *Rosa suffulta* did not fill their scopas although they made the usual motions and pollen was abundant. Probably these were young, inexperienced foragers, since most bees on *Rosa* rapidly filled their scopas. Females in the field returning to nests with incomplete pollen loads (July, 1963) were like those returning with full loads with respect to mandibular and wing wear and ovarian development. Factors other than immaturity apparently were responsible for the partial pollen loads in this instance.

Females in the insectary room were induced to collect pollen of *Alnus* sp. (which *L. zephyrum* is not known to visit in nature) from a petri dish. Flowers of *Aster* sp., from which bees were collecting pollen, were dusted with the pollen of *Alnus*, which they then picked up. The *Aster* plants were placed near some yellow plastic imitation sunflowers, each of which had a small pile of *Alnus* pollen on its disc. Bees began collecting this pollen, and the asters were removed. A petri dish, having a circular piece of yellow paper beneath it, was placed near the sunflowers. A black "disc" and black "rays" had been drawn on the paper. The following day, foragers were collecting *Alnus* pollen from a small heap placed over the "disc" area. Because these females had not been marked, it is not known which individuals learned to collect this pollen. They were probably later replaced by young untrained bees as they died off. A colony of bees was maintained through the winter, using this pollen alone. Foragers usually hovered over the dish for a few seconds, alighting at the edge of the pile of pollen. When bees were collecting the loose *Alnus* pollen, foraging trips were brief, lasting only one or two minutes, unless they also visited the honey-feeding stations. This suggests that the duration of a foraging trip depends in part on the ease with which pollen is gathered.

When crude paintings of flowers were made on one wall of an insectary room (1962), several females were attracted, alighting on the "stems" and "leaves." They also alighted at the centers of asterisk-shaped blue "flowers." After two days, bees were no longer attracted to the paintings, apparently having learned to ignore them.

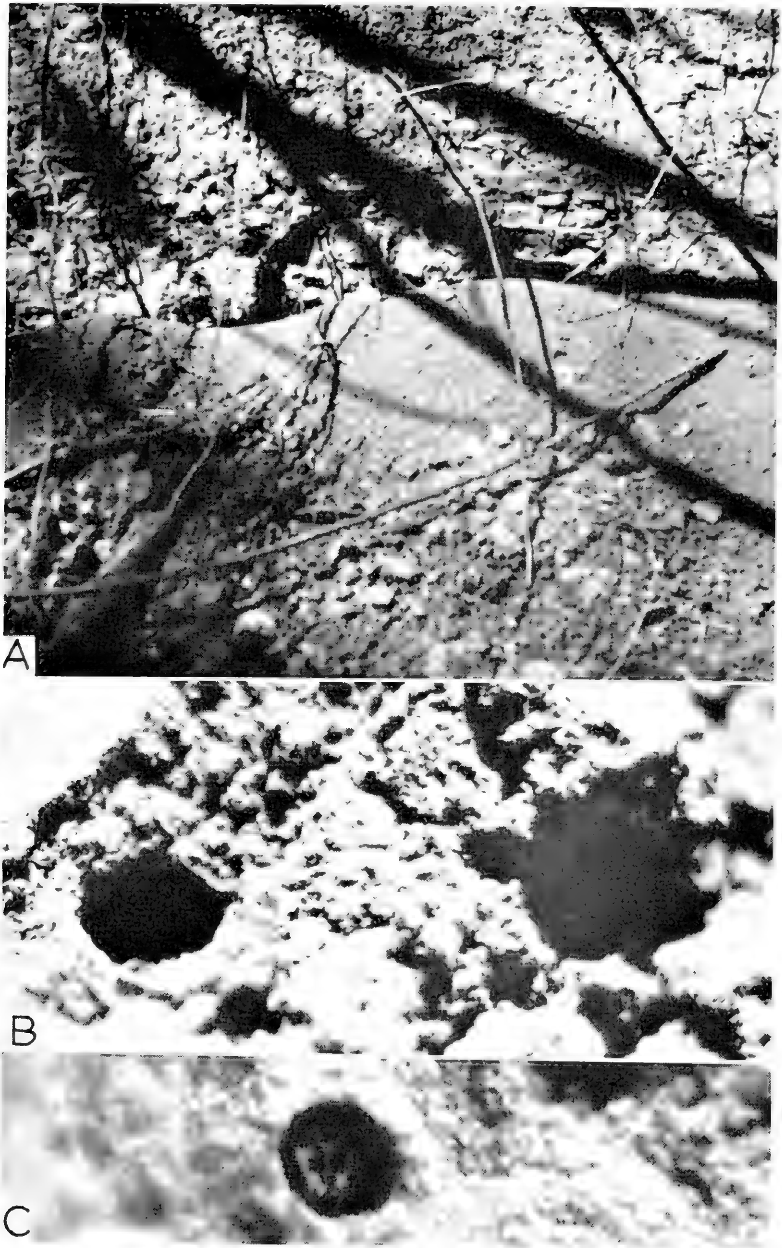
Artificial flowers were effective competitors with real flowers for attention outdoors as well as in the insectary rooms. Females in the field fed on honey at plastic flowers placed near the nesting site.

Halictine bees are well known for their annoying tendency to lick up human perspiration. Males and females of *L. zephyrum* do this occasionally. Both sexes also licked the stems, tendrils, and both sides of the leaves of *Vitis* sp. growing near the nesting site. Females were observed licking stems and buds of *Aster* sp. in the insectary rooms, and they licked dry sugar at a feeding stand. In the field, they licked the honeydew on stems and leaves of suckers of *Populus deltoides* that were infested with aphids. When licking skin or plants, the bees were unusually persistent and not easily frightened away. One female that was licking a pencil was caught and squeezed tightly so that she buzzed and struggled. She immediately flew back to the pencil and resumed licking when released. This treatment and response were repeated three times. As the bee walked slowly over the pencil, the antennae moved about, lightly contacting it. A trace of liquid could sometimes be seen at the rapidly moving apex of the glossa, which was extended back under the thorax. Moisture was readily available at streams near the nesting sites, but bees were never seen drinking water. They may have been licking up sugars (of plants) or salts (in perspiration).

GUARDS

Overwintered solitary females that are actively provisioning their nests in spring usually guard them intermittently. In the insectary rooms, such females often plugged the nest entrance with a little soil when they had finished provisioning for the day, and were about to oviposit (usually in the afternoon), and the nests remained plugged for several hours or overnight. When the overwintered females had ceased activity in May and were waiting for their brood to mature, the nest entrances were plugged with soil or were left open (Fig. 9) and were usually without guards. When several overwintered females stay together in a nest in spring, it is guarded. After the young females emerge at the end of May, most nests are always guarded. Guarding by solitary females does not occur in *L. imitatum* and other halictines (Michener and Wille, 1961).

Observations of colonies in the insectary rooms have indicated that the youngest females guard their nests and excavate for several days before leaving on foraging trips. Figure 7 shows that many large, overwintered females were probably replaced as guards in summer by their smaller daughters. Many of the overwintered females (group A) as well as smaller group E bees were guarding in June, perhaps accounting for the relatively large standard error of mean size of guards in that month. Throughout the summer, the mean mandibular wear of guards remains at about three, and wing wear did not show increases associated with brood production as did wing wear of pollen collectors (Figs. 7, 21). There were differences between wing wear of guards and pollen-collectors in spite of the fact that many foragers guard before leaving nests on foraging trips, and some of them were probably included in the samples of guards. Females parasitized by gregarines, nematodes, female Strepsiptera and conopid larvae were seen guarding nests.



IG. 9. A. Excavated soil forming a heap at the base of a bank that contains many active nests. B. Entrances of two new nests in spring. C. Entrance of a nest in summer, with a guard.

Percentages of guards belonging to each ovarian group in June and August are indicated below:

Group	A	B	C	D	E
June (N = 29)	34%	7%	24%	4%	31%
August (N = 39)	3%	19%	61%	3%	14%

Guards of *L. zephyrum* in general resemble those of *L. imitatum* (Michener and Wille, 1961) in behavior. Aggressiveness of guards in defending the nest entrance seemed to depend on time of day and temperature. When the soil temperature was less than 16° C and few or no bees were flying, guards were timid. After about 7:00 p.m. (in summer) when all bees had ceased flying, guards were timid and retreated into their nests when disturbed. Solitary overwintered females that had finished provisioning were also timid and often retreated to the bottoms of their nests, leaving them unguarded. Possibly guards are females "intending" to fly out of the nest and the stronger the urge to leave, the more aggressive the guard (Legewie, 1925). In the insectary room, females that had emerged from their cells 24 hours earlier were aggressively guarding nests and flying.

Guards defend the nests against small organisms such as phorid flies and ants simply by blocking the constricted nest entrance with the head (Fig. 9), or by striking out with open mandibles. More aggressive organisms, such as mutillids, are kept out of the nest by plugging the entrance with the posterior abdominal terga. Guards frequently leave their nests to attack nearby females of *Pseudomethoca frigida* (Batra, 1965). When heavy rain falls on the nest entrances, guards sometimes block the burrows with their abdomens or plug them with a little soil to protect the nests from flooding. Guards engaged in attacking an intruder would, at the same time, briefly withdraw to permit nest mates to enter, but when guards block the nest entrances with the abdomen, other females can neither enter nor leave.

When nests are well populated, usually several females stay in the burrow just below the guard. Marked guards in such nests were replaced as guards by other individuals every 15 to 30 minutes.

Females occasionally guard shallow burrows (1 or 2 cm deep) excavated as overnight sleeping places, and bees have been found resting in detached turrets at nesting areas as if guarding them. One female, collected as she was guarding a nest in the field, was put into a nest in the insectary room. Within one minute, she began to repair the entrance of this nest, apparently not disturbed by the transfer. (See Batra, 1964, for additional information on guards.)

LOST BEES

As in *L. imitatum* (Michener and Wille, 1961), young females make more elaborate orientation flights when leaving the nest than experienced females do, and they appear to have difficulty locating their nests on their return. In the insectary rooms, newly emerged females and overwintered females often flew up toward the lights when first leaving their nests, but after a few days in the rooms, were no longer attracted to the lights. Overwintered females, in the field and in the insectary rooms, at first had difficulty finding their newly established nests. By the time they began collecting pollen, however, they usually entered and departed rapidly. One forager, that had been searching for her nest for about ten minutes, alighted and brushed off her pollen load before continuing. Females, like some other Hymenoptera, apparently relate the positions of their nests to landmarks. One disoriented bee was attracted to the southwest side of several clumps of grass before she found her nest, which was at the southwest side of a grass clump. Another female flew to the wrong nest-box in the insectary room and spent about five minutes flying and walking over the soil at its right side, minutely examining the surface with her antennae and occasionally digging. Finally she flew to the neighboring nest box, where she immediately entered her nest in the soil at the right side of the box. Many lost bees were seen when floods or trampling by cattle had apparently destroyed landmarks. On the other hand, bees readily located nest entrances covered with dirt or debris by the observer, if the surrounding area was undisturbed.

Disoriented bees sometimes enter the wrong nests and are usually not repulsed by the guards. Most of these females leave the nests immediately but rarely a bee, marked as a member of the population of one nest, was later found behaving normally in another nest. In early spring, when overwintered females are establishing nests, they frequently enter nests of other females when inspecting holes for nest sites. One overwintered female that was excavating a burrow only about 2 cm deep, was joined by a second bee. Both females tried to stay in the nest, first one, then the other being pushed to the surface, each briefly taking a guarding position before trying to crowd deeper into the nest; one of them finally left. In two instances, a previously marked overwintered female left her own nest and was found living in the nest of another bee, along with the original inhabitant. Probably the newly established nests containing two females (relatively common in *L. zephyrum*) arise in this way.

During summer, disoriented bees were sometimes much worn or parasitized individuals. In early June, several "lost" females that were dissected appeared to be old, overwintered bees of groups A or B; but others were newly emerged. In the insectary room, one senile marked queen was apparently stung to death by the guard of a nest (not her own) that she had persisted in attempting to enter during the morning. That afternoon, the guard, still in the entrance, was biting one of the front legs of the weakly quivering bee. Occasionally dying bees were found near nest entrances in the field.

These females of various ages, may have been also injured by guards. Guards sometimes refused to let certain individuals enter their nests, although at the same time other bees were permitted to enter. The females that were attempting to enter frequently stood near the nest entrances, facing the guards, as if waiting. They made orientation flights around the nests at intervals and occasionally tried to push into the nests past the guards, which bit at the intruders, sometimes grasping their mandibles. Females that had been repulsed by guards repeatedly cleaned their heads and antennae while waiting near the nests. Some of these bees were apparently lost, for they later entered other nests, but some belonged in the nests they were trying to enter. Bees that had left their nests to attack mutillids were often kept from re-entering immediately. Probably bees that approached the guards rapidly were more readily allowed to enter than those that hesitated, such as lost, inexperienced, senile or parasitized females. In 1957 many disoriented females were seen in July at an area in which most bees were infected by the nematode, *Hexamermis*. Six of a sample of eight such lost females contained the nematode. Bees containing puparia of male *Halictoxenos* (Strepsiptera) were found walking or weakly flying about the nesting site as if lost.

NEST STRUCTURE

INTRODUCTION

The structure of nests changes somewhat during the year as the population of bees in each nest varies in number and in composition. The generalizations made below are based in part on statistics given in Table 5 and in Fig. 10. Nests characteristic of various phases of the life cycle are illustrated in Figs. 11 to 17.

HIBERNACULA

Inseminated females overwinter in nests constructed and occupied during the summer. One exception may have been a female in a new unbranched burrow 4 cm deep, collected in November.

The entrances of overwintering nests in banks are about 2 mm in diameter, and not plugged with soil, but those in horizontal ground are usually closed by rain or other disturbances. Each hibernating female usually occupies a branch burrow (hibernaculum) 1 to 1.5 cm long, of the same diameter as the main burrow (about 4 mm). These branch burrows may be homologous to the resting places seen in nests during summer and also to "sleeping places" excavated by females that have no nests. Overwintering nests were 24 to 40 cm deep, the bees in branches at depths of 12 to 37 cm (Fig. 11). The overwintering females apparently make the side branches

TABLE 5. Characteristics of nests throughout the year. Means ($\bar{X}$), standard errors (S.E.), range (R) and number of nests examined (N) are indicated. "New" July nests are those newly excavated after a flood in July, 1963.

		Maximum Nest Depth	Minimum Depth Eggs	Maximum Depth Eggs	Number of Branches	Bees Per Nest	Brood Cells Per Nest
April	$\bar{X}$	9.42	5.00	8.00		1.14	2.69
(New Nests)	S.E.	0.66	0.51	0.42		0.08	0.54
	(R)N	(2-15)26	(3-9)18	(3.5-14)18	0	(1-2)21	(0-9)26
April	$\bar{X}$	20.63				4.63	
(Old Nests)	S.E.	3.53				0.89	
	(R)N	(5-39)8	0	0	0	(1-8)8	0
May 1-15	$\bar{X}$	12.06	5.43	8.14	0.29	1.42	3.12
	S.E.	0.91	0.84	1.31	0.19	0.09	0.93
	(R)N	(7-18)17	(2-15)14	(3-19)14	(0-3)17	(1-3)36	(0-16)17
May 16-30	$\bar{X}$	14.79	6.62	10.19	0.48	2.43	3.86
	S.E.	0.96	0.62	0.80	0.16	0.28	0.78
	(R)N	(9-28)19	(2-14)21	(4-16)21	(0-3)21	(1-6)21	(0-17)21
June 1-15	$\bar{X}$	21.45	14.85	17.55	1.65	5.30	9.80
	S.E.	2.09	1.69	1.68	0.67	1.56	1.78
	(R)N	(7-50)20	(5-40)20	(5-40)20	(0-13)20	(1-34)20	(1-37)20
June 16-30	$\bar{X}$	25.42	17.74	22.91	2.00	3.86	19.58
	S.E.	1.62	1.43	1.84	0.20	0.96	3.03
	(R)N	(11-42)26	(5-33)23	(9-41.5)22	(0-16)26	(1-22)21	(0-57)26
July 1-15	$\bar{X}$	31.00	20.60	22.60	2.43	12.71	14.43
	S.E.	3.46	1.36	2.02	0.72	2.78	5.39
	(R)N	(20-44)7	(17-24)5	(17-28)5	(0-5)7	(8-26)7	(0-36)7
July 16-30	$\bar{X}$	26.83	18.18	22.18	5.42	11.18	24.92
	S.E.	3.07	3.50	2.93	1.55	3.18	6.22
	(R)N	(14-48)12	(9.5-36)11	(10.5-38)11	(1-17)12	(4-38)11	(0-65)12
July 15-30	$\bar{X}$	6.67	4.40	5.60	0.50	1.08	1.08
(New)	S.E.	0.91	1.21	1.50	0.26	0.08	0.47
	(R)N	(2-11)12	(1-8.5)5	(1-10)5	(0-3)12	(1-2)12	(0-4)12
August 1-15	$\bar{X}$	39.67	29.13	35.50	10.30	14.30	45.30
	S.E.	7.85	3.36	3.45	2.72	4.08	10.81
	(R)N	(32-57)9	(16-45)8	(24-55)8	(3-29)10	(5-45)10	(0-85)10
September 1-15	$\bar{X}$	31.56			5.60	8.30	18.40
	S.E.	3.81			2.37	3.81	7.82
	(R)N	(15-49)9	0	0	(0-26)10	(1-41)10	(0-81)10
Winter	$\bar{X}$	32.36			4.88	4.44	
	S.E.	1.50			1.88	1.39	
	(R)N	(24-40)11	0	0	(0-16)8	(1-14)9	0

which are sometimes plugged with a little soil, but do not deepen the main burrow.

Polygynous Spring Nests

In spring, some females remain together in the nests in which they hibernated; others leave these nests to begin new ones.

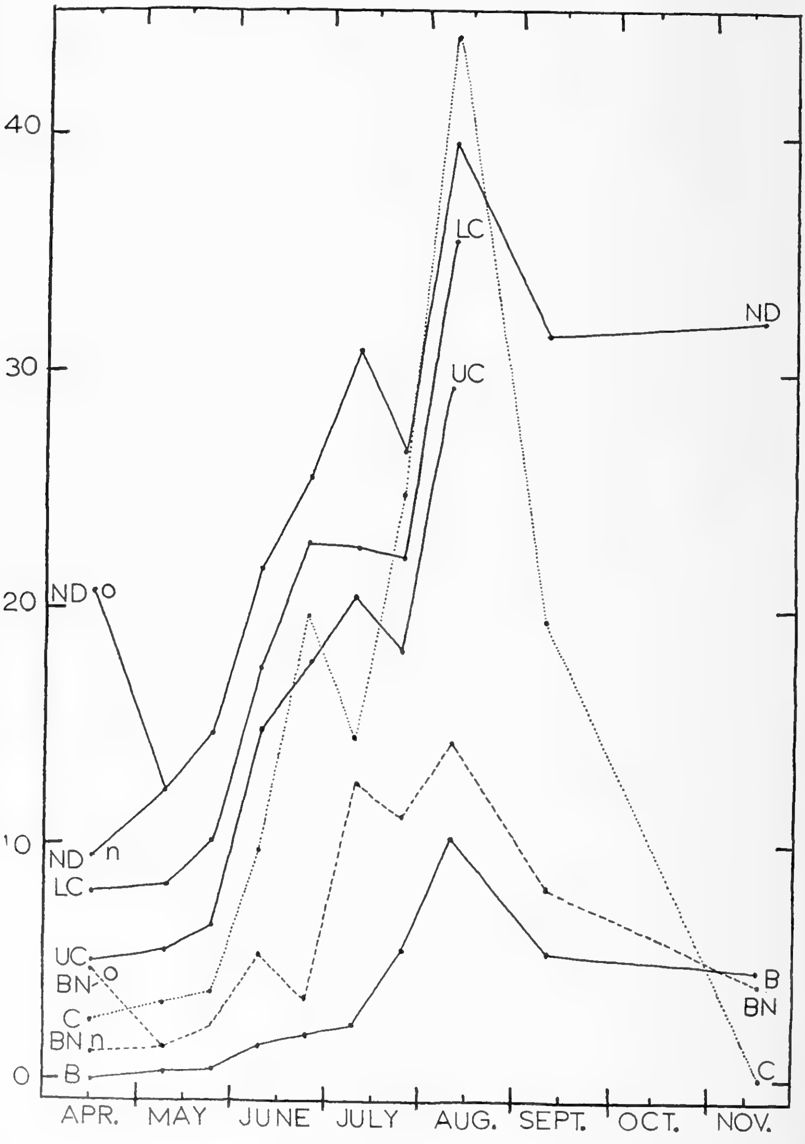


Fig. 10. Characteristics of nests during the year. ND, mean nest depth in cm; LC, mean depths of lowest cells containing eggs in cm; UC, mean depths of uppermost cells with eggs in cm; C, mean number of cells per nest; BN, mean number of females per nest; B, mean number of branches per nest. (o), old spring nest; (n), new spring nest.

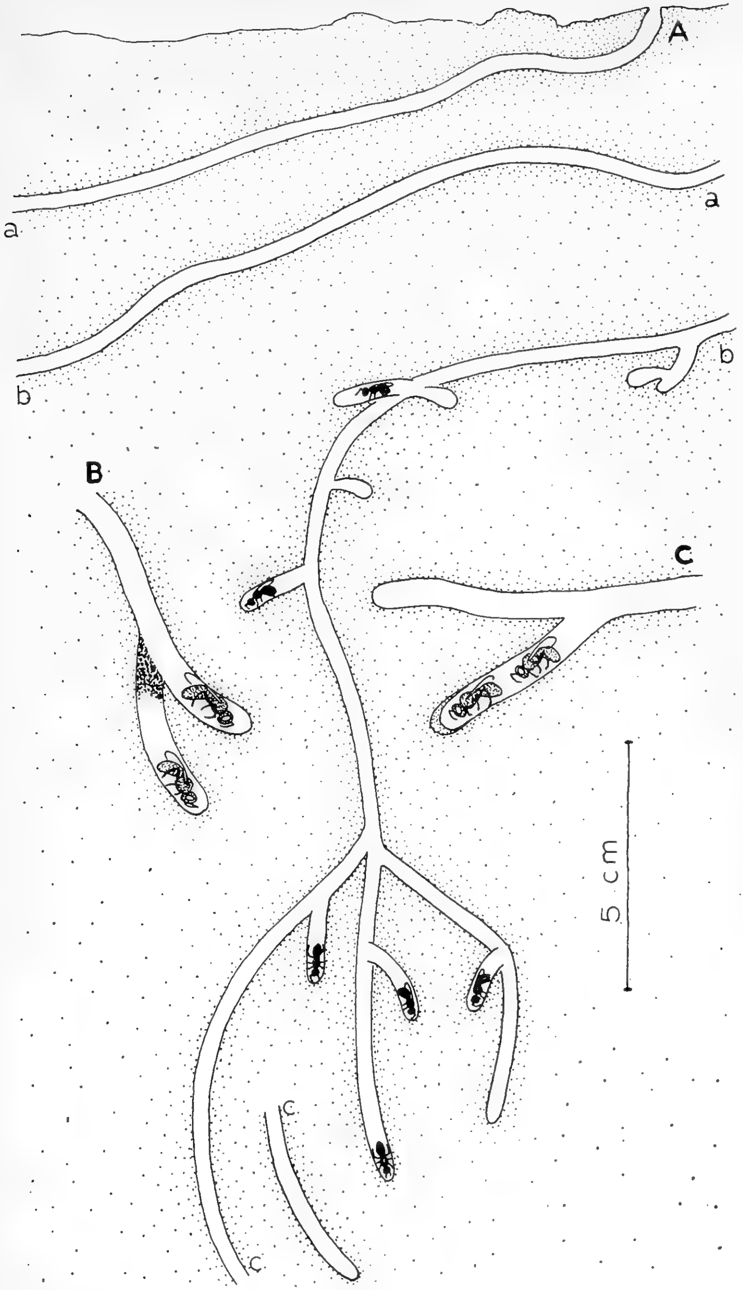


FIG. 11. Hibernacula. A, Overwintering females in short branch burrows. Nest opened October 3, 1957; B and C. Females in characteristic hibernation attitude, January 3, 1964. In diagrams of nests, the following symbols are used: N, new empty cell; B, pollen ball or loose pollen in cell; E, egg; S, small larva; M, medium larva; L, large larva or prepupa; ♂, male pupa; ♀, female pupa; X, dead or parasitized brood. Stippled areas indicate cells or burrows that have been filled with soil by the bees. Small letters indicate connecting points, when diagrams have been broken to conserve space.

When several overwintered females were found using the same nest during early spring, it seemed probable that they had hibernated together if old earth filled cells were found near the burrow or if the nest had been marked the previous year. Females emerging from hibernation fill the side branches and lower part of the burrow with soil before beginning to make new cells (Fig. 12). New spring cells in old nests were excavated at about the same depths as those of new nests in spite of the availability of deep burrows. Nests containing several bees were constantly guarded and had well-maintained, constricted entrances.

NEW SPRING NESTS

Shallow nests, with no traces of old cells or burrows, containing one or sometimes two females, were often known to be new. They often have a branch burrow about 1 cm long near the entrance, but most have no other branches. Burrows made in banks are fairly straight but those in horizontal ground are often more crooked. New nests in spring frequently have unrepaired entrances 3 mm or more in diameter and are guarded only intermittently. Such nests usually are not guarded after the females finish provisioning the cells (Fig. 14). New nests were about three times as numerous as old polygynous nests in spring. Nests resembling new spring nests in structure were excavated in July by females whose original nests had been destroyed by a flood.

SUMMER NESTS

After the young females emerge in late May, nests are gradually extended deeper into the earth. The number of branches and cells is directly proportional to the number of bees per nest (Fig. 10). The level of occupied cells descends with the deepening of the burrows. The deepest nest reached 57 cm (August), the maximum number of branch burrows was 38 (July), the largest number of occupied cells was 85 (August), and the maximum number of females per nest was 45. Other data are given in Table 5 and Fig. 10. In late summer, the number of bees and inhabited cells rapidly decreases, until by October only the overwintering females are left in the nests where they stay to hibernate. Summer nests in horizontal ground are in general vertically oriented but often tortuous, with many branches ramifying in various directions. Those in banks are somewhat straighter, the branches being usually fairly straight and running into the bank (Figs. 15, 16, 17). Perhaps nests in horizontal ground are tortuous because *L. zephyrum* usually nests in banks; such nests often have subhorizontal sections like nests in banks. The actual amount of tortuousness is difficult to draw in two dimensions.

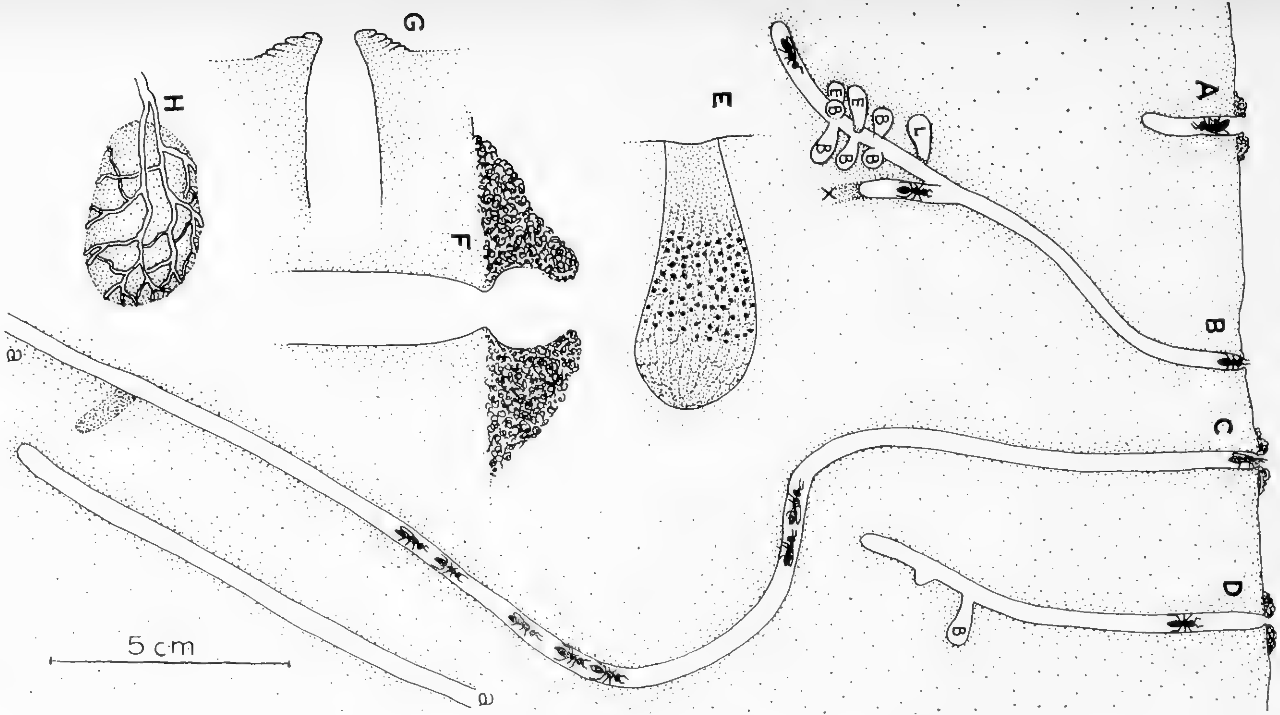


FIG. 12. Nests in early spring and details of nest structure. A, Female beginning to excavate a nest, April 1, 1961; B, Females in a nest in which they had hibernated. The old burrow (X) has been filled with soil before May 13, 1961; C, Bees emerging from hibernation April 1, 1961. The short branches in which they overwintered have apparently been filled with soil and only one was found; D, Female in new nest, May 13, 1961; E, Newly made cell, showing grooves underlying polished lining and droplets of moisture on its surface; F, Funnel-like region in tumulus above nest entrance; G, Short turret built up of concentric layers of soil; H, Compact mass of soil and fecal material from abandoned cell that is surrounded by thick rootlets of plants.

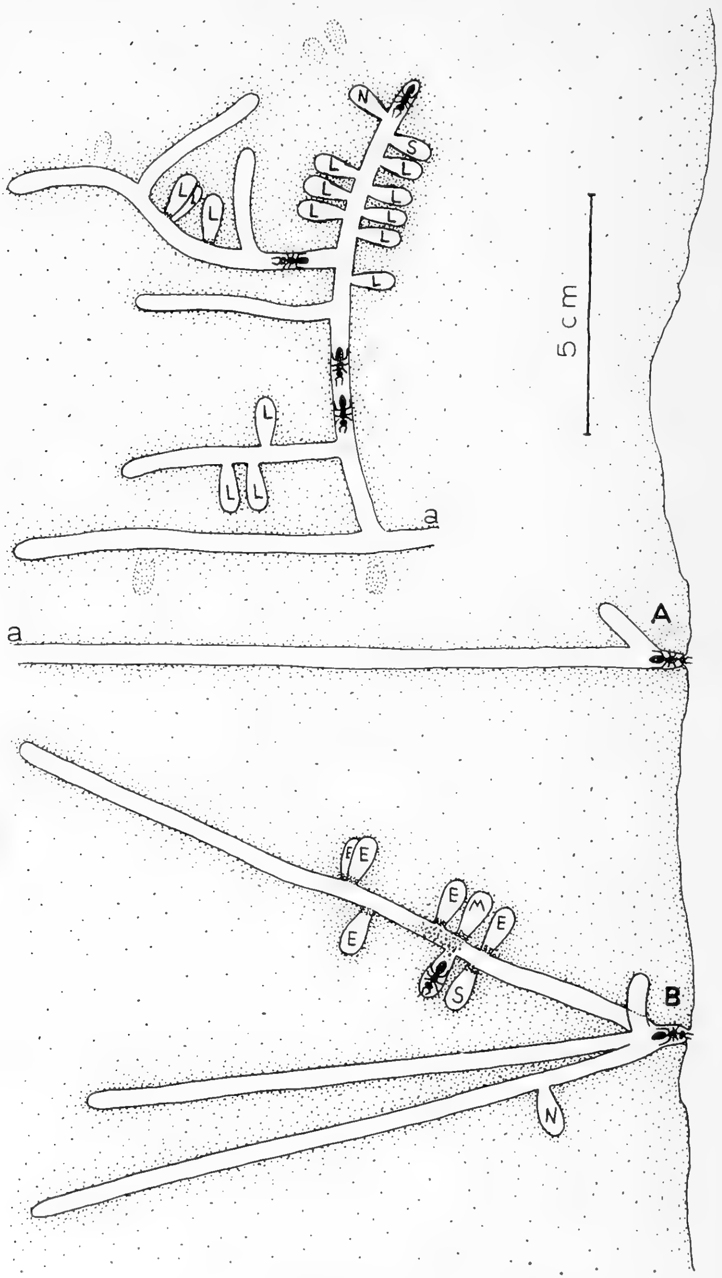


FIG. 13. Spring nests in a bank, as viewed from above. A, Polygynous nest with old cells, May 7, 1963; B, New nest with two bees, April 23, 1963.

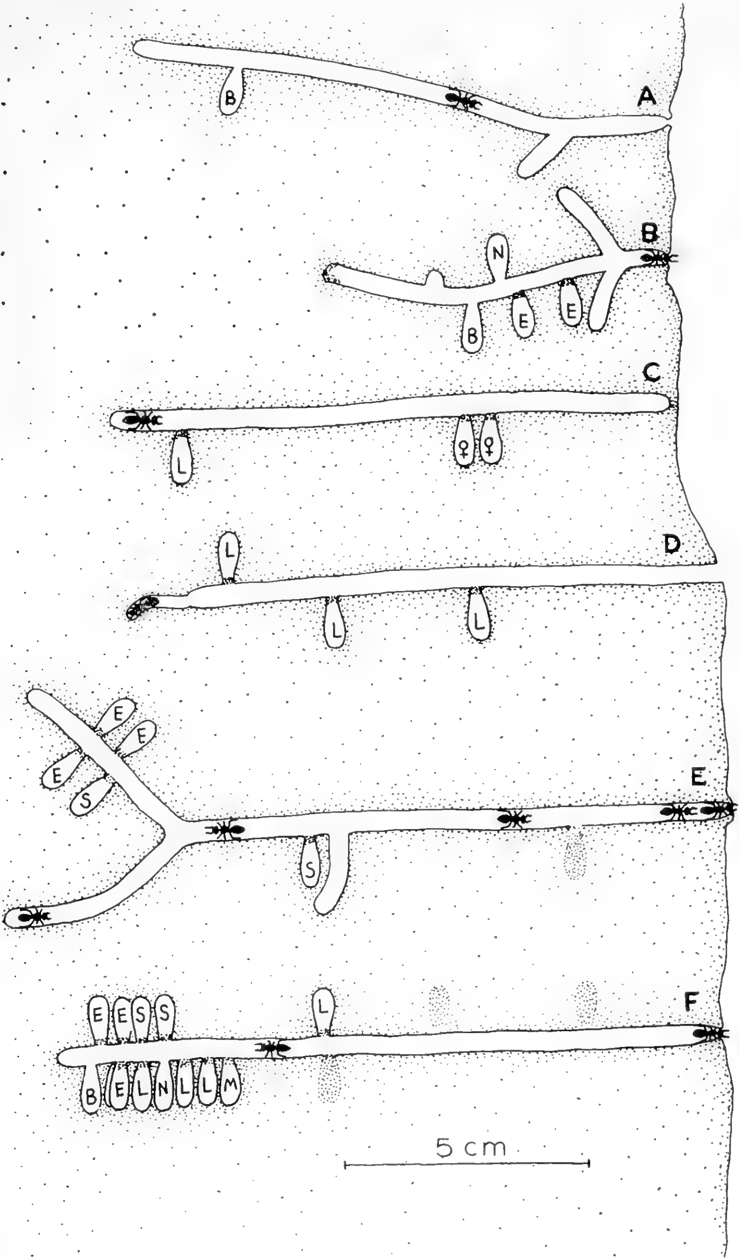


FIG. 14. New spring nests and early summer nests in banks as viewed from above. A, April 24, 1963; B, May 2, 1963; C, Resting female in closed nest with maturing brood, May 10, 1963; D, Resting female in open nest. She dug a narrow escape tunnel when the nest was dug up for study, May 10, 1963; E, and F, Nests with young summer females and new cells, June 8, 1963.

GENERAL CONSIDERATIONS

Nest entrances are usually constricted to about 2 mm in diameter at the County Line site, where guards have relatively large heads. At the Wakarusa site, entrance diameters average about 1.8 mm. Nests in horizontal ground often have radial tumuli of granular excavated soil particles surrounding the entrance. Depending on the activity of the bees and the weather, tumuli reach diameters of 4.5 cm and heights of 3 cm. The inner wall of the tumulus is sometimes made of compressed soil, leaving a turret when loose soil blows away. Soil particles pushed from nests excavated in banks form piles up to 8 cm deep on ledges and at the bases of the banks (Fig. 9). Nests in banks sometimes have short turrets up to 7 mm in outside diameter and 6 mm in length, apparently made of concentric rings of mud pushed out of the nest when the soil is wet. Funnel-like depressions are rarely seen around the entrances of nests in horizontal ground (Fig. 12). No subsurface enlargements of the burrows ("sentry boxes") are made by the populations studied although L. Chandler (personal communication) reports such structures in nests of *L. zephyrum* in Indiana.

The main burrow and branch burrows are usually about 4 mm in diameter (range 3.2-4.5 mm). Burrows maintain very roughly a 90° angle to the surface of the soil, so that those in horizontal ground are more or less vertical and those in steep banks are approximately horizontal in orientation although sections of nests are often oriented differently. Intermediates were seen, depending on the steepness of the slopes. Branch burrows were of various lengths, some of them nearly equalling the main burrow, others only 1 cm long. Usually a short blind burrow is present as a continuation of the main burrow or branch burrows beyond the deepest cells. The burrow walls are smooth and sometimes a lining of compressed soil, about 0.5 mm thick, can be detected. This lining is conspicuous when burrows pass through differently colored layers of soil or through rotten wood buried in the soil.

In arrangement of cells, nests of *L. zephyrum* belong to subtype IIIb, $\mathrm{OCH}^{n}\mathrm{B}$ or to subtype IIIc, $\mathrm{OCH}'^{n}\mathrm{B}$ of the classification of Sakagami and Michener (1962). Vertical sections of burrows often have cells arranged radially but in burrows or sections running horizontally the cells are arranged serially along each side of the tunnel (Figs. 15, 16), with few exceptions. The degree of concentration of the cells is variable, but in general, spring or summer nests containing several females have cells more crowded together than nests occupied by only one or two bees. Cells are sometimes separated by only 0.5 mm to 1 mm of soil. Excavating females probably detect the secretion that soaks into the soil around cells, thus being able to avoid cells already completed when making new cells or burrows.

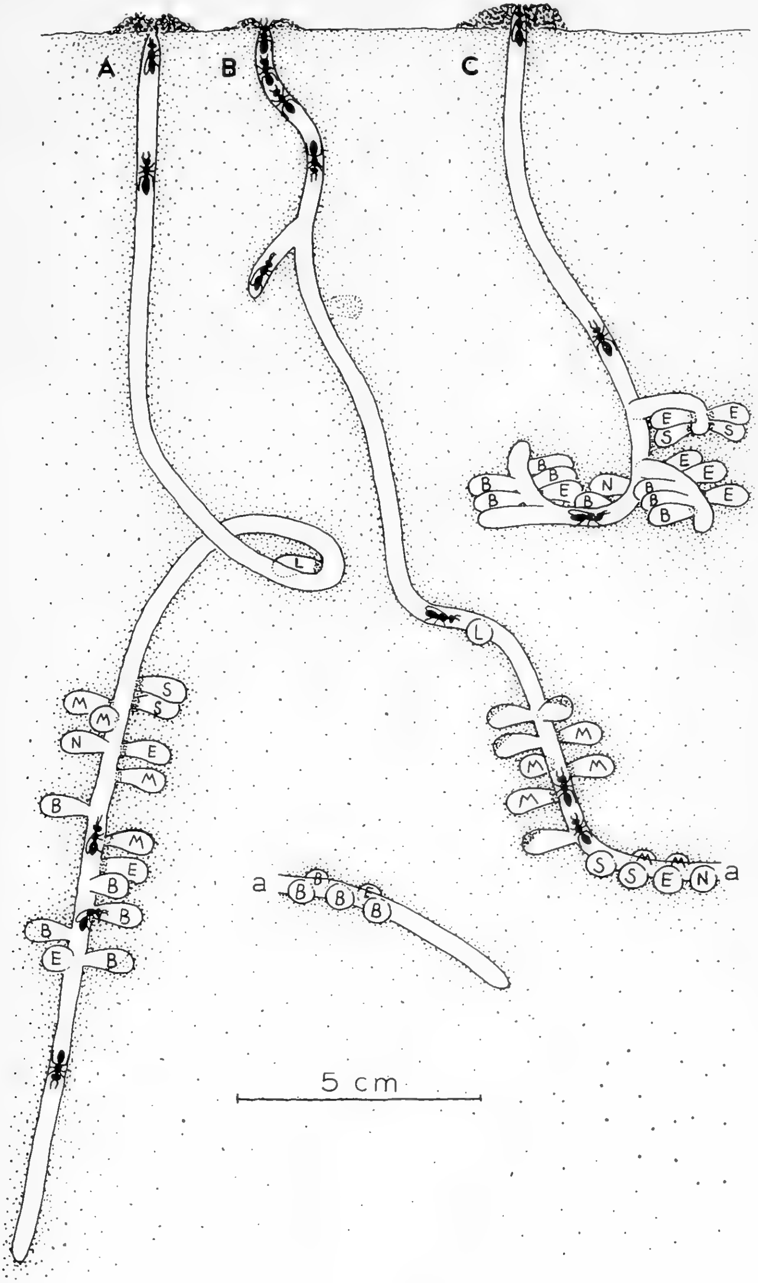


FIG. 15. Early summer nests and polygynous spring nest in horizontal ground. A, June 8, 1962; B, June 11, 1962; C, May 13, 1961.

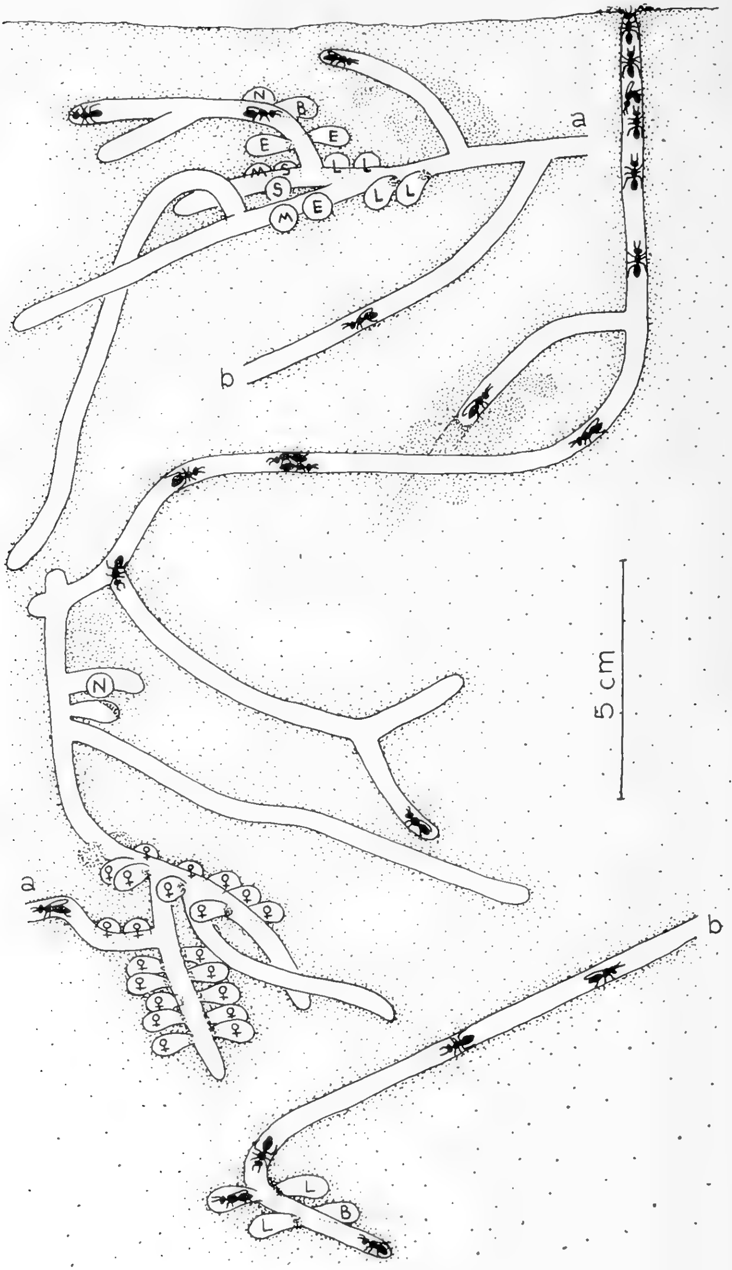


FIG. 16. Summer nest in horizontal ground, July 17, 1957. The diagram has been broken to conserve space. Letters indicate connecting points.

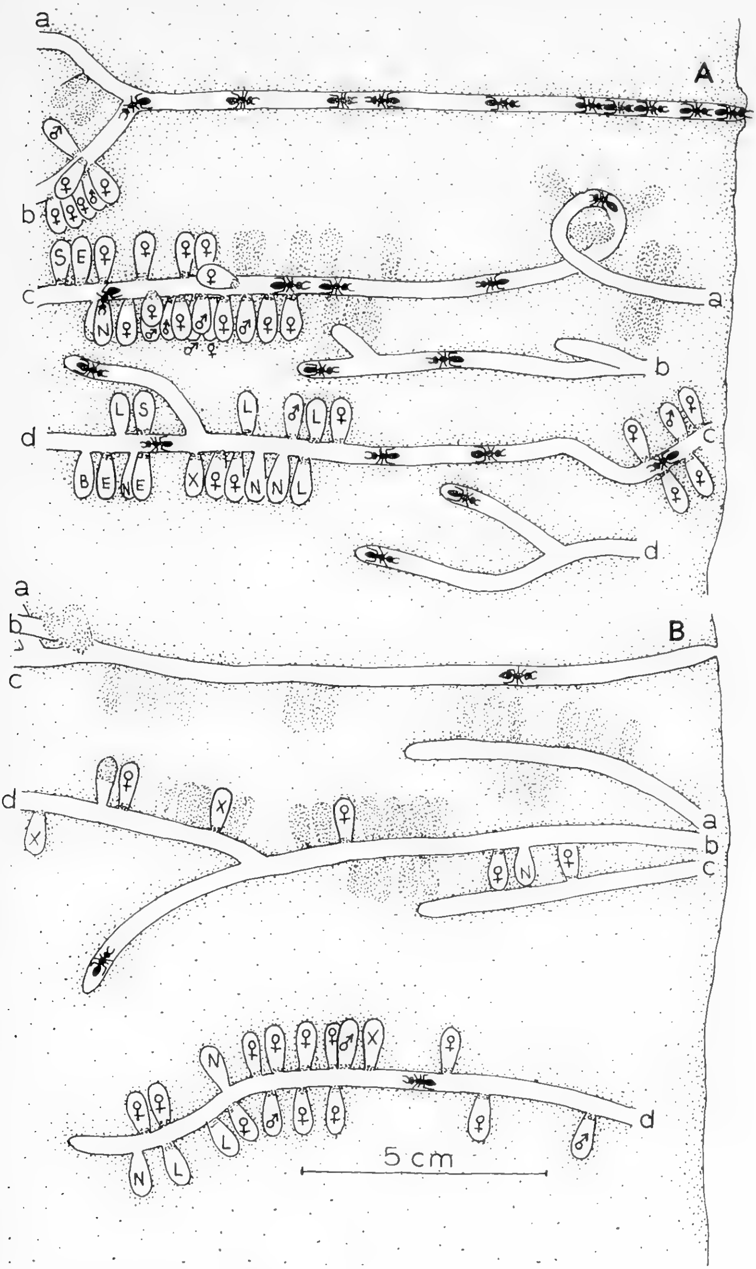


FIG. 17. Two summer nests in banks, viewed from above. A, July 18, 1962; B, September 13, 1962. The diagrams have been broken to conserve space and letters indicate connecting points.

Cells are subhorizontal and bilaterally symmetrical, 9 to 11 mm in total length including the neck (extremes 8 to 15 mm), 4 mm in maximum vertical width (3.5 to 4.5 mm), and slightly more in maximum horizontal width. The necks of the cells are usually about 2 mm wide (1.7 to 2.5 mm) and 2 to 4 mm long. Cells are closed after oviposition with a plug of loose soil pellets which extends into the neck for a distance of about 2 mm. The portion of the plug forming part of the burrow wall is of smooth compressed soil, so that there are no visible differences in the burrow surfaces between regions where there are plugs and those without plugs. An area about 7 mm long, occupying the widest end of the cell, is lined with a thin, shiny, transparent, waterproof film that can be flaked off when cells are soaked in water. Observations in the insectary room have shown how this film is applied over a layer of compressed soil. Completed cells in the insectary room nest-boxes had distinct halos where a liquid apparently had soaked into the soil for a distance of about 1 mm around each cell. In the field, newly-made cells with wet, sweet-smelling walls were occasionally found, the secretion penetrating the surrounding soil for about 1 mm. It appears unlikely that this amount of secretion could be produced by the salivary glands alone, although the glossa was used by bees lining cells in the insectary rooms (Batra, 1964). Bordas (1894) has shown that the Dufour's glands of the sting apparatus of young females of *L. leucozonium* (a solitary species) are greatly enlarged in spring. Semichon (1906) noticed that the Dufour's glands of freshly killed *Anthophora personata* were greatly enlarged and filled with an oily liquid, which when dried, became a white waxy solid that resembled the lining of the cells of this bee in solubility and melting point. These glands were most enlarged at the time when the bees were making cells. He believed that the secretion of Dufour's gland was used by *Anthophora* in making cells. In *L. zephyrum*, 11 of 14 solitary females taken from nests with newly made, empty cells in April had greatly enlarged Dufour's glands, but only two of six females taken from closed nests during the resting period in May had enlarged Dufour's glands. During summer, enlarged Dufour's glands were found mainly in females belonging to groups C, B, and A in this order of frequency. Observations in the insectary room have shown that foragers (probably most in groups C and B) made cells. Possibly the secretion from Dufour's glands soaks into the soil and is spread about by the glossa or augmented by a salivary secretion. One cell, excavated in the field, had a polished lining with minute droplets on its surface, which suggested that two secretions may have been used (Fig. 12). The waterproof layer becomes brown in old abandoned cells. Small grooves, probably made by the pygidial plate in tamping and smoothing the earthen walls, are often seen underlying the shiny secreted linings of the cells (Fig. 19).

IMMATURE STAGES AND PROVISIONS

PROVISIONS

In the field as well as in the insectary rooms, more than one female usually provisions each cell during summer. As in *L. imitatum* (Michener and Wille, 1961) and *L. calceatum* (Plateaux-Quénu, 1963), there are often more pollen-collectors per nest than cells being provisioned at that time, indicating cooperative activity. For instance, five marked individuals were carrying pollen into a nest that yielded only three newly provisioned or empty cells when excavated that day. Of course, the number of foragers that were supplying nectar alone could not be counted.

Cells opened in the field while being provisioned contained one or another of the following sorts of pollen masses: (1) a small amount of loose, dry pollen, (2) a small, moist but crumbly pollen ball, (3) a similar small pollen ball on top of a mass of dry pollen, (4) a large amount of dry pollen (Fig. 18), sometimes in differently colored layers, (5) a mass of loose, somewhat moist pollen that may be molded by the fingers like dough, (6) a small pollen ball with a mass of loose pollen on top of it, (7) a pollen ball with a few flakes of agglutinated pollen grains on top of it, and (8) a full-sized, smooth pollen ball. The consistency of completed pollen balls varies from that of butter at room temperature to that of dough. The different types of provisions listed above may be related to the stage at which provisioning was interrupted; the process of provisioning is discussed by Batra (1964).

Pollen balls collected in the field are frequently more moist outside than in the center. When females from several nests were fed a honey and water mixture to which blue food color had been added, some of the pollen balls that were removed from the nests a few days later were stained blue. One of them, bearing an egg, was blue only in its upper half. This suggested that honey was added to the pollen ball after it had been shaped, and either that the working over of the ball by the egg-layer just before oviposition did not disturb its surface, or that the honey may have been added after oviposition (progressive provisioning). Usually pollen balls appear dull in texture, but glossy nectar oozes out when their surfaces are scratched.

The flattened, subspherical pollen balls of *L. zephyrum* measure 3 to 4.1 mm in diameter and 2.0 to 2.5 mm in height; there is no depression for the egg. Completed pollen balls, each bearing one egg, are usually somewhat tilted in the cells (Fig. 18), unlike those of other halictines. No loose pollen or nectar is visible on the walls of cells that contain completed pollen balls. Pollen balls have a strong, pungent, sweet odor.

EGGS

As in other halictines, the eggs are white, smooth and curved. Eggs, including those laid by a single female, vary in curvature. Some contact the

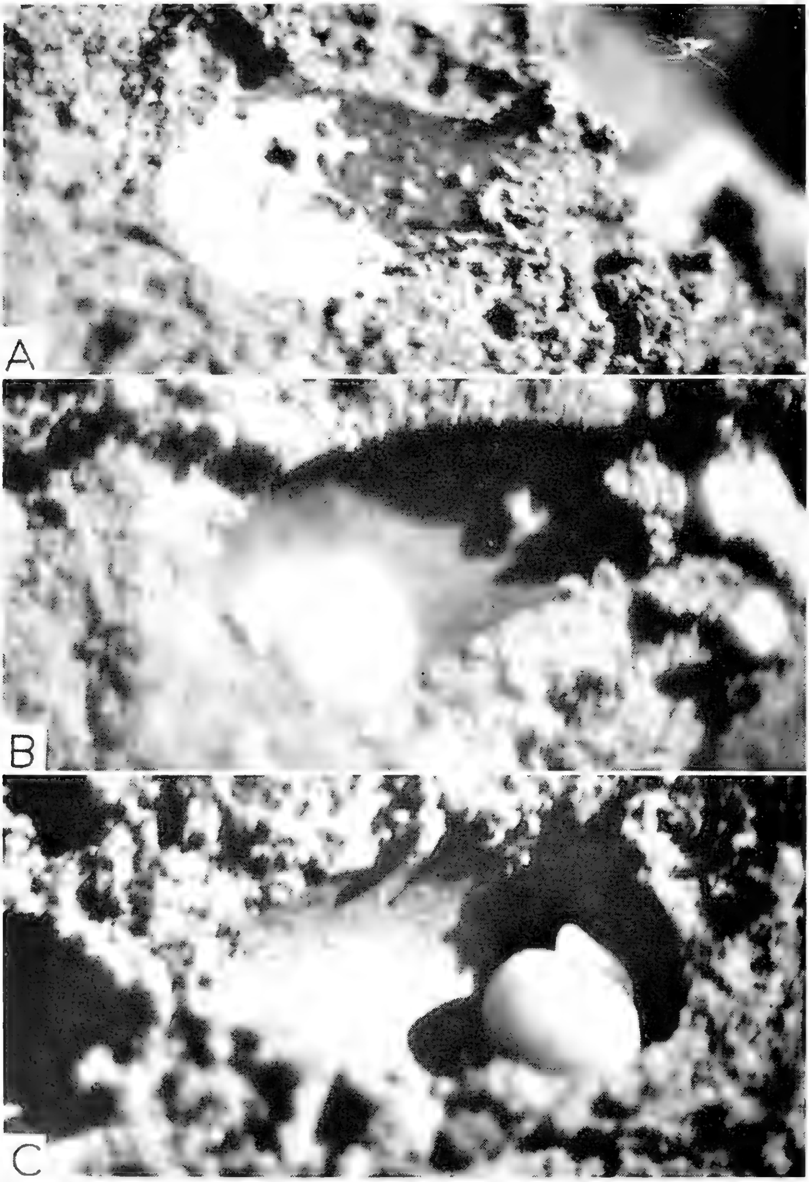


Fig. 18. Development of the brood. A, Loose pollen in a partly provisioned cell; B, Egg on a characteristically tilted pollen ball. The upper end of the egg will develop into the head of the larva. C, Young (probably first instar) larva, with head raised.

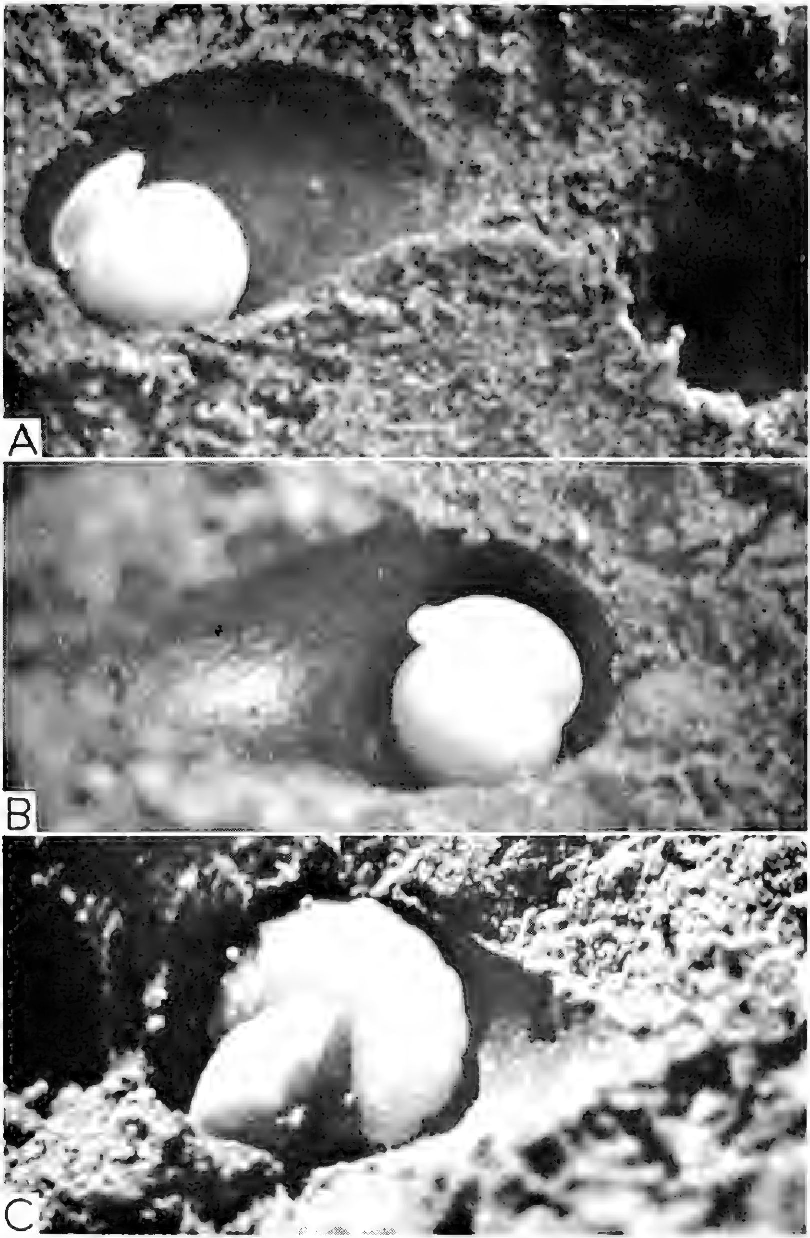


Fig. 19. Development of the brood. A, Second or third instar larva. A cross-section of the burrow is at the right; B, Larva (probably third instar), with head raised in alarm pose. The grooves in the shiny wall of the cell may have been made by the pygidial plate of the female that constructed it; C, Fourth or fifth instar larva eating a pollen ball.

pollen ball only at each end, but others contact it throughout their entire lengths. The widest, blunt end of the egg is directed toward the neck of the cell, and develops into the head of the larva. The tapering, narrower end terminates as a transparent area. A few eggs had a small watery droplet on their upper surfaces (some such eggs hatched). Eggs were 1.39 to 1.53 mm long and 0.44 to 0.48 mm across the widest end (Fig. 18, 20).

LARVAE

Larvae were reared in cavities made in a layer of embedding paraffin in large, covered Stender dishes kept in darkness at 16° C in an incubator. Each egg or larva, with its pollen ball, was placed in a separate cavity as soon as its cell was opened in the field. Larvae survived best if kept cool and not exposed to the sun or allowed to dry out. Each Stender dish contained a piece of moist cotton to maintain high humidity (usually so that water condensed on the lid). A honey and water mixture was added to the pollen balls periodically, for the larvae did not eat provisions that became dry (in spite of the apparently high humidity). Larvae were examined and measured at intervals of two or three days. Dead ones were removed to discourage growth of fungi. About one-third to one-half of the eggs and larvae died within two days of collection. Many of these had probably been injured by handling with forceps and showed black areas at the sites of injury, which spread over the entire body within an hour or two. Twenty-five eggs and young larvae lived for considerable periods in the Stender dishes, although only one developed completely from egg to pupa. Prepupae and pupae were relatively easy to raise and required little attention.

Before hatching, the segments and pulsating head of the young larvae could be seen. As in *L. duplex* (Sakagami and Hayashida, 1960), the chorion was first removed from the anterior part of the larva in hatching. Larvae began to eat and raise their heads if disturbed within 24 hours after hatching, although the rear half was still encased in the chorion. Eggs in the laboratory hatched after two to ten days.

Five larval instars (Fig. 20) could be distinguished by observing discrete increases in widths of the head capsules of growing individuals. The duration of each instar was highly variable, perhaps because of adverse conditions in the rearing dishes. Head capsules of first instar larvae were 0.41 to 0.48 mm[4] in width and the first instar lasted two to ten days (N=4). Second instar head capsules were 0.54 to 0.58 mm in width, this stage lasting two to ten days (N=4). Third instar head capsules were 0.65 to 0.75 mm wide, this stage lasting two to four days (N=8). Fourth instar head capsules were 0.78 to 0.88 mm wide, this stage lasting one to three days (N=6). Fifth

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[4] Some larvae were larger than others throughout all instars. This may account for the near overlap of head capsule widths of different instars.

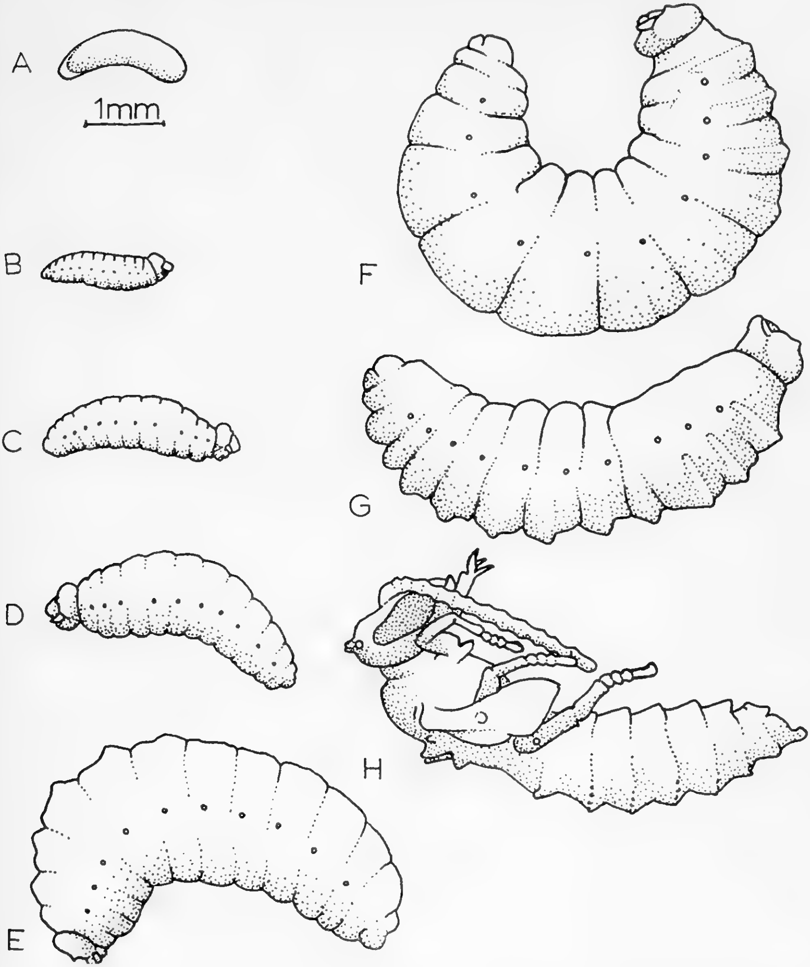

FIG. 20. Immature stages, drawn from fixed specimens all to same scale. A, Egg, with hyaline region at narrow end; B, First instar larva; C, Second instar larva; D, Third instar larva; E, Fourth instar larva; F, Fifth instar larva about to defecate; G, Prepupa; H, Pupa of male.

instar larvae defecated and became prepupae without an additional molt (N=9). Their head capsules were 1.03 to 1.16 mm wide and they lived three to thirteen days before defecating. Although the size of the head capsule increased only at each molt, the rest of the body grew gradually larger. A sample of preserved larvae from the field had the same distribution of head capsule widths, which suggested that five larval instars are normal for this species. During molting, the old larval skin was gradually pushed back from the head (the delicate transparent skins had been dusted with pollen grains to make them visible).

Behavior of larvae is in general like that of *L. duplex* (Sakagami and Hayashida, 1960) and *L. imitatum* (Michener and Wille, 1961). The youngest larvae (first to fourth instars) eat the portions of the pollen balls near their mouths and are relatively inactive. Last instar larvae curl around their pollen balls (Figs. 18, 19). They consume about two-thirds of the provisions, moving the head from side to side as they chew. These larger larvae are less sensitive to disturbances and desiccation of pollen balls than are earlier instars. When the pollen balls have been consumed, such larvae continue to make chewing motions until ready to defecate. In the insectary room, a large larva that had eaten all of its provisions continued to chew and actively moved about in the cell as if looking for more food, completing a 360° revolution within 35 minutes.

In the insectary rooms, at 28° to 33° C, the egg and larval stages combined lasted eight to 11 days (one egg developed to about second instar in 4.5 days from time of oviposition). Development from egg-laying to adult, regardless of sex, required 21 to 24 days at these temperatures. In the field, at a mean soil temperature of about 18.5° C, development from egg to adult required about 38 days.

PUPAE

Defecation and pupal development are essentially as outlined for *L. duplex* (Sakagami and Hayashida, 1960). Pupae in the insectary rooms occasionally rotate on their long axes in the cells by twisting their abdomens. Almost all pupae and prepupae excavated in the field had their heads directed toward the plugs of their cells, although fifth instar larvae were oriented in various ways. The only exceptions were one prepupa (parasitized by two small mutillid larvae) and one normal black-eyed male pupa, excavated in July and August, 1963, after a flood. Jay (1951) found that honeybee larvae depend on differences in texture of cell and cap for orientation. Possibly, the flood disoriented these *L. zephyrum* larvae by somehow changing the texture of the plugs or walls of their cells.

Teneral adults of both sexes usually stand with their heads pressed against the plugs of the cells (in rearing dishes, they pressed against the sides of the wax cavities). Females attempt to sting when their cells are opened but do not try to escape.

After bees have emerged, their cells are filled with soil brought from other parts of the burrow. The fecal material, decomposed by fungi, small oligochaetes and mites, is gradually converted into a yellow or brown powdery material. Roots of plants sometimes penetrate abandoned cells and surround the masses of soil and the probably nitrogenous fecal material in them (Fig. 12).

GENERAL CONSIDERATIONS

Peaks in production of young were seen in June and early August (Fig. 21 and Table 6), but the broods are not as distinct as in some species of *Lasioglossum* (such as the Palearctic *malachurum, duplex*). Probably the relatively short lives of overwintered females and oviposition by successive groups of young females are responsible for the fluctuations in brood production that are not seen in *L. imitatum* (Michener and Wille, 1961), a species with a long-lived queen and few egg-laying workers. The condition in *L. zephyrum* seems to be intermediate between that of solitary species with distinct broods and that of the more social Nearctic species with fairly constant production of young.

In general, cells nearest the soil surface are constructed and provisioned first, so that there is a sequence in ages of the immature stages from oldest above to youngest below. Cells along a branch burrow usually contain the older stages of brood nearest the origin of the branch. However, many irregularities occur, especially when there are several females in the nest.

As in other halictines (Sakagami and Michener, 1962), solitary females as well as females nesting together often make and provision two or more cells simultaneously.

MALES

SEASONAL CYCLE

Males first appear at the nesting areas during the third week of May, at the same time that the first female progeny of the overwintered females appear, but they are scarce. They gradually become more abundant until the second half of September when their numbers begin to decrease somewhat. The last males were seen during the second week of October, none being found after the first frost. The relative abundance of males observed flying around the nesting sites corresponds with fluctuations in the percentage of pupae that were males (Fig. 22). Males leave their nests permanently after emerging from their cells; Marshall and Musgrave (1937) found them sleeping in large aggregations in curled leaves. The few non-teneral males found in nests were not used to estimate abundance. The probable relationship between number of group C females and number of males produced has been discussed.

Fluctuations in the mean number of wing nicks of males flying around the nest sites during the season agrees well with the fluctuations in production of males. When many young males are being produced during July to September, males on the average, are less worn than in June.

TABLE 6. Composition of the brood during the year. For each month and each immature stage, the percentage (%), mean number of cells per nest ($\overline{X}$), standard error (S.E.) and range (R) of cells containing that stage are given. "New" July nests are those newly excavated after a flood in July, 1963.

		Empty Cell	Pollen	Egg	Small Larva	Larva Med.	Large Larva	Prepupa
April 1-30	%	20.8	18.0	41.6	6.9	12.5	0.0	0.0
	$\overline{X}$	0.555	0.481	1.111	0.185	0.428		
	S.E.	0.154	0.154	0.294	0.093	0.506		
	R	0-3	0-3	0-5	0-2	0-3		
May 1-15	%	21.7	11.5	4.3	4.3	1.4	18.8	23.1
	$\overline{X}$	0.750	0.400	0.150	0.150	0.050	0.650	0.800
	S.E.	0.228	0.133	0.109	0.150	....	0.418	0.451
	R	0-3	0-2	0-2	0-1	0-1	0-8	0-8
May 16-30	%	7.3	21.9	15.8	2.4	0.0	1.2	0.0
	$\overline{X}$	0.285	0.857	0.619	0.095	....	0.047	....
	S.E.	0.122	0.474	0.335	0.095	....	....	....
	R	0-2	0-9	0-5	0-2	....	0-1	....
June 1-15	%	9.6	17.2	19.2	11.1	15.7	13.1	6.5
	$\overline{X}$	0.950	1.700	1.900	1.100	1.550	1.300	0.650
	S.E.	0.303	0.391	0.397	0.176	0.426	0.616	0.335
	R	0-5	0-6	0-5	0-2	0-6	0-12	0-6
June 16-30	%	3.1	3.3	3.9	6.2	5.5	11.5	18.5
	$\overline{X}$	0.615	0.653	0.769	1.230	1.076	2.269	3.653
	S.E.	0.205	0.166	0.217	0.310	0.293	0.771	0.686
	R	0-4	0-4	0-3	0-4	0-17	0-5	0-12
July 1-15	%	7.9	1.0	0.0	2.0	2.0	5.0	12.9
	$\overline{X}$	1.142	0.142	....	0.285	0.285	0.714	1.857
	S.E.	0.705	....	....	0.286	0.286	0.421	1.320
	R	0-5	0-1	....	0-2	0-1	0-3	0-9
July 16-30	%	5.3	5.3	9.9	10.6	4.0	11.9	8.6
	$\overline{X}$	1.333	1.333	2.500	2.666	1.000	3.000	2.166
	S.E.	0.541	0.284	1.005	0.964	0.407	1.700	0.860
	R	0-5	0-3	0-10	0-20	0-4	0-20	0-10
July 16-30 (New)	%	84.6	0.0	15.4	0.0	0.0	0.0	0.0
	$\overline{X}$	0.916	....	0.166				
	S.E.	0.313	....	0.112				
	R	0-3	....	0-1				
August 1-15	%	4.4	1.5	9.5	11.0	7.5	9.1	8.6
	$\overline{X}$	2.000	0.700	4.300	5.000	3.400	4.100	3.900
	S.E.	1.265	1.158	2.128	3.066	1.905	1.581	1.225
	R	0-13	0-3	0-18	0-31	0-18	0-13	0-10
September 1-15	%	4.4	0.5	0.0	1.6	4.4	19.7	2.2
	$\overline{X}$	0.800	0.100		0.300	0.800	3.600	0.400
	S.E.	0.327			0.213	0.416	1.694	0.267
	R	0-2	0-1		0-2	0-3	0-17	0-2
October 1-15	%	0.0	16.7	0.0	0.0	0.0	0.0	0.0
	$\overline{X}$		0.150					
	S.E.		0.433					
	R		0-2					

TABLE 6. (Continued)

		Female Pupa	Female Imago	Male Pupa	Male Imago	Total Cells	Total Nests
April 1-30	%	0.0	0.0	0.0	0.0		
	$\bar{X}$					72	27
	S.E.						
	R						
May 1-15	%	14.0	0.0	0.0	0.0		
	$\bar{X}$	0.500				69	20
	S.E.	0.211					
	R	0-3					
May 16-30	%	41.4	4.7	0.0	0.0		
	$\bar{X}$	1.619	0.380			82	21
	S.E.	0.428	0.128				
	R	0-7	0-2				
June 1-15	%	6.0	0.0	1.0	0.0		
	$\bar{X}$	0.600		0.100		197	20
	S.E.	0.550		0.100			
	R	0-11		0-2			
June 16-30	%	35.3	4.9	6.2	1.6		
	$\bar{X}$	6.961	0.961	1.230	0.307	513	26
	S.E.	1.060	0.306	0.547	0.198		
	R	0-29	0-5	0-9	0-5		
July 1-15	%	40.6	18.8	6.9	3.0		
	$\bar{X}$	5.857	2.714	1.000	0.428	101	7
	S.E.	2.711	1.208	0.655	0.297		
	R	0-16	0-8	0-4	0-2		
July 16-30	%	27.8	7.0	7.9	1.7		
	$\bar{X}$	7.000	1.750	2.000	0.416	302	12
	S.E.	2.243	0.780	1.095	0.260		
	R	0-22	0-8	0-11	0-3		
July 16-30	%	0.0	0.0	0.0	0.0		
(New)	$\bar{X}$					13	12
	S.E.						
	R						
August 1-15	%	30.9	2.9	11.7	2.9		
	$\bar{X}$	14.000	1.300	5.300	1.300	453	10
	S.E.	4.119	0.578	2.724	0.989		
	R	0-47	0-5	0-26	0-10		
September 1-15	%	45.9	2.7	19.1	0.0		
	$\bar{X}$	8.400	0.500	3.500		184	10
	S.E.	3.949	0.307	2.007			
	R	0-37	0-3	0-20			
October 1-15	%	77.8	0.0	5.6	0.0		
	$\bar{X}$	3.500		0.250		18	4
	S.E.	1.817					
	R	0-12		0-1			

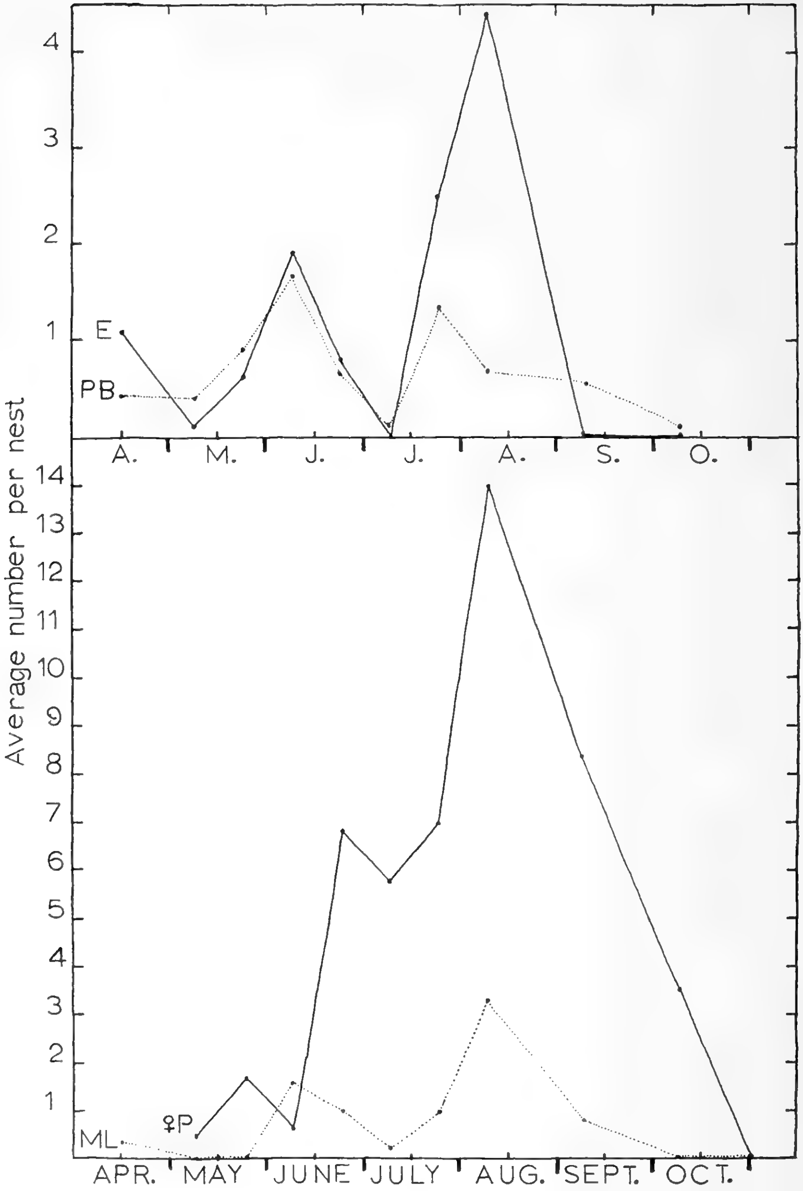

FIG. 21. Fluctuations in the production of brood. PB, pollen balls without eggs; E, eggs; ML, medium sized larvae; P, female pupae. The probable relationships between the number of pollen balls without eggs and the number of eggs are discussed in the text and additional figures are given in Table 6.

Flight Behavior of Males

Males of *L. zephyrum* usually fly around the nesting sites, although they visit flowers for nectar and sometimes mate there. In the field, males apparently are attracted by conspicuous objects. At the County Line nesting area, swarms of males were seen flying around large plants or bushes on which some of them rested at intervals. They also flew back and forth, 7 to 30 cm above the surfaces of banks or horizontal areas that contained nests. At the

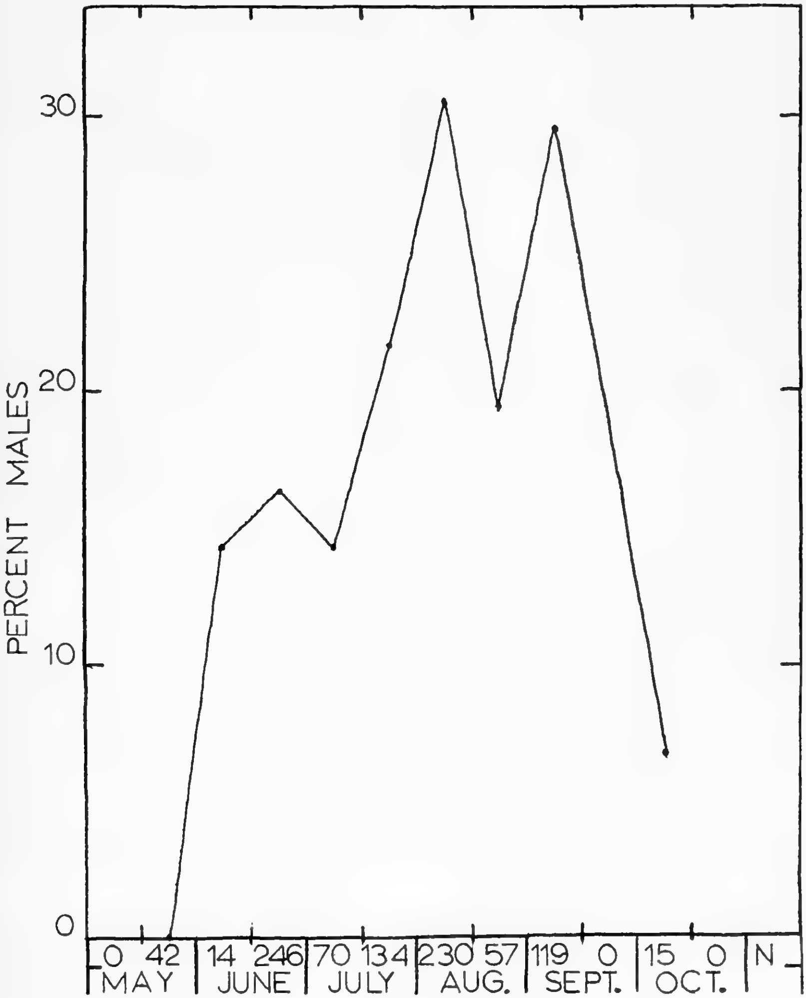

Fig. 22. Percentages of pupae and teneral adults that are males. The total number of pupae and teneral adults examined is shown for each half-month. A few adult males are found at nesting areas in May although none were in the small sample of pupae examined during that month.

Wakarusa nesting area, the greatest concentrations of males were found along the upper edges of the banks and among the hanging roots of plants that had been exposed by erosion. Males flew along the upper edges of concavities in the bank where I had removed nests. After a flood in 1962 that destroyed many nests in the left side of a bank, males no longer swarmed there (where formerly they were most abundant), but flew over the remaining nests in the right side of the bank, perhaps attracted by the heads of guarding females. In the insectary rooms, males established flight patterns around high, conspicuous objects, such as strips of corrugated cardboard on the wall (where they also rested), beams, the door frame, tall flowers, and the feeding stations that were suspended from the ceiling. They did not aggregate around the nesting boxes which were relatively low and inconspicuous. Males generally zig-zagged upward along a cardboard strip or other object. On reaching the top, they usually flew to another landmark

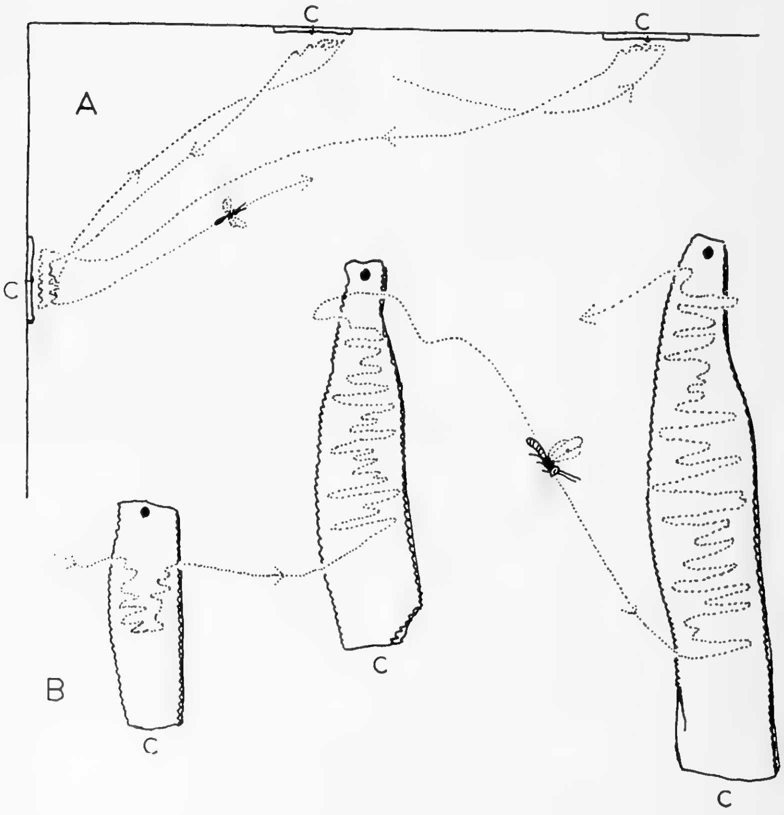

FIG. 23. Flight pattern of a male in the insectary room, semi-diagrammatic. A, Viewed from above; B, Side view. Cardboard strips are indicated (C).

and then flew upward along it. Objects were not visited in any definite sequence by individual males (Fig. 23). When lights above one side of an insectary room were turned off, males confined their flights to the lighted side. Males apparently flew independently, but when they were numerous, a swarm (the "sun-dance" of Rau, 1926) was seen around the landmarks. They usually faced toward the bank or other vertical object as they rapidly flew back and forth, and upward along its surface. Males were continuously active from 8:00 a.m. until 7:00 p.m. in summer. In the insectary rooms, they usually did not begin activity until one and one-half hours after the lights were turned on, although some females were active within one-half hour.

Mating Behavior

Mating occurs when females are standing or walking at one of the landmark areas visited by males. In the field, mating usually occurred at the banks where males were flying, but in the insectary rooms, females were attacked when they alighted on feeding stations or other objects that attracted males. Males do not attack females in flight, although groups of males or single males often followed females that were about to enter their nests, and pounced on them as soon as they alighted.

Attempted matings, lasting a few seconds, are more common than true matings, during which the bees remain together for 20 to 35 seconds (as determined by stopwatch). In June, six attempts were seen for every successful copulation observed.

Visual stimuli apparently initiate attack by males, but actual copulation is probably controlled by chemical stimuli. Males pounce on many objects but only attempt to mate with females. When offered stunned or headless females, they often persistently tried to copulate but were unsuccessful, perhaps because some cooperation by the female is necessary.

Males, like those of other halictines (Bohart, 1950; Michener and Wille, 1961), are not discriminating, and attack various objects of about the same size as females of *L. zephyrum*. They pounced at small pebbles, nail heads, female mutillids, millipeds, rhipiphorids and stationary males, but immediately flew away. When a female was contacted, the male grasped her with his legs and immediately attempted to insert his genitalia. Whether mating occurs apparently depends on the amount of resistance by the female. Frequently, females let go of the banks or other surfaces on which they are walking so that the pair falls or rolls a meter or more, and the males are often dislodged at this time. If the male continues to hold on, most females effectively resist him by curling away the abdomen, pushing him off with the hind legs or sometimes biting at his abdomen. Males usually let go after five seconds or less in such cases. Some females do not struggle or merely fall down. These are usually successfully mated. During copulation, females are passive, standing still or walking a few millimeters (they are able to fly if provoked). The male usually maintains a horizontal position above the female, with the end of his abdomen curled around the tip of the female's abdomen. The male's head is above the abdomen of the female, with the antennae slanting backwards, the legs lightly contacting the female or the nearby soil (Fig. 25). The male's abdomen expands and contracts about once per second during copulation. If the female begins to move, the male sometimes assumes a perpendicular position. The male terminates the copulation by abruptly detaching and immediately flying away. The female usually flies up as soon as the male leaves her but sometimes first cleans herself for a few seconds. Copulating pairs can be gently lifted up and sometimes aspirated without disturbing them.

By placing laboratory-reared virgin females with clipped wings on a bank were males were numerous and allowing them to mate, it was determined that spermatozoa had not entered the spermathecae of females killed immediately after mating. Spermatozoa were found in spermathecae of such females killed 36 hours after true mating, but not in those that resisted and were contacted by males for ten seconds or less.

Samples of females were collected in the field in July as they were copulating or struggling to avoid copulation, in order to determine if willingness to mate was related to age, condition of ovaries or presence of spermatozoa already in the spermatheca. These females were killed immediately, before the newly received spermatozoa could be transferred to the spermatheca. Females passively accepting the male for 15 seconds or more included: two in group E, one in group C (unfertilized), four in group D, and three in group B (fertilized). Indices of total wear of these females ranged from one to four. Females violently struggling to free themselves for ten seconds or more included: two in group E (unfertilized), four in group D, one in group E (fertilized) and one parasitized by a female *Halictoxenos*. Index of wear ranged from one to nine. No clear difference was seen between females accepting copulation and those resisting it.

When males were numerous, two or three were often seen simultaneously attempting to mate with a single female, which sometimes succeeded in avoiding all of them. Males were attracted to the heads of guards at nest entrances but were struck at by them. They unsuccessfully tried to copulate with guards that had blocked nest entrances with their abdomens. In autumn, males appeared to be more aggressive than during the summer. They frequently darted into unguarded nests. When entrances of occupied nests were artificially widened, males entered and could be seen attempting to copulate with the inhabitants. None were seen entering guarded nests with normal constricted entrances, however. Copulation within the nest is little known among bees but is usual in *L. marginatum* (Plateaux-Quénu, 1959). Worn males of *L. zephyrum* sometimes taken in nests containing females probably had entered them and were not newly emerged bees.

Males usually attacked females that hesitated before entering their nests. Such females included many young, inexperienced bees. Probably females entering hibernation are all inseminated because (a) males are numerous in fall; (b) males enter the nests; (c) the many young inexperienced females about to overwinter are attacked outside the nests; and (d) males are somewhat more active than females at low fall temperatures.

Males probably mate repeatedly. Individuals lived in vials for one week after mating. In the insectary room, marked individuals (with one antenna clipped) lived for 32 days.

VARIATIONS IN COLOR

Claude-Joseph (1926) observed considerable variation in color of the abdomens of males, and to a lesser extent, of females, of *Ruizantheda mutabilis*. Males, but not females, of *L. zephyrum* as well as of various European species of *Lasioglossum* show great variation in color of the abdomen. Abdomens of males range from almost entirely orange to uniform dark brown or black. Intermediates show different patterns and degrees of banding (Fig. 24), apparently similar to patterns seen in *R. mutabilis*.

The color of the abdomen is not associated with the age or size of the

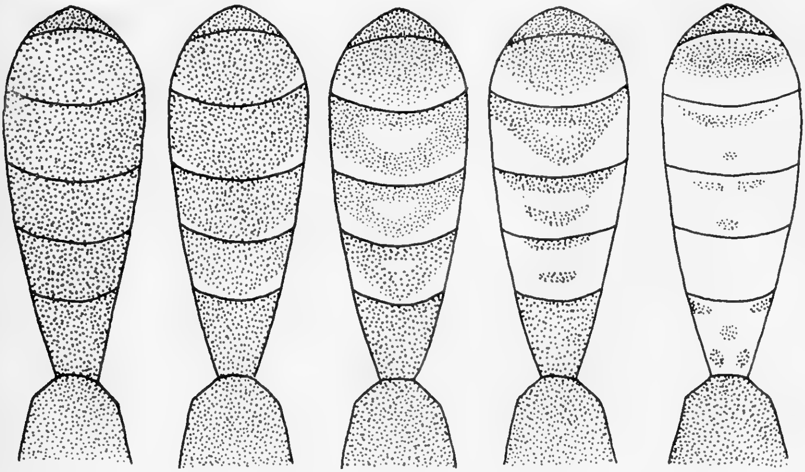

FIG. 24. Range of variation in color of the abdomens of males, semidiagrammatic. Black areas are represented by stippling.

FIG. 25. Activities at the nesting site. A, Copulating pair; B and C, Guards watching a nearby mutillid *(P. frigida)*.

male. No overall seasonal differences in abdominal color were noted and males reared at 16° C were no darker than usual; temperature probably is not a factor in determining color. Males reared from pupae of the same summer nest showed a wide range of color variation, and males of both the County Line and Wakarusa populations showed similar variations in color. These variations are probably genetically determined.

CONCLUSION

Lasioglossum zephyrum is of special interest due to its weakly social behavior. The nest founding female (queen) lives usually for several weeks with her daughters which cooperatively work in their natal nests. As the daughters grow older, they gradually equal or replace the queen as egg-layers, many simultaneously acting as foragers. Apparently these daughters tend to behave like solitary bees because they provision cells when their ovaries contain large eggs; however, they do not individually establish new nests as do solitary species.

In other social Hymenoptera, workers have small or atrophied ovaries and normally do not fully replace the queen as egg-layers. Probably in *L. zephyrum* there is little or no inhibition of ovarian development in workers by the queen. Physiological and biochemical studies to elucidate the mechanisms of colony maintenance and integration in this species need to be made. *Lasioglossum zephyrum* may be a species taking early steps in the evolution of social behavior.

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Mr. Roy Stecher generously permitted me to study a nesting area on his farm and Mr. William Kerfoot located another nesting area.

I wish also to thank my husband, Lekh, for his self-sacrifice, patience and many helpful suggestions.

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THE UNIVERSITY OF KANSAS
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A Report On The Occurrence And Distribution Of Cladocera And Copepoda In Lewis And Clark Lake, South Dakota

By

Jerry C. Tash,[1] George A. Swanson,[2] and Richard E. Siefert[2]

INTRODUCTION

North Central Reservoir Investigations, Bureau of Sport Fisheries and Wildlife, Yankton, South Dakota, is conducting biological studies on Lewis and Clark Lake, a main-stem reservoir on the Missouri River separating South Dakota from Nebraska. This is the smallest reservoir on the Missouri River and the lowest point of control in the reservoir system.

In South Dakota, most limnological investigations have emphasized vegetational, ichthyological, or physicochemical aspects (Over and Churchill, 1927; Gastler and Moxon, 1948; Shields, 1957). A few studies include records of microcrustacea (Galtsoff, 1924; Berner, 1951; Nash, 1959; Nelson, 1960). No study has considered the distribution of microcrustacea within a single aquatic locality such as a reservoir. The distribution of microcrustacea in a reservoir correlated with stomach analyses of fishes collected in that habitat may provide information on trophic dynamics, feeding areas, and movements of some fishes. This report provides information on the occurrence and distribution of Cladocera and Copepoda in Lewis and Clark Lake.

METHODS

One-hundred and four samples, collected during 1962-1963, were analysed for Cladocera and Copepoda. Eighty-six of these samples were collected

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from a boat using a Miller plankton sampler with a conical net of #10 mesh, and were taken either by towing the sampler or by hanging the sampler over the side of the boat while anchored in a swift current. The remaining 18 samples were collected in a stationary sampler installed inside Gavins Point Dam, using a conical net of #10 mesh.

Conductivity, expressed as micromhos at 25°C., was measured with an Industrial Instruments conductivity bridge, turbidity (ppm) with a Hach "Direct Reading" colorimeter, and temperature with an electronic thermometer. Zooplankton were identified with the aid of keys by Brooks (1957, 1959), Pennak (1953), Wilson (1959), and Yeatman (1944, 1959).

DESCRIPTION OF COLLECTING STATIONS

Shields (1957) and Schmullbach (1962) described Lewis and Clark Lake. The collecting stations were grouped according to river, littoral, or limnetic characteristic (Fig. 1).

River Areas

Fifteen samples were analysed from collections taken during June-August, 1963, in swift currents near the junction of the Missouri and Niobrara rivers, and from collections taken during October, 1962, and June-August, 1963, in downstream areas at Running Water and Springfield. The river level varies due to fluctuating discharges from Ft. Randall Reservoir upstream.

At station 1, samples were collected along the south edge of the Missouri River about 100 meters upstream from the Niobrara River junction. Turbidity was 12-37 ppm., conductivity 785-820 micromhos/cm, and water temperature 15.8-24.2°C. The river in this area remains relatively clear yeararound because streamflow is stabilized by Ft. Randall Reservoir about 35 miles upstream.

At station 20, samples were collected in water 1-2 meters deep at midchannel of the Niobrara River, approximately 100 meters from the mouth. Turbidity was 190-1,250 ppm., conductivity 260-445 micromhos/cm, and temperature 21.1-26.4°C.

At stations 2 and 4, samples were collected along the north edge of the Missouri River channel. Turbidity was 52-83 ppm., conductivity 735-800 micromhos/cm, and temperature 16.9-24.9°C.

Littoral Areas

Thirty-five samples were analysed from collections taken during June-August, 1963, in creeks, bays, basins, and the western end of the lake. Increased currents caused by rainfall influence all of these areas except the boat basins.

Stations 7, 8, and 9 are creeks of 15-60 meters wide at their mouths, 1.5-2.4 meters deep, have silt bottoms, lack aquatic vascular plants, and are protected from most wind action. Snatch Creek is land-locked during dry periods.

Stations 12, 16, and 17 are open bays of 1.2-4.0 hectares, 5.4-6.1 meters deep, have silt or sand bottoms, and are influenced by wind. Only station 17 has aquatic vascular plants (two species of *Potamogeton*).

Stations 3, 5, 14, and 18 are boat basins of 0.4-12.0 hectares, 1-5 meters deep, have silt bottoms, lack aquatic vegetation, and are protected from wind action. Boats entering and leaving create waves and mixing.

Station 5, in the western end of the lake, is 1.5-3.1 meters deep except in the river channel, has a silt bottom, and contains scattered aquatic vascular plants of *Scirpus* sp., *Typha* sp., and *Polygonum* sp. This area is protected from wind, but it is influenced by currents coming from the Missouri River.

LIMNETIC AREAS

Fifty-four samples were analysed from collections taken in five limnetic zones of the lake. All collections were taken during July-October, 1962, and during January-August, 1963, in water 6-20 meters deep.

Stations 9, 10, 11, and 13 are in the old river channel that winds the length of the lake. Turbidity was 12-65 ppm., conductivity 740-805 micromhos/cm, and temperature 19.4-25.8°C. These areas are influenced by wind action.

Station 15 is adjacent to the southwest side of the dam and water passes from it through the turbines. The area is protected from the wind.

SPECIES ACCOUNT

Collections from the 20 stations yielded 37 species of Cladocera and Copepoda (Table 1). Eighteen were present in river samples, 13 from the Missouri River and 15 from the Niobrara River. Few individuals of any species were in Niobrara River samples, but many individuals per species were common in Missouri River samples. Most of the species found in the Missouri River samples probably originated in Ft. Randall Reservoir. Of the 37 species distinguished, 6 were found in only littoral samples, 5 in only limnetic samples, 9 in both littoral and limnetic samples, and 7 in samples from all areas.

Table 2 summarizes relative abundance of Cladocera and Copepoda from all collecting stations. *Diaptomus forbesi, D. clavipes, D. ashlandi, Cyclops bicuspidatus thomasi, Daphnia galeata mendotae, D. pulex,* and *Bosmina longirostris* showed the greatest relative abundance throughout the year. *Mesocyclops edax, Leptodora kindtii, Diaphanosoma brachyurum, Daphnia retrocurva,* and *Moina* spp. were relatively abundant from May to October. All of the above species except *L. kindtii* were found in river samples, suggesting the possibility that river-introduced species may influence the population dynamics of the same species occurring in the lake.

DISCUSSION

Pennak (1957) reported that, at any one time, most limnetic habitats include 2-4 species of Cladocera and 1-3 species of Copepoda. The limnetic zone of Lewis and Clark Lake contained as many as 13 species of Cladocera and 11 species of Copepoda during July, 1963. Collections taken during the winter of 1962-1963 contained 3 species of Cladocera and 4-6 species of Copepoda in the limnetic samples, and the number of species during this period of time more readily fit Pennak's proposal of a typical limnetic species composition. Pennak's proposal was based on studies conducted on lakes more stable than those through which large rivers flow, as Lewis and Clark. The complex species composition of Cladocera and Copepoda in Lewis and Clark Lake can be accounted for if the varieties of habitats and modes of species introduction are considered. The large drainage area of the tributaries entering the lake introduce different species from a variety of habitats; these species may establish themselves in the niches provided by the diverse littoral and limnetic areas.

Despite the rapid movement of water through the lake (it takes approximately eight days for a volume of water equal to the holding capacity of the lake to pass through), the introduction of plankton by several large tributaries, and the extreme wind action, populations of Cladocera and Copepoda species have developed and maintained themselves. Past records (Galtsoff, 1924; Siebrass, 1960; Nelson, 1960) of species composition in the Missouri River and in Lewis and Clark Lake compared to the species listed in this paper indicate a high degree of stability in species composition of Cladocera and Copepoda of the river and lake. Only four of the 15 species of Cladocera and Copepoda recorded by Galtsoff (1924) for the upper Missouri River and only one of the 11 species of Cladocera and Copepoda recorded by Siebrass (1960) and Nelson (1960) for Lewis and Clark Lake were absent from the species listed in this report.

Further discussion on the ecology of the Cladocera and Copepoda in Lewis and Clark Lake is beyond the scope of this report. A program is now in progress to collect data on the biological and environmental parameters affecting the entire biota.

SUMMARY

Distribution and relative monthly abundance of Cladocera and Copepoda during July-October, 1962, and January-August, 1963, have been studied in Lewis and Clark Lake, Gavins Point, South Dakota. Thirty-seven species of Cladocera and Copepoda were identified from 104 samples collected from 20 different stations on Lewis and Clark Lake and on the Missouri and Niobrara rivers. Distribution of Cladocera and Copepoda were related to river, littoral, and limnetic areas. Only seven species occurred year-around while all others showed seasonal periodicity.

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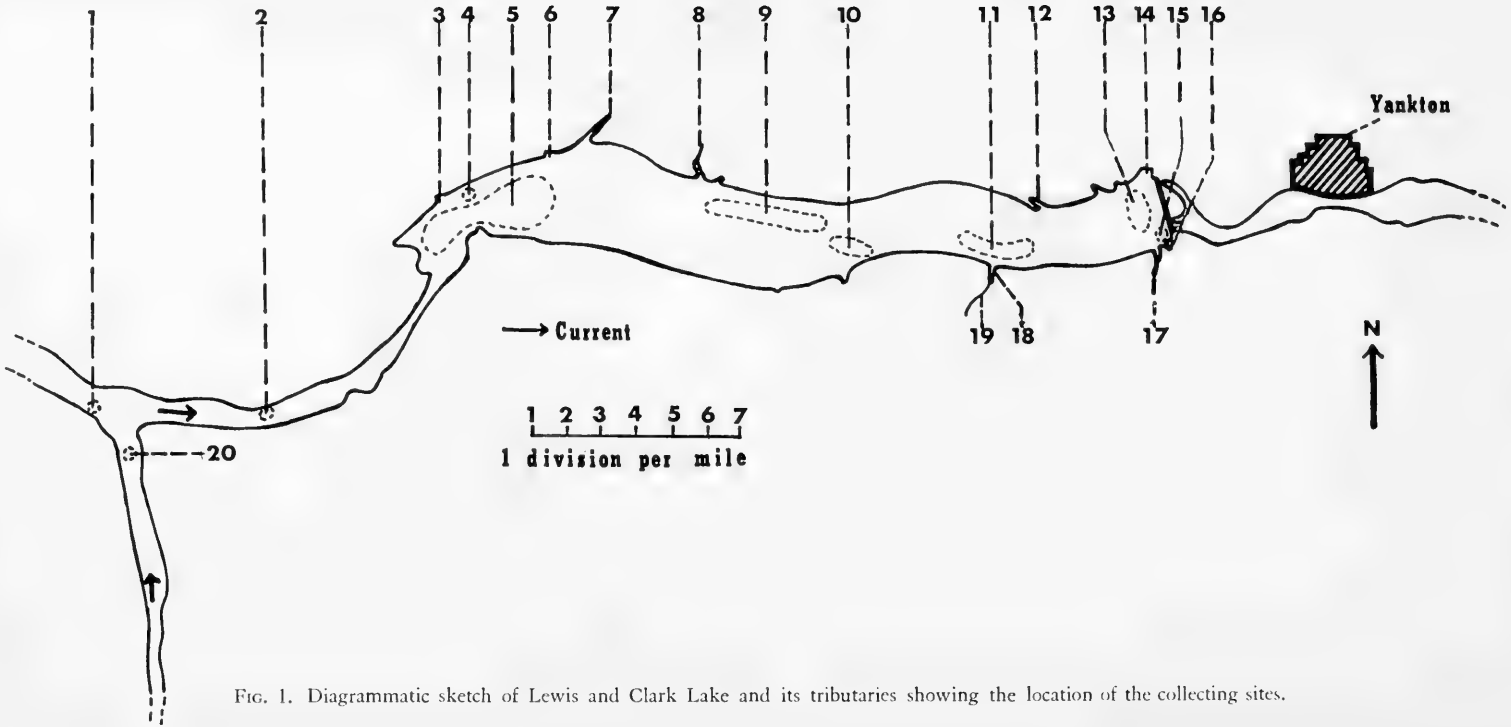

FIG. 1. Diagrammatic sketch of Lewis and Clark Lake and its tributaries showing the location of the collecting sites.

Legend:

1. Missouri River
2. Running Water
3. Propeck Boat Basin
4. Springfield Bottoms
5. Western End of Lake
6. Appletree Boat Basin
7. Snatch Creek
8. Charley Creek
9. Channel Limnetic Area
10. Channel Limnetic Area
11. Channel Limnetic Area
12. Gavins Point Bay
13. Channel Limnetic Area
14. Marina
15. Gavins Point Dam
16. Bay East of South Shore
17. South Shore Bay
18. Weigand Boat Basin
19. Weigand Creek
20. Niobrara River

TABLE 1. Distribution of Cladocera and Copepoda in study areas of Lewis and Clark Lake and in the Missouri and Niobrara rivers during July-October, 1962, and January-August, 1963. The numbers in the habitat columns indicate the numbers of separate collections from each type of environment in which the species was encountered.

	Habitat		
Species Composition	River	Littoral	Limnetic
Cladocera			
Leptodora kindtii (Focke) 1844	—	11	18
Sida crystallina (O. F. Müller) 1785	—	1	1
Diaphanosoma brachyurum (Liéven) 1848)	9	23	25
Daphnia parvula Fordyce 1901	3	1	14
D. galeata Sars 1864 *mendotae* Birge 1918	10	3	29
D. retrocurva Forbes 1882	5	8	20
D. pulex Leydid 1860 amend. Richard 1896	11	11	38
D. schødleri Sars 1862	—	—	1
Scapholeberis kingi Sars 1903	—	4	—
Ceriodaphnia reticulata (Jurine) 1820	—	—	1
C. pulchella Sars 1862	1	4	6
Moina spp.	1	21	22
Bosmina longirostris (O. F. Müller) 1785	4	21	33
Macrothrix laticornis (Jurine) 1820	—	2	1
Camptocercus rectirostris Schødler 1862	1	—	—
Leydigia quadrangularis (Leydid) 1860	—	1	3
Alona costata Sars 1862	—	1	—
A. rectangula Sars 1861	—	3	—
Pleuroxus denticulatus Birge 1878	—	2	—
Chydorus globosus Baird 1850	—	1	—
C. sphaericus (O. F. Müller) 1785	1	6	15
Alonella sp. Sars 1862	—	1	9
Copepoda			
Diaptomus forbesi Light 1938	8	12	37
D. clavipes Schacht 1897	10	4	39
D. sicilis S. A. Forbes 1882	—	—	2
D. ashlandi Marsh 1893	8	16	31
D. siciloides Lilljeborg 1889	5	3	16
D. pallidus Herrick 1879	—	—	1
Eucyclops agilis (Koch) 1838	—	5	12
E. agilis montanus (Brady)	—	8	7
Trophocyclops prasinus (Fisher) 1860	1	3	5
Cyclops vernalis Fischer 1853	3	19	18
C. bicuspidatus thomasi S. A. Forbes 1882	12	15	42
C. varicans rubellus Lilljeborg 1901	—	1	3
Mesocyclops edax (S. A. Forbes) 1891	10	2	22
Macrocyclops albidus (Jurine) 1820	—	—	2
Ergasilus chautauquensis Fellows	—	10	9
Total number of Samples taken	15	35	44

TABLE 2. The monthly relative abundance of Cladocera and Copepoda in study areas of Lewis and Clark Lake and in the Missouri and Niobrara rivers during July-October, 1962, and January-August, 1963. Code to letters in the columns under the dates: A—more than 50 individuals per sample; C—10 to 50 individuals per sample; R—1 to 9 individuals per sample.

Species	1962				1963							
	J	A	S	O	J	F	M	A	M	J	J	A
Leptodora kindtii	C	C	-	-	-	-	-	-	-	-	A	C
Sida crystallina	-	-	-	-	-	-	-	R	-	R	-	-
Diaphanosoma brachyurum	A	A	A	A	-	-	-	-	-	A	A	A
Daphnia galeata mendotae	C	A	C	C	A	C	R	R	R	C	C	C
D. parvula	R	R	C	-	-	-	R	-	-	C	C	R
D. retrocurva	R	A	C	C	-	-	-	-	-	A	A	C
D. pulex	C	C	R	A	A	C	C	C	A	C	C	R
D. schødleri	-	-	-	-	-	-	-	-	-	-	R	-
Scapholeberis kingi	-	-	-	-	-	-	-	-	-	-	C	-
Ceriodaphnia reticulata	-	-	R	-	-	-	-	-	-	-	-	-
C. pulchella	C	C	R	-	-	-	-	-	-	-	C	R
Moina spp.	A	C	C	-	-	-	-	-	-	A	A	C
Bosmina longirostris	C	A	C	C	A	A	C	C	R	A	A	C
Macrothrix laticornis	-	-	-	-	-	-	-	-	-	R	R	-
Camptocercus rectirostris	-	-	-	-	-	-	-	-	-	-	R	-
Leydigia quadrangularis	-	-	-	R	-	-	-	-	R	-	R	-
Alona costata	-	-	-	-	-	-	-	-	-	-	R	-
A. rectangula	-	-	-	-	-	-	-	-	-	-	R	-
Pleuroxus denticulatus	-	-	-	-	-	-	-	-	-	-	R	-
Chydorus globosus	-	-	-	-	-	-	-	-	-	-	R	-
C. sphaericus	C	R	R	C	-	-	-	-	R	R	R	R
Alonella sp.	-	R	C	A	-	-	-	-	-	-	R	R
Diaptomus forbesi	C	C	C	R	A	C	C	C	C	C	C	C
D. clavipes	R	C	C	A	R	C	R	C	C	C	C	C
D. sicilis	-	-	-	-	-	-	-	-	R	-	R	-
D. ashlandi	C	C	R	R	A	C	C	A	A	A	C	C
D. siciloides	A	C	C	A	C	-	-	-	-	-	R	C
D. pallidus	R	-	-	-	-	-	-	-	-	-	-	-
Eucyclops agilis	-	R	R	R	-	-	-	-	R	R	R	R
E. a. montanus	R	R	R	R	-	-	R	-	-	R	R	-
Trophyocyclops prasinus	-	C	C	-	-	-	-	-	-	-	R	R
Cyclops vernalis	C	-	R	C	-	-	-	-	-	A	A	C
C. bicuspidatus thomasi	C	C	R	A	A	A	A	A	A	A	A	C
C. varicans rubellus	-	-	-	-	-	-	-	R	R	R	R	R
Mesocyclops edax	-	C	-	C	-	-	-	R	C	R	C	C
Macrocyclops albidus	-	-	-	-	-	-	-	R	-	R	-	-
Ergasilus chautauquensis	-	R	R	R	-	-	-	-	-	-	R	R

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Mosses Of The Great Plains And Arkansas River Lowlands Of Kansas

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Abstract. The purpose of this investigation is to increase the knowledge and understanding of the mosses of the Great Plains and Arkansas River Lowlands of Kansas. Climatic, edaphic, lithologic, and topographic factors have a very important influence upon the growth and distribution of mosses in Kansas. From east to west in Kansas there is a decrease in mean temperature, in the length of the growing season, in precipitation, and in humidity, and an increase in the number of sunny days and wind velocity. These environmental factors operate together to produce a progressively less favorable habitat from east to west for the growth of mosses. Sandstone and the soil produced from it have a coarse texture and hence good moisture-retention properties; shale, limestone, chalk, and gypsum and the soils derived from them are fine-grained and hence contain a relatively small amount of moisture. Mosses are most common where there is enough topographic relief to provide north-facing slopes and ravines with favorable moisture conditions. Mosses are able to exist on the dry plains because of a protoplasm with a high resistance to desiccation and morphological features such as awns, involute and revolute margins, photosynthetic filaments, lamellae, and papillae which hold a capillary film of water onto the surface of the leaf. The pygmy mosses are mosses which are less than 5 mm in height and have a seta less than 2 mm long and a capsule which is round, less than 1 mm in diameter, with or without deciduous operculum, but always without peristome teeth. The ten genera of pygmy mosses in Kansas have arisen by specialized evolution in six different families. Four genera reveal step-wise evolutionary reduction from larger and morphologically more complex relatives. Three genera, all with morphological adaptations of the leaves to hold a film of capillary water, are very important in the moss floras of the Great Plains. The exceptional ability to complete a life cycle on the dry plains is evidence that the pygmy mosses are highly adapted for existence on the prairies of the Great Plains. The mosses of the Great Plains and Arkansas River Lowlands are discussed as a unit for each of the following physiographic areas: the Smoky Hills, the Blue Hills, the Red Hills, and the High Plains (all in the Great Plains), and the Wellington Lowland, the Great Bend Lowland, and the Finney Lowland in the Arkansas River Lowlands. Each physiographic area provides unique microhabitats which select a characteristic assemblage of mosses. From east to west in Kansas there is a decrease in the importance of mosses of both eastern and western geographical affinities in the United States and an increase in importance of mosses of western affinities. A total of 117 species and varieties in the Great Plains and Arkansas River Lowlands with 23 new records for the state of Kansas are reported. Although knowledge of the mosses is still incomplete, this study should establish without doubt that the Great Plains and Arkansas River Lowlands of Kansas are areas of great bryological interest.

INTRODUCTION

The purpose of this investigation is to increase the knowledge and understanding of the mosses of the Great Plains and Arkansas River Lowlands of Kansas. Previous collections of mosses from this area have been reported by McGregor (1950) and McGregor and Hartman (1956). In the present investigation, the western two-thirds of Kansas is approached from the physiographic standpoint with special emphasis on the microhabitats of the different rock outcrops of the various physiographic divisions. The discussion begins with a section on general physiography and is followed by one on ecology. Following, there is a morphological and an evolutionary consideration of the pygmy mosses, uniquely adapted to existence on the dry plains. In the section on mosses of the Great Plains and Arkansas River Lowlands the moss floras of the following areas are discussed and compared to each other: the Smoky Hills, the Blue Hills, the Red Hills, and the High Plains (all in the Great Plains), and the Wellington Lowland, the Great Bend Lowland, and the Finney Lowland in the Arkansas River Lowlands. A list of species is provided.

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GENERAL PHYSIOGRAPHY

Physiographically, Kansas is a plain (Schoewe, 1949). The surface of the plain slopes gradually eastward at a rate of 10 to 15 ft. per mile. The highest spot, located in Wallace County, is 4,135 feet above sea level; the lowest spot, located in Montgomery County, is slightly less than 700 feet above sea level. The surface of this plain is not everywhere flat and featureless. On the contrary, hills and valleys interrupt the flatness of the plain with slopes that are sometimes steep and precipitous. Local relief attains a maximum of 300 ft. in a mile in areas along the major streams. Elsewhere it is seldom more than 100 ft.

The classification of major and minor physiographic divisions of Kansas is given in Table 1 (Schoewe, 1949). The area of Kansas under consideration includes parts of two major physiographic provinces of the United States: the Great Plains Physiographic Province and the Central Lowlands Physiographic Province (Plate 1). The Great Plains Physiographic Province is represented in Kansas by two sections: the Dissected High Plains and the High Plains. Of the Central Lowlands the only section occurring in the study area is the Arkansas River Lowlands.

Table 1. Classification of major and minor physiographic divisions of Kansas (Schoewe, 1949). Used by permission of the author. Mosses have been collected from areas starred.

Major Division	Province	Section	Minor Division
Interior Highlands	Ozark Plateaus	Springfield-Salem Plateaus	
*Interior Plains	*Central Lowland	Osage Plains	Flint Hills Osage Cuestas Chautauqua Hills Cherokee Lowlands
		Dissected Till Plains	Kansas Drift Border Attenuated Drift Border
		*Arkansas River Lowlands	*Wellington Lowland McPherson Lowland *Great Bend Lowland *Finney Lowland
	*Great Plains	*Dissected High Plains	*Smoky Hills *Blue Hills *Red Hills
		*High Plains	

THE GREAT PLAINS

The Great Plains Physiographic Province in Kansas lies west of a line drawn from Washington County along the northern border of the state, southwestward to Harper County on the southern border. According to Fenneman (1931), the Great Plains is a broad belt of highland which slopes gradually eastward from the Rocky Mountains to the Central Lowland. The Great Plains surface is not continuous but is separated into a northern area and a southern area by the Arkansas River Lowland extension of the Central

Lowland Province. The eastern boundary of the Great Plains north of the Arkansas River is delimited by the eastern margin of the outcropping of Cretaceous rocks (Plate 2). South of the Arkansas River the eastern boundary of the Great Plains is formed by the outcropping of resistant sandstones interbedded in soft shales of Permian age. The Great Plains Province is divided into two physiographic sections: the Dissected High Plains section and the High Plains section.

The flatness of the Great Plains is due to the low angle of dip of the bedrock. According to King (1951) the structure of the rocks beneath the Great Plains is a homocline known as the Prairie Plains homocline, the eastern limb of the very asymmetric Great Plains syncline. The rocks of the homocline dip westward at a low angle. In the western part of the Great Plains the homocline is buried beneath Pliocene fluviatile deposits forming the High Plains. In the eastern part of the Great Plains, erosion has removed the fluviatile mantle and has exposed sedimentary rocks of Cretaceous and Permian ages. Because the different westward-dipping, sedimentary formations vary in resistance to erosion, differential erosion has here produced east-facing escarpments upheld by the more resistant layers of rock. This strip of eroded cuestas along the eastern front of the High Plains is known as the Dissected High Plains.

THE DISSECTED HIGH PLAINS

The Dissected High Plains form the eastern part of the Great Plains. In this area erosion has removed the Pliocene fluviatile mantle and has exposed Cretaceous and Permian rocks. There are three minor divisions included in the Dissected High Plains: the Smoky Hills, the Blue Hills, and the Red Hills. The Smoky Hills and the Blue Hills divisions are located north of the Arkansas River and are underlain by Cretaceous rocks; the Red Hills division is located south of the Arkansas River and is underlain by Permian rocks.

SMOKY HILLS.—The Smoky Hills, a belt trending from Washington County southwestward to Rush County, form the eastern part of the Dissected High Plains north of the Arkansas River. These maturely dissected hills are carved in the Cretaceous Dakota Formation, the dark color of which gives the area its name. Numerous outlying hills and mounds occur in the Smoky Hills.

BLUE HILLS.—The Blue Hills, so called because of the bluish haze which frequently invests them, form the western part of the Dissected High Plains north of the Arkansas River. This area extends from Republic and Jewell counties southwestward to Hodgeman and Finney counties. The rocks consist of inter-stratified limestones and shales of Cretaceous age. Two dissected cuestas occur in the Blue Hills. Other topographic features present are flat-topped buttes and small mesas.

RED HILLS.—The Red Hills represent the Dissected High Plains south of the Arkansas River. The name Red Hills comes from the red soil and rocks present in the area. Included in the Red Hills are parts of Kingman, Harper, Barber, Comanche, Clark and Meade counties. Underlying rocks are red shales, siltstones, and sandstones, along with gypsum and anhydrite, of Permian age. Topographic features include scarps, bluffs, mesas, and steep-sided buttes.

THE HIGH PLAINS

The High Plains in Kansas is a locally featureless area lying between 2,000 and 4,000 feet above sea level. According to Fenneman (1931), they are remnants of a former great fluviatile plain which stretched from the mountains on the west to the Central Lowland. Rivers have cut broad valleys into this plain, forming a dissected plateau with extensive flat uplands. The High Plains are generally underlain by unconsolidated or poorly cemented deposits of Pliocene (Ogallala) and Pleistocene ages. The lime-cemented part of the Ogallala Formation is known as mortar beds. These mortar beds uphold cliffs which are an important topographic feature of the High Plains. Cretaceous chalk and shale formations are exposed along the river valleys. Schoewe (1949) includes the area of outcrop of these Cretaceous rocks in the High Plains; Fenneman (1931) places this area, along with the Smoky Hills, the Blue Hills, the Red Hills, and the Great Bend Lowland, in the Plains Border. Along the river valleys there occur Pleistocene alluvium and terraces and low sand dunes.

ARKANSAS RIVER LOWLANDS

The Arkansas River Lowlands are low-lying areas extending east and west along the Arkansas River. The surface rocks are of two major kinds: unconsolidated gravels, silts, and clays of Pleistocene age and red silty shales of Permian age. The Arkansas River Lowlands are divided into the Wellington Lowland, the McPherson Lowland, the Great Bend Lowland, and the Finney Lowland. All but the McPherson Lowland are considered.

WELLINGTON LOWLAND.—The Wellington Lowland lies mostly in Sumner and Harper counties with small areas in Barber, Sedgwick, and Reno counties. Unlike the flat topography of the rest of the Arkansas River Lowlands, the Wellington Lowland topography is decidedly rolling. The surface is underlain by Permian shales.

GREAT BEND LOWLAND.—The Great Bend Lowland is an undulating plain of little relief, extending from Dodge City in Ford County eastward to Hutchinson in Reno County and southeastward to Wichita in Sedgwick County and Arkansas City in Cowley County. The surface of the lowland is covered by Pleistocene dune sand, terraces, and alluvium.

FINNEY LOWLAND.—The Finney Lowland comprises all of the Arkansas River Valley in Kansas west of Dodge City. The topography of the inner valley or valley bottom is essentially flat. The outer valley includes the terraces and land sloping toward the river but lying below the level of the High Plains. An extensive area of sand dunes occurs in the outer valley.

ECOLOGY

As an area for the growth of mosses, the Great Plains has long been misunderstood. Dr. Henry S. Conard, a well-known bryologist who has done extensive moss collecting in a state as close to Kansas as Iowa, has written (1956): "There is no moss among the grasses of the Tallgrass Prairies or the Shortgrass Plains. Moist spots or bare spots or wooded spots among these Plant Associations have their mosses." Yet, in many areas of the Great Plains mosses abound in spots that are neither moist, bare, nor wooded. Many mosses grow on soil on slopes of hills and ravines where the grass cover does not produce too much shade. Other mosses grow on rocks forming cliffs or outcropping along the sides of hills or in ravines. A few mosses grow on the bark of trees; a few others grow on sand dunes with grass or sagebrush cover.

Climatic factors have a very important influence upon the growth and distribution of mosses in Kansas. The authority for the climatic data of Kansas is S. D. Flora (1948). The annual mean temperature for the state is 55.0°F. The normal annual mean Fahrenheit temperatures for Cheyenne, Morton, Washington, and Sumner counties, located respectively at the northwest, southwest, northeast, and southeast corners of the study area are as follows:

Cheyenne	52.1	Washington	54.3
Morton	55.9	Sumner	58.0

The average length of the growing season in days for the same counties is:

Cheyenne	160	Washington	171
Morton	179	Sumner	185

The average number of clear days per year increases from 162 at Wichita at the eastern border of the study area to 177 at Dodge City in the High Plains. The average annual precipitation decreases from 30 inches at Wichita to 17 inches at the western border of the state. The mean relative humidity in the spring for Wichita and Dodge City is as follows:

	March	April	May
Wichita	60%	59%	64%
Dodge City	57%	56%	60%

The average hourly wind velocity increases from 12.1 at Wichita to 12.9 at Dodge City. Thus, from east to west there is a decrease in mean temperature, in the length of the growing season, in precipitation, and an increase in the number of sunny days and wind velocity. These environmental factors operate together to produce a progressively less favorable habitat from east to west for the growth of mosses.

Edaphic and lithologic factors, as well as climatic factors, have an important effect upon the growth and distribution of mosses in Kansas. Because soils differ in texture and moisture-retention properties, they differ in their capacity to support the growth of mosses. Soils derived from sandstone have a coarse texture due to the presence of sand grains and moisture retention is good. Soils derived from shale and limestone have a fine texture with poor moisture-rention properties. However, the moisture retention of soils derived from shale and limestone is often improved by the presence of thin layers of fine-grained sands interbedded in the shale and limestone. Like soils, the rocks differ in their ability to support growth of mosses. Because shale, limestone, gypsum, and chalk are fine-grained and relatively nonporous, they contain relatively small amounts of water. Sandstone and lime-cemented sands are coarser grained, more porous, often friable, and contain a better supply of water. Except where they are situated in ravines where there is seepage of water to moisten the rocks, shale, limestone, gypsum, and chalk are devoid of mosses. In contrast, sandstone and the lime-cemented sands support the growth of mosses, not only in ravines, but even where the rocks are exposed on wind-swept ledges and cliffs.

Because of the heat and dryness of the Great Plains in the summer, mosses growing there must have the ability to withstand extreme desiccation. An experiment was conducted to see what would result if mosses that had been stored in herbarium packets three to 20 months were placed on moist peat or sand. Of 32 species tested, the following 17 showed renewed growth: *Amblystegium juratzkanum, Astomum muhlenbergianum, Bryum argenteum, B. bicolor, B. caespiticium, Ceratodon purpureus, Desmatodon plinthobius, Grimmia apocarpa, G. laevigata, G. pulvinata, G. wrightii, Hedwigia ciliata, Leskea gracilescens, Phascum cuspidatum* var. *americanum, Physcomitrium pyriforme, Pterigoneurum subsessile,* and *Ptychomitrium incurvum.* All species except *Desmatodon plinthobius* and *Grimmia wrightii* produced new rhizoids and axillary shoots from the pieces of shoots that had been dried. *Desmatodon plinthobius* and *Grimmia wrightii* started new growth from the apex of the old stem. In some cases renewed growth started within two weeks after the dried mosses were placed upon a moist substrate. In other cases it was a month before growth was renewed. The presence of mosses on the Great Plains year after year and the results of the above experiment indicate that they have protoplasm with a very high resistance to desiccation.

In addition to a very resistant protoplasm, mosses have various morphological adaptations of the leaves which tend to hold a capillary film of water on their surfaces (Goebel, 1905). These morphological adaptations are awns or hairpoints, involute and revolute margins, photosynthetic filaments, lamellae, and papillae. The most common mosses with smooth to slightly-toothed awns are *Bryum argenteum, B. caespiticium, Desmatodon plinthobius, Phascum cuspidatum* var. *americanum, Grimmia rauei,* and *G. wrightii.* Mosses with toothed awns, the irregular surfaces of which can hold considerable capillary water, are *Grimmia laevigata, Pterigoneurum subsessile,* and *Tortula ruralis.* The strongly involute leaves of the genera *Astomum* and *Weissia* form small receptacles which can serve as a reservoir for water. A film of capillary water can be held by revolute leaf margins, a morphological adaptation common in the Pottiaceae. The genus *Aloina* has chains of photosynthetic cells attached to the upper surface of the leaves. These filaments serve both to increase the photosynthetic area and to increase the amount of capillary water held by the leaf. Lamellae, thin sheets of cells standing perpendicular to the upper surface of the leaf, perform a similar function in the genus *Pterigoneurum.* Papillae, small knobs on the outer cell wall, are an effective capillary device. Papillae are present on the leaves of many species of mosses in the Great Plains. Two species, *Hedwigia ciliata* and *Weissia glauca,* have branched papillae which are especially effective in holding a film of capillary water. These morphological adaptations enable the moss leaf to obtain moisture from dew, mist, and light rain. Since precipitation on the Great Plains is often in the form of mist or light rain, these morphological adaptations play a vital role in the existence of mosses in the area.

All of the most common mosses of the Great Plains have one or more of the morphological adaptations discussed in the paragraph above. *Bryum caespiticium* and *B. argenteum,* both common in the Great Plains and found even growing under sagebrush on sand dunes, have awned leaves. In *B. argenteum* the upper leaf cells are dead and form a protective mantle for the living cells of the lower part of the leaf (Goebel, 1905). *Grimmia laevigata,* the characteristic moss of dry wind-swept rocks in the Smoky Hills, has leaves with toothed awns. *Grimmia rauei* and *G. wrightii* with somewhat spinulose leaf awns occur on the dry wind-swept Ogallala rocks in the High Plains. *Barbula unguiculata,* common on dry limestone outcrops in the Blue Hills and on the Ogallala Formation in the High Plains, has papillose leaf cells and revolute leaf margins. The morphological adaptations found in *Phascum cuspidatum* var. *americanum,* a moss distributed from the Smoky Hills and the Red Hills west to the High Plains, are awns, papillose leaf cells, and revolute leaf margins. *Tortula ruralis* has leaves with papillose leaf cells, revolute margins, and toothed awns, features of importance in adapting this moss to its habitat on dry ravine slopes on the Ogallala Formation in the High Plains. *Pterigoneurum subsessile,* a moss which grows most abundantly under sagebrush plants on sand dunes, has leaves with lamellae and toothed awns. In both *Astomum muhlenbergianum* and *Weissia controversa* papillose leaf cells and strongly involute leaf margins are combined in a leaf with an especially good morphology to hold capillary water. These two mosses are of great importance on the Great Plains. From the foregoing discussion it can readily be seen that mosses of the Great Plains show considerable diversity in their adaptations to hold capillary water.

PYGMY MOSSES

The term "pygmy mosses" is here used to denote a group of unrelated mosses with the same growth form. The plants, gametophytes and sporophytes, together are less than 5 mm in height; the setae are less than 2 mm long; the capsule is round, less than 1 mm in diameter, cleistocarpous or with deciduous operculum, but always without peristome teeth. Thus, the pygmies are minute mosses with the leaves of the gametophyte surrounding the immersed capsule. On the Great Plains of Kansas ten genera have been found which can be considered pygmy mosses: *Archidium, Ephemerum, Aschisma, Pterigoneurum, Pleuridium, Bruchia, Pyramidula, Phascum, Acaulon,* and *Astomum.* The evolutionary relationships of the genus *Archidium* are obscure; Conard (1956) places this genus in the monogeneric Archidiaceae. Similarly, the genus *Ephemerum* is placed in the monogeneric Ephemeraceae. The relationships of the genera *Aschisma* and *Pterigoneurum* in the Pottiaceae are unclear. However, within the genus *Pterigoneurum* there is an evolutionary trend from *P. ovatum* with an exserted, cylindrical capsule to *P. subsessile* with immersed spherical capsule. The genera *Pleuridium* and *Bruchia* belong to the Ditrichaceae and the Dicranaceae, respectively (Bryan, 1956). The remaining four genera of pygmy mosses reveal a step-wise evolutionary reduction from larger and morphologically more complex relatives. Three such specialized evolutionary trends are illustrated by mosses growing on the Great Plains: one in the Funariaceae, one in the subfamily Pottioideae of the Pottiaceae, and one in the subfamily Trichostomoideae of the Pottiaceae. Each trend begins with a moss with a large gametophyte, long seta, and a large, cylindrical, operculate capsule with single or double peristome. From this stage different genera and species have undergone diminution in size and loss of structures until the pygmy condition is attained. Since the particulars of each trend differ in detail, each will be discussed separately.

The most morphologically complex species in the Funariaceae is *Funaria hygrometrica* with nodding annulate capsules with both inner and outer peristomes well developed. *Funaria flavicans* is similar, but the inner peristome teeth are short and truncate. *Funaria americana* has a peristome like that of *F. hygrometrica,* but the capsule is smaller, almost erect, and lacks an annulus. In *Entosthodon drummondii* the capsule is erect and has only a single peristome. Further reduction is illustrated by *Physcomitrium pyriforme* in which the setae are shorter and the capsule lacks peristome teeth. *Physcomitrium pyriforme* var. *serratum* has setae about 2 mm long and thus approaches the pygmy habit. The pygmy condition in the Funariaceae is represented by *Pyramidula tetragona,* a moss with a short seta and operculate capsule covered by the 4-angled calyptra.

The trend in the subfamily Pottioideae of the Pottiaceae begins with *Tortula ruralis* which has long seta, and a cylindrical, operculate capsule with long, spirally twisted peristome teeth. *Desmatodon obtusifolius* is a smaller moss with shorter, untwisted peristome. In some species of the genus *Pottia* the peristome is lacking, although the capsule is operculate. The pygmy mosses represented in this trend are *Phascum cuspidatum* var. *americanum* and *Acaulon rufescens.* Both are perfect examples of the pygmy habit with small, inoperculate, spherical capsules immersed in a bud-like cluster of gametophytic leaves.

The forms present in the subfamily Trichostomoideae of the Pottiaceae illustrate in a striking manner the specialized evolution of normally developed mosses to the pygmy condition. The trend begins with *Barbula unguiculata,* a species with seta 5 mm long, a cylindrical, operculate capsule with twisted single peristome teeth. *Didymodon tophaceus* is similar, but in this species the peristome is shorter and not twisted. The genus *Weissia* has species showing two stages in reduction from the condition represented by *Barbula* and *Didymodon. Weissia controversa* has seta 4 mm long and an operculate capsule with shorter peristome. *Weissia microstoma* is still more reduced; this species has seta 1 mm long and an operculate capsule with a closing membrane in place of the peristome teeth. Although the operculum separates as a unit when the capsule is moist, spores are released from capsules maturing in the dry prairies in June by irregular breaking of the capsule wall. This loss of function of the operculum leads in a natural way to the next genus. The genus *Astomum* represents the pygmy habit in the Trichostomoideae. In all three species the capsule is inoperculate; the spores are not released until the wall of the capsule is broken. However, in *Astomum ludovicianum* the apiculus, the tip end of the capsule, is delimited from the rest of the capsule by a distinct ridge. Thus, the apiculus represents a vestigial operculum and the ridge represents a vestigial annulus. In *A. phascoides* and *A. muhlenbergianum* the apiculus is merely the pointed tip end of the capsule. In *A. ludovicianum* the short-cylindrical capsule is up to 1 mm long, the apiculus up to 0.3 mm long, and the seta is about 0.5 mm long. In *A. phascoides* the spherical capsule is 0.7 mm in diameter, the apiculus 0.4 mm long, and the seta is 1.5 mm long. Thus, compared to *A. ludovicianum, A. phascoides* has a longer seta and apiculus, but a smaller capsule with no dividing line separating the apiculus from the rest of the capsule. *A. muhlenbergianum* represents the most reduced condition in this trend. The seta, less than 0.2 mm long, supports a spherical capsule 0.4 mm in diameter with an apiculus 0.1 mm long.

Although seven genera of the pygmy mosses are rare, three genera, all in the Pottiaceae, are of great importance in the moss flora of the Great Plains. *Astomum muhlenbergianum* is a common moss in the Smoky Hills, the Red Hills, the Blue Hills, the Wellington Lowland, and the Great Bend Lowland, and is present in the High Plains. Only in the Finney Lowland is this species absent. *Phascum cuspidatum* var. *americanum* is present in all seven physiographic regions in the area studied except for the Blue Hills and is an important moss in the Smoky Hills and the Wellington Lowland. *Pterigoneurum subsessile* is an important moss in the Finney Lowland, is fairly common in the High Plains, and is present in the Red Hills, the Blue Hills, and the Wellington Lowland. The leaves of these pygmy mosses have morphological adaptations to enable the leaf to hold a film of capillary water. *Astomum muhlenbergianum* has leaves with papillose cells and involute margins. The leaves of *Phascum cuspidatum* var. *americanum* have papillose cells, revolute margins, and awns. *Pterigoneurum subsessile* has leaves with lamellae and toothed awns. With the exception of *Grimmia rauei* and *G. wrightii,* which could be considered pygmy mosses except for the peristome teeth, these three pygmy mosses are the only ones that regularly fruit throughout the Great Plains of Kansas. This exceptional ability to complete a life cycle on the dry plains is evidence that these pygmy mosses are highly adapted for existence on the prairies of the Great Plains.

Bryan (1956, 1956a) has reported chromosome numbers of four genera of pygmy mosses. Species of *Bruchia* have chromosome numbers of n=14, n=15, and n=28. Because of the similarities of the chromosomes of *Bruchia* and *Trematodon* (n=28), the genus *Bruchia* is removed from the Ditrichaceae and placed in the Dicranaceae. The similarities of the chromosomes of *Ditrichum pallidum* (n=26) and the pygmy moss *Pleuridium subulatum* (n=13) substantiate their classification in the Ditrichaceae. The genera *Weissia* and *Astomum* are closely related taxonomically and cytologically. *Weissia controversa* has 13 bivalents, including one M-chromosome. The chromosomes of *Astomum ludovicianum* (n=13) are of similar size although two are somewhat smaller. *Astomum muhlenbergianum* is a sporophytic tetraploid with 26 bivalents, including one large elongated bivalent resembling the M-chromosome of *Weissia controversa. Acaulon rufescens* (n=26) and *Phascum cuspidatum* var. *americanum* (n=26) are also sporophytic tetraploids.

MOSSES OF THE GREAT PLAINS AND ARKANSAS RIVER LOWLANDS

The mosses of the Great Plains and Arkansas River Lowlands are discussed as a unit for each of the following physiographic areas: the Smoky Hills, the Blue Hills, the Red Hills, the High Plains of the Great Plains, the

Wellington Lowland, the Great Bend Lowland, and the Finney Lowland of the Arkansas River Lowlands. The discussion of the mosses of each area follows the same pattern. First, there is a treatment of geology and physiography in greater detail than in the section on General Physiography. Then, there is an ecological comparison of each area to the Smoky Hills where conditions for the growth of mosses are the most favorable of all regions under study. Next, the flora is analyzed from the standpoint of how many species are both eastern and western in their distribution in the United States, how many are eastern, and how many are western. Then, the most common species are listed and their distributional affinities stated, after which the rest of the mosses are listed. Following, there is a discussion of the various mosses and their microhabitats. Finally, the mosses on the microhabitats not characteristic of the area in general are considered. At the end of the section there is a comparison of the floras of the different physiographic areas. Plate 1 shows the localities from which mosses have been collected by the author.

MOSSES OF THE SMOKY HILLS

The Smoky Hills form the eastern part of the Dissected High Plains north of the Arkansas River. Outcropping rocks belong to the Dakota Formation of Cretaceous age. The Dakota Formation is divided into the lower Terra Cotta Clay Member and the upper Janssen Clay Member (Plummer and Romary, 1947). The Terra Cotta Clay Member consists of massive clay, silt, and sandstone and comprises approximately the lower two-thirds of the Dakota Formation. The Janssen Clay Member includes beds of lignite, massive clay, silt, and some shale. Approximately three-fourths of the thickness of the Dakota Formation is clay. The case-hardened, iron oxide-cemented silt beds and sandstone lenses are more resistant to erosion than the clays and form the cap rock of steep-sided hills of irregular shape. The Dakota Formation is an important aquifer. Springs and seeps are numerous due to the abundance of saturated sandstone outcropping. An area of special interest is Rock City, a group of concretions located 2½ miles southwest of Minneapolis in Ottawa County. According to Schoewe (1949), there are over 200 concretions, spherical to irregular, and 8 to 27 ft. in diameter. The sandstones forming the concretions are distinctly cross-bedded. The concretions are areas in the sandstone where the quartz sand grains have been cemented together by calcite. Because of the resistant nature of the concretions, weathering and erosion have removed the uncemented, softer sandstone, thus exposing the concretions. Pleistocene alluvium and alluvial terraces and dune sand occur in the river valleys.

More species of mosses grow in the Smoky Hills than in any other physiographic area in the region under study. The reasons for the comparative richness of the moss flora are the following:

1. Due to their eastern position, the Smoky Hills receive a relatively large amount of precipitation.
2. The dissected topography has many ravines and north-facing hill slopes favorable to the growth of mosses.
3. The sandstone is porous and contains a good supply of water. As an important aquifer, the Dakota Formation provides water for many springs and seeps on hill slopes and in ravines.
4. The soils formed from the Dakota Formation contain fine to medium sand which provides a comparatively good soil texture as far as moisture retention is concerned.

All of the above factors operate together to make the Smoky Hills the most favorable area in the Great Plains of Kansas for the growth of mosses.

Of the 81 species and varieties collected in the Smoky Hills, 77% are distributed in both the eastern and the western United States. Seventeen per cent are eastern species extending as far west as Kansas. Six per cent are of western affinity.

Ten of the 81 species and varieties are especially important in the moss flora:

Astomum muhlenbergianum
Bryum argenteum
B. caespiticium
Campylium chrysophyllum
Chamberlainia salebrosa
Desmatodon obtusifolius
Grimmia laevigata
Phascum cuspidatum var. *americanum*
Physcomitrium pyriforme
Weissia controversa

All of these mosses are distributed in both the eastern and the western United States.

Thirteen other species are common to fairly common in the Smoky Hills:

Astomum ludovicianum
Atrichum angustatum
Barbula unguiculata
Campylium hispidulum
Ceratodon purpureus
Ditrichum pallidum
Entodon seductrix
Grimmia apocarpa
Hedwigia ciliata
Homomallium adnatum
Mnium cuspidatum
Pohlia nutans
Ptychomitrium incurvum

Fifty-eight species and varieties are rare:

Acaulon rufescens
Amblystegium juratzkanum
A. serpens
A. varium
A. varium var. *ovatum*
Atrichum undulatum
A. undulatum var. *minus*
Barbula fallax
Bryum bicolor
B. cuspidatum
B. pendulum
B. pseudotriquetrum
Campylium chrysophyllum var. *brevifolium*
Chamberlainia acuminata
C. oxyclada
Desmatodon plinthobius
Dichodontium pellucidum
Dicranella varia
Didymodon rigidulus
Drepanocladus aduncus var. *polycarpus*
Entodon compressus
Ephemerum spinulosum
Eurhynchium hians
E. serrulatum
Fabronia imperfecta
Fissidens bryoides
F. obtusifolius
F. osmundioides
F. sublimbatus
Funaria americana

F. flavicans
F. hygrometrica
Grimmia plagiopodia
G. pulvinata
G. wrightii
Hygroamblystegium irriguum
Leptobryum pyriforme
Leptodictyum riparium
L. trichopodium
Leskea gracilescens
L. obscura
Orthotrichum pumilum
O. strangulatum
Philonotis longiseta
Physcomitrium hookeri
P. pyriforme var. *serratum*
Plagiothecium geophilum
Platygyrium repens
Pleuridium subulatum
Pohlia wahlenbergii
Polytrichum juniperinum
P. piliferum
Pylaisia selwynii
Pyramidula tetragona
Thuidium virginianum
Timmia megapolitana
Tortula pagorum
T. ruralis

Mosses are commonly found in ravines and on northfacing hill slopes. Most of the 81 species and varieties grow on rocks and soil in such situations. Some, however, grow in distinctive habitats. One striking example is the common occurrence of little hummocks of *Grimmia laevigata* on dry, wind-swept rocks on the sides and tops of hills. Also growing on dry rocks are *Weissia controversa, Desmatodon obtusifolius,* and *Hedwigia ciliata.* Plants of the genus *Fissidens* are usually found on rock ledges or soil on vertical ravine banks where grass leaves hang over and form a protective cover. The various pygmy mosses most often grow on small level areas on hill slopes. At the opposite ecological extreme from the dry wind-swept rocks, there are shaded spring areas characterized by the presence of the following corticolous species: *Amblystegium juratzkanum, A. serpens, A. varium, Hygroamblystegium irriguum, Leptodictyum riparium, L. trichopodium, Leskea gracilescens,* and *Orthotrichum pumilum.*

Some interesting mosses have been found growing on the sandstone concretions at Rock City. The cross-bedded sandstones of the concretions have been weathered to produce many ledges and crevices, ideal places for the growth of mosses. In a paper on the flora of Rock City, Horr (1937) mentioned two mosses but did not specify them by name. The following mosses have been found growing on the sandstone concretions: *Bryum argenteum, Campylium hispidulum, Desmatodon plinthobius, Fissidens obtusifolius, Grimmia apocarpa, G. wrightii,* and *Weissia controversa.* Of special interest is the presence at Rock City of *Desmatodon plinthobius* and *Grimmia wrightii,* two species of mosses, unknown elsewhere in the Smoky Hills, normally growing in Kansas only on the lime-cemented rocks of the Ogallala Formation in the High Plains. The occurrence of these mosses at Rock City is to be explained by the calcite cement of the concretions.

Dune sand occurs in small areas along the river valleys in the Smoky Hills. Mosses growing on these dunes are *Bryum argenteum, B. caespiticium, Phascum cuspidatum* var. *americanum,* and *Weissia controversa.* On a north-facing vertical roadbank covered by grass and shaded by a box elder tree the following species were found: *Amblystegium serpens, Astomum muhlen-*

bergianum, Barbula unguiculata, Bryum argenteum, B. caespiticium, Campylium hispidulum, Chamberlainia salebrosa, Eurhynchium serrulatum, Funaria hygrometrica, and *Mnium cuspidatum.*

MOSSES OF THE BLUE HILLS

The Blue Hills form the western belt of the Dissected High Plains north of the Arkansas River. The underlying rocks are inter-stratified limestones and shales belonging to the Gulfian Series of Cretaceous rocks. In ascending order the formations are the Graneros Shale, the Greenhorn Limestone, the Carlile Shale, and the Fort Hays Limestone. According to Fishel and Leonard (1955), the Graneros Shale is a fissile, black non-calcareous, marine shale with some sandstone, siltstone, and limestone beds. The Greenhorn Limestone consists of a blue-gray calcareous shale alternating with thin beds of dark crystalline or white chalky limestone. The Carlile Shale is represented by a lower member of fissile, light gray to buff, calcareous, marine shale and an upper member of fissile, non-calcareous, black, marine shale with a thin sandy zone. The Fort Hays Limestone of the Niobrara Formation is a massive, white, chalky limestone. The two limestone formations uphold two dissected cuestas in the Blue Hills, the Greenhorn Limestone cuesta in the east and the Fort Hays Limestone cuesta in the west. Areas underlain by the nonresistant shales have a rolling topography. Along the foot of the Fort Hays Limestone escarpment the Carlile Shale is intricately dissected into local small badlands. The more resistant limestones form the cap rock of flat-topped buttes and small mesas bounded by steep rocky escarpments up to 100 ft. high.

Several factors are responsible for the fact that the Blue Hills are decidedly less favorable than the Smoky Hills as an area for the growth of mosses. Because the Blue Hills lie to the west of the Smoky Hills, the annual precipitation is one to five inches less. The topography of the Blue Hills is not as favorable as that of the Smoky Hills. Much of the Blue Hills is underlain by nonresistant shale which produces a rolling topography with insufficient relief for exposures suitable for moss growth. However, where the shale is overlain by resistant limestone, erosion has produced hills and ravines where mosses can be found. Unlike the porous sandstone of the Smoky Hills, the shale and limestone of the Blue Hills are non-porous and do not support the growth of mosses. The fine-textured soil in the Blue Hills does not provide as much moisture for the growth of mosses as does the sandy soil in the Smoky Hills. Thus, the precipitation, topography, lithology, and edaphic conditions in the Blue Hills compare unfavorably with those of the Smoky Hills.

Of the 33 species and varieties of mosses growing in the Blue Hills, 67% are distributed in both the eastern and the western United States. Twenty-four per cent are eastern species extending as far west as Kansas. Nine per cent are western in their distribution.

The most common mosses of the Blue Hills are *Astomum muhlenbergianum, Barbula unguiculata, Bryum caespiticium, Didymodon rigidulus,* and *Weissia microstoma.* Their distributional affinities are varied. *Bryum caespiticium, Astomum muhlenbergianum,* and *Barbula unguiculata* are distributed in both the eastern and the western United States. *Weissia microstoma* is an eastern species that does not grow west of Kansas. *Didymodon rigidulus* is a western species that reaches its eastern limit in Iowa and Michigan. Thus, the Blue Hills have selected an unusual assemblage of mosses as the characteristic elements of the flora.

The other 28 species and varieties are rare:

Amblystegium juratzkanum
A. serpens
Astomum phascoides
Barbula cruegeri
B. fallax
Bryum argenteum
B. bicolor
B. cuspidatum
Campylium chrysophyllum
C. hispidulum
Ceratodon purpureus
Chamberlainia acuminata
C. oxyclada
C. salebrosa
Ditrichum pallidum
Drepanocladus aduncus
Ephemerum cohaerens
Eurhynchium serrulatum
Fissidens minutulus
Grimmia apocarpa
Leptodictyum trichopodium
Leskea gracilescens
Orthotrichum diaphanum
O. pumilum
Physcomitrium pyriforme var. *serratum*
Pterigoneurum subsessile
Pylaisia selwynii
Weissia controversa

Mosses in the Blue Hills are found growing on north-facing slopes developed along the contact between nonresistant shales and overlying resistant limestones. Shale and limestone rocks are too dry to support the growth of mosses, but a number of interesting species grow on soil and bark. The most commonly encountered mosses on soil in limestone areas are *Astomum muhlenbergianum, Barbula unguiculata,* and *Bryum caespiticium. Didymodon rigidulus,* a moss characteristic of the Ogallala rock in the High Plains, is frequent on soil in the Blue Hills. Of special interest is *Weissia microstoma.* This moss is abundant on soil at certain horizons of the Greenhorn and Fort Hays limestone outcrops where there are numerous flat pieces of limestone rock scattered upon the surface of the soil. The association of *Weissia microstoma* with such outcrops is striking, inasmuch as this moss is rare or altogether lacking in other physiographic areas of Kansas. The prominent corticolous species are *Campylium hispidulum, Leskea gracilescens, Orthotrichum diaphanum,* and *O. pumilum.*

Shale outcrops vary greatly in their capacity to support the growth of mosses. In one area there are within one-quarter mile of each other three microhabitats, each with its own moss flora. *Astomum muhlenbergianum* and *Barbula unguiculata* (not fruiting) were found on a dry hill slope. At the bottom of a moist ravine there were *Bryum cuspidatum, Leptodictyum* *trichopodium,* and *Drepanocladus aduncus.* On a hill slope at a sandy horizon in the shale the following mosses were found: *Astomum muhlenbergianum, Barbula unguiculata* (fruiting), *Bryum cuspidatum, Physcomitrium pyriforme* var. *serratum, Campylium hispidulum, Chamberlainia salebrosa, Eurhynchium serrulatum,* and *Ceratodon purpureus.*

The following species have been found growing on sandy Pleistocene alluvium: *Bryum caespiticium, B. argenteum, Barbula unguiculata, Physcomitrium pyriforme* var. *serratum,* and *Funaria hygrometrica.*

MOSSES OF THE RED HILLS

The Red Hills form the Dissected High Plains south of the Arkansas River. According to Swineford (1955), the Red Hills are developed on predominantly red Permian rocks consisting of very fine-grained sandstones and siltstones, silty shales and shales, and extensive thin beds of gypsum and anhydrite. The red color is due to a hematite stain on the mineral grains. Topographic features present in the Red Hills include jagged scarps, mesas, steep-sided buttes, and stream valleys with steep bluffs. Fenneman (1931) states that it is gypsum, a resistant rock in dry climates, that upholds the topographic features of the Red Hills. The prominent scarp forming the eastern boundary of the Red Hills is upheld by resistant sandstones (Bayne, 1960). Thus, the topographic relief, which locally reaches a maximum of 300 ft., is to be explained by the differential erosion of nonresistant shales and resistant sandstones and gypsum.

Swineford (1955) has classified the Permian rocks in the Red Hills in the following formations, listed in ascending order: the Salt Plain Formation, the Cedar Hills Sandstone, the Flowerpot Shale, the Blaine Formation, and the Dog Creek Shale of the Nippewalla Group of the Leonardian Series, and the Whitehorse Sandstone, the Day Creek Dolomite, and the Taloga Formation of uncertain classification. These formations outcrop from east to west in the same order. The Salt Plain Formation consists of reddish-brown, flaky siltstones, thin, sandy siltstones, and very fine-grained sandstones. A plain of low relief has developed upon most of the outcrop area. The Cedar Hills Sandstone includes brownish-red, massive, very fine-grained sandstones and sandy siltstones with beds of argillaceous siltstone and silty shale. Box canyons have developed in the thick sandstones. The Flowerpot Shale consists of reddish-brown gypsiferous shale and silty shale with a few thin beds of sandstone and siltstone; the Blaine Formation above contains massive gypsum, thin dolomite, and brownish-red shale. The resistant Blaine gypsum forms the cap rock of mesas and buttes, the slopes of which are developed upon the nonresistant Flowerpot Shale lying below the gypsum. Where the protective gypsum cover has been removed by solution, deep ravines have been eroded into the soft shales. Prominent benches formed by resistant sandstones outcrop on the shale slopes. The Dog Creek Shale consists of thin beds of dark red, silty shale, brownish-red and greenish-gray siltstone, and very fine-grained sandstone, dolomite, dolomitic and gypsiferous sandstone, and gypsum. The Whitehorse Sandstone includes red, friable sandstone, siltstone, and shale, with minor quantities of white to buff sandstone and dolomite. The Day Creek Dolomite is a single bed of pale gray to pink, dense, fine-grained dolomite with some chert. The Taloga Formation consists of montmorillonitic shale, silty shale, siltstones, and some very fine-grained sandstones. A rolling topography has developed in this formation.

Like the Smoky Hills, the Red Hills are located toward the eastern part of the study area and receive a relatively large amount of precipitation. The topography of the Red Hills, like that of the Smoky Hills, is dissected with many ravines and north-facing hill slopes favorable for the growth of mosses. However, the shale, siltstone, and gypsum of the Red Hills are less porous and contain less water than the more porous sandstone of the Smoky Hills. Although the texture of the soil in the Red Hills is in places improved by the addition of fine sand, the soil of the Red Hills does not compare favorably with the predominantly sandy soil of the Smoky Hills in regard to the retention of moisture. As a result of the comparatively unfavorable lithologic and edaphic conditions in the Red Hills, there are only half as many species of mosses growing in the Red Hills as in the Smoky Hills.

Most of the mosses growing in the Red Hills also grow throughout all or nearly all of the United States. Of the 31 species and varieties of mosses found in the Red Hills 68% are widely distributed throughout the United States. Ten per cent are eastern species extending as far west as Kansas. Nineteen per cent are essentially western species. *Aschisma kansanum* is endemic to Kansas.

The most common mosses in the Red Hills are *Astomum muhlenbergianum, Barbula unguiculata, Campylium chrysophyllum, Weissia controversa,* and *Didymodon rigidulus.* Except for *Didymodon rigidulus,* which is of western affinity, the mosses characteristic of the Red Hills are species widely distributed throughout all or most of the United States.

The remaining 26 species and varieties are rare:

Acaulon rufescens
Aloina rigida
Amblystegium juratzkanum
A. serpens
Aschisma kansanum
Barbula fallax
Bryum argenteum
B. caespiticium
B. cuspidatum
Campylium hispidulum
Didymodon tophaceus
Ditrichum pallidum
Fabronia ciliaris
Fabronia imperfecta
Fissidens minutulus
F. sublimbatus
Homomallium mexicanum
Leskea gracilescens
Orthotrichum diaphanum
O. pumilum

Phascum cuspidatum var. *americanum*
Pterigoneurum subsessile
Pylaisia selwynii
Tortula pagorum
T. ruralis
Weissia microstoma

The most characteristic mosses on slopes of hills and ravines are *Astomum muhlenbergianum, Barbula unguiculata, Campylium chrysophyllum,* and *Weissia controversa.* Mosses are not abundant on gypsum, but the notable ones are *Amblystegium juratzkanum, A. serpens, Didymodon rigidulus, Fissidens minutulus,* and *F. sublimbatus.* The important corticolous species include *Fabronia imperfecta, Leskea gracilescens, Orthotrichum diaphanum, O. pumilum,* and *Tortula pagorum. Aschisma kansanum* grows beneath and around the edges of small, round, white quartz pebbles.

In the Red Hills there are several habitats quite unlike those found on the Permian rocks. The Cheyenne Sandstone of the Dakota Formation of Cretaceous age outcrops in local areas. *Desmatodon obtusifolius, Grimmia laevigata,* and *G. rauei* grow on the sandstone rocks, while *Bryum argenteum, B. caespiticium, Ceratodon purpureus, Ditrichum pallidum,* and *Weissia controversa* grow on the sandy soil. Except for *Grimmia rauei,* which normally grows on the Ogallala Formation in the High Plains, these mosses are most commonly found on the Dakota Formation in the Smoky Hills. Rocks of the Ogallala Formation outcrop at Big Basin, a sink located in the western part of the Red Hills. *Didymodon rigidulus* and *Grimmia wrightii* grow on rocks; *Aloina rigida, Bryum argenteum, B. caespiticium, Pterigoneurum subsessile, Phascum cuspidatum* var. *americanum,* and *Weissia controversa* grow on the soil. All of these species are also found in the High Plains. The mosses common on sandy Pleistocene alluvium are *Bryum argenteum, B. caespiticium, Barbula unguiculata,* and *Phascum cuspidatum* var. *americanum.* Other mosses found on alluvium are *Archidium ohioense, Aloina rigida, Astomum muhlenbergianum, Bryum bicolor, Ephemerum cohaerens, Physcomitrium pyriforme* var. *serratum, Pterigoneurum subsessile,* and *Pottia arizonica.* Except for *Pottia arizonica,* which is known in Kansas from only one area, these mosses are found on sandy substrates in other physiographic areas in Kansas.

MOSSES OF THE HIGH PLAINS

The High Plains include approximately the western one-third of Kansas. The surface materials are of Pleistocene and Pliocene (Ogallala) ages. According to Frye, Leonard, and Swineford (1956), the Ogallala Formation consists of feldspathic sand, silt, and gravel with irregular calcareous cementation. The cemented deposits of the Ogallala Formation, known as mortar beds, are resistant and form cliffs along the sides of hills and ravines. Where the Ogallala Formation is covered by Pleistocene deposits, the topography is flat. Cretaceous chalk and shale outcrops are exposed along the river valleys. Also in the river valleys are Pleistocene alluvium and alluvial terraces and low sand dunes.

Insofar as topographic, lithologic, and edaphic conditions are concerned, the High Plains compare favorably with the Smoky Hills as an area suitable for the growth of mosses. Away from the flat inter-stream divides there are prominent cliffs and ravines. The Ogallala Formation, porous and often friable, is the only rock formation other than the Dakota Formation in the Smoky Hills to support the growth of mosses. Likewise, the soil texture is such as to contain moisture for moss growth. However, precipitation in the High Plains is 3 to 10 inches less than in the Smoky Hills. Also, the humidity is lower and the wind velocity is higher in the High Plains than in the Smoky Hills. As a result, considerably fewer species of mosses grow in the High Plains than in the Smoky Hills.

Of the 44 species and varieties of mosses growing in the High Plains, 61% are distributed in both the eastern and the western United States. Sixteen per cent are eastern species extending as far west as Kansas, and 20% are western. *Aschisma kansanum* is endemic to Kansas.

The most common mosses of the High Plains are *Grimmia wrightii, G. rauei, Didymodon rigidulus, Barbula unguiculata,* and *Bryum caespiticium*. *Grimmia wrightii, G. rauei,* and *Didymodon rigidulus* are mosses of western affinity, while *Barbula unguiculata* and *Bryum caespiticium* are distributed in both the eastern and the western United States.

Four other species of mosses fairly common in the High Plains are *Bryum argenteum, Desmatodon plinthobius, Pterigoneurum subsessile,* and *Tortula ruralis.*

The remaining 35 species and varieties are rare:

Aloina brevirostris
A. rigida
Amblystegiella subtilis
Amblystegium americanum
A. juratzkanum
A. serpens
Aphanorhegma serratum
Aschisma kansanum
Astomum muhlenbergianum
Barbula fallax
Bryum bicolor
B. gemmiparum
Campylium chrysophyllum
C. hispidulum
Chamberlainia acuminata
C. salebrosa
C. velutina
Desmatodon obtusifolius
Didymodon tophaceus
Eurhynchium serrulatum
Fissidens bryoides
F. minutulus
F. sublimbatus
Grimmia teretinervis
Hygroamblystegium irriguum
Hypnum cupressiforme
Leptodictyum riparium
L. trichopodium
Oreoweisia serrulata
Orthotrichum diaphanum
Phascum cuspidatum var. *americanum*
Physcomitrium hookeri
Weissia controversa
W. glauca
W. microstoma

The Smoky Hill Chalk Member of the Niobrara Formation is exposed in areas bordering the major streams. Mosses growing on north-facing slopes of ravines are *Astomum muhlenbergianum, Barbula unguiculata, Didy-*

modon rigidulus, Bryum caespiticium, Campylium hispidulum, Weissia controversa, and *W. microstoma.* All of these are known also from Ogallala outcrop areas in the High Plains.

Pleistocene alluvium and alluvial terraces and sand dunes occur in the river valleys. Mosses collected on sandy alluvium in the western part of the High Plaines include *Barbula unguiculata, Bryum argenteum, B. caespiticium, Phascum cuspidatum* var. *americanum,* and *Pterigoneurum subsessile.* On sandy terraces in Kingman and Reno counties of the eastern part of the High Plains the following mosses are abundant: *Astomum muhlenbergianum, Bryum argenteum, B. caespiticium, Phascum cuspidatum* var. *americanum,* and *Weissia controversa.* Also present are *Acaulon rufescens, A. schimperianum, A. triquetrum, Archidium ohioense, Astomum ludovicianum, Barbula unguiculata, Bryum cuspidatum, Ephemerum cohaerens, E. spinuolsum, Funaria flavicans,* and *Pleuridium subulatum. Bryum argenteum, B. caespiticium,* and *Pterigoneurum subsessile* grow abundantly on sand dunes, but *Barbula unguiculata, Phascum cuspidatum* var. *americanum,* and *Physcomitrium pyriforme* var. *serratum* are rare.

The Cockrum Sandstone of the Dakota Formation of Cretaceous age is exposed in local outcrops along streams in Stanton and Morton counties. *Grimmia rauei, Weissia glauca,* and *Didymodon rigidulus* grow on rock, while *Aloina rigida, Barbula unguiculata, Bryum argenteum, B. caespiticium, Phascum cuspidatum* var. *americanum, Pterigoneurum ovatum,* and *P. subsessile* grow on sandy soil. At present *Pterigoneurum ovatum* is known in Kansas only at Cockrum Sandstone outcrops in Stanton County.

MOSSES OF THE WELLINGTON LOWLAND

The Wellington Lowland is situated mostly in Sumner and Harper counties. The rocks that outcrop in the Wellington Lowland are of Permian and Pleistocene ages (Bayne, 1960; Walters, 1961). Although bedrocks are Permian, they are in many areas mantled by Pleistocene deposits. The Permian rocks are represented by the Sumner Group below and the Nippewalla Group above, both of the Leonardian Stage. The Sumner Group underlies the eastern part of the Wellington Lowland and consists of two formations: the Wellington Formation below and the Ninnescah Shale above. The Nippewalla Group underlies the western part of the Wellington Lowland and includes the Harper Siltstone below and the Salt Plain Siltstone above. The Wellington Formation consists of mostly shale and silty shale, usually of gray and green color, but sometimes red. The Ninnescah Shale is a reddish-brown, silty shale with beds of thin calcareous siltstone, blocky, reddish-brown shale, and a very fine-grained sandstone. The Harper Siltstone consists of reddish-brown, argillaceous siltstone and silty shale and a few thin beds of silty sandstone. The Salt Plain Siltstone consists of red silty shale with thin, silty sandstone and siltstone beds. Since the Permian shales and siltstones are easily eroded, and topography of the Wellington Lowland is characterized by gently rolling hills.

Although the average annual precipitation for the counties in the Wellington Lowland is three inches more than those in the Smoky Hills, the Smoky Hills is a much better area for the growth of mosses. The topographic expression of the nonresistant shales and siltstones in the Wellington Lowland is a rolling area with only rare development of hills and ravines with protected exposures favorable for the existence of mosses. The shales and siltstones and the soils produced upon them are poor substrates as far as a moisture supply for mosses is concerned. The best growth of mosses occurs at sandy horizons of the Ninnescah Shale where a fine sand improves the texture of the soil, and the shale is eroded to produce north-facing slopes. Thus, despite a more favorable precipitation, the less favorable topographic, lithologic, and edaphic conditions in the Wellington Lowland make moisture conditions for the growth of mosses there less suitable than in the Smoky Hills.

Of the 14 species of mosses known presently from the Wellington Lowland, 79% are distributed in both the eastern and the western United States. Fourteen per cent are eastern species and 7% are western species.

The characteristic mosses of the Wellington Lowland are *Astomum muhlenbergianum*, *Barbula unguiculata*, *Bryum argenteum*, and *Phascum cuspidatum* var. *americanum*. All of these are known from both the eastern and the western United States.

The other 10 mosses are rare:

Astomum ludovicianum
A. phascoides
Bryum caespiticium
Chamberlainia salebrosa
Leskea gracilescens
Physcomitrium pyriforme
P. pyriforme var. *serratum*
Pterigoneurum subsessile
Pyramidula tetragona
Weissia controversa

The most common mosses growing on sandy Pleistocene alluvium are *Barbula unguiculata*, *Bryum caespiticium*, and *Phascum cuspidatum* var. *americanum*. Others include *Astomum ludovicianum*, *A. muhlenbergianum*, *Barbula fallax*, *Bryum argenteum*, *Chamberlainia oxyclada*, and *Ephemerum cohaerens*. Those growing on bark are *Leskea gracilescens*, *Orthotrichum diaphanum*, *O. pumilum*, and *Tortula pagorum*.

MOSSES OF THE GREAT BEND LOWLAND

The Great Bend Lowland extends along the Arkansas River from Arkansas City in the east to Dodge City in the west. Much of the area is underlain by Pleistocene dune sand. The dune sand consists of fine- to medium-grained quartzose sand with minor amounts of clay, silt, and coarse sand (Latta, 1950). Erosion has reduced the older dunes to a low, hummocky topography. The younger dunes, subjected to erosion for a shorter time, form moderately steep, irregular, grass-covered hills surrounding shallow, undrained basins (Bayne, 1956). Small ponds form in some of these undrained basins. Most of the Great Bend Lowland is covered by the older subdued dunes which are often in cultivation. However, younger, irregular dunes occur in various places, notably between the Arkansas and the Little Arkansas rivers. Pleistocene terraces and alluvium also occur in the Great Bend Lowland.

Precipitation in the Great Bend Lowland compares favorably to that in the Smoky Hills. However, the topographic diversity present in the Smoky Hills is lacking in the former. Furthermore, dune sand does not have the good moisture retention properties characteristic of the sandy soil of the Smoky Hills. As a result of these factors, the Great Bend Lowland does not have as rich a moss flora as the Smoky Hills.

Of the 30 species and varieties of mosses growing in the Great Bend Lowland, 70% are species found in both the eastern and the western United States. Twenty-seven per cent are eastern species extending as far west as Kansas, and three per cent are western species.

The characteristic mosses of the Great Bend Lowland are *Astomum muhlenbergianum, Bryum argenteum, B. caespiticium,* and *Physcomitrium pyriforme.* All of these are distributed in both the eastern and the western United States.

The remaining 26 species and varieties are rare:

Amblystegium serpens
Archidium ohioense
Atrichum angustatum
Barbula unguiculata
Bruchia sullivanti
Bryum bicolor
B. pseudotriquetrum
Campylium chrysophyllum
Ceratodon purpureus
Chamberlainia acuminata
Ditrichum pallidum
Ephemerum cohaerens
E. crassinervium
E. spinulosum
Funaria flavicans
F. hygrometrica
Leskea gracilescens
Orthotrichum diaphanum
O. pumilum
Phascum cuspidatum var. *americanum*
Physcomitrium pyriforme var. *serratum*
Pleuridium subulatum
Pohlia nutans
Pylaisia selwynii
Tortella humilis
Weissia controversa

Mosses are most commonly found on young sand dunes which provide enough relief to form shallow depressions. The only species commonly found where the dunes are above the water table are *Astomum muhlenbergianum, Bryum argenteum, B. caespiticium,* and *Physcomitrium pyriforme.* The remaining species are normally found only in areas where the water table intersects the surface of the depressions and moist spots and small ponds are formed. Species growing on bark include *Amblystegium serpens, Chamberlainia acuminata, Leskea gracilescens, Orthotrichum diaphanum, O. pumilum, Pylaisia selwynii,* and *Tortella humilis.*

At Pawnee Rock in southwestern Barton County there is an isolated outcrop of the Dakota Formation. Mosses growing there are *Barbula unguiculata, Bryum argenteum, B. caespiticium, Desmatodon obtusifolius,* and *D. plinthobius. Desmatodon plinthobius* is a moss occurring elsewhere in Kansas on the lime-cemented sands of the Ogallala Formation in the High Plains and on the lime-cemented sandstone concretions in the Smoky Hills.

MOSSES OF THE FINNEY LOWLAND

The Finney Lowland includes the Arkansas River Valley west of Dodge City. Extensive sand dunes occur in the outer valley of the river. Mosses have been collected from several areas in the sand dunes along the Arkansas River west of Syracuse in Hamilton County. The altitude of the dunes is only a few tens of feet higher than the Arkansas Valley and is more than 150 feet lower than the upland area of the High Plains (McLaughlin, 1943). The maximum relief in the dunes is 70 feet. The dunes are bare or are covered by grass and sagebrush.

Because the precipitation is only 17 inches per year and the dunes lie above the water table, only a few drought-resistant mosses grow in the area. However, the species present occur abundantly, mostly under the protective cover of sagebrush plants. The sagebrush bushes serve to collect dew and light rain and direct it toward the mosses growing underneath. As a result, even light rains can be effective in providing moisture.

Only six species of mosses have been found growing on the sand dunes. *Pterigoneurum subsessile, Bryum argenteum,* and *B. caespiticium* are abundant, while *Phascum cuspidatum* var. *americanum, Barbula unguiculata,* and *Funaria hygrometrica* are rare. These six mosses represent four different geographical patterns in the United States. *Bryum argenteum, B. caespiticium,* and *Funaria hygrometrica* are distributed throughout the United States. *Barbula unguiculata* is known throughout the United States but is rare in the West Coast States. *Phascum cuspidatum* var. *americanum* is known from the eastern United States and Arizona. In contrast, *Pterigoneurum subsessile* is a western species occurring mostly from Arizona to Texas and Kansas, but also reported from North Dakota and Illinois. The moss flora of the sand dunes of the Finney Lowland is, then, a unique assemblage.

All mosses growing on the sand dunes have morphological adaptations of the leaves to hold capillary water. *Bryum argenteum* and *B. caespiticium* have leaves with slightly toothed awns. In addition to awns, the leaves of *Phascum cuspidatum* var. *americanum* have papillose leaf cells and revolute margins. *Pterigoneurum subsessile,* growing in irregularly shaped hummocks up to 5 cm across and fruiting profusely, has even more specialized adaptations. Both the erect lamellae attached to the upper surface of the leaves and the toothed awns projecting from the surface of the hummocks serve as very effective devices to hold capillary water.

COMPARISON OF THE FLORAS OF THE SEVEN PHYSIOGRAPHIC AREAS

Table 2 shows the geographical affinities of the entire moss floras of the seven physiographic areas in the region under study.

Table 2. Percentage of the species of the total moss floras of the seven physiographic areas with geographical distribution in both the eastern and the western United States, only in the eastern United States, and only in the Western United States.

	Eastern and Western	Eastern	Western
Smoky Hills	77	17	6
Blue Hills	67	24	9
Red Hills	68	10	19
High Plains	61	16	20
Wellington Lowland	79	14	7
Great Bend Lowland	70	27	3
Finney Lowland	83	0	17

From east to west in the Great Plains there is a decrease in the percentage of mosses of both eastern and western affinities and an increase in the percentage of mosses of western affinities.

Table 3 shows the geographical affinities of the characteristic mosses of each of the seven physiographic areas. As in the comparison of the entire moss floras, the comparison of the most characteristic elements of each of the floras of the seven physiographic areas shows from east to west a decrease in the percentage of mosses of both eastern and western distribution in the United States and an increase in the percentage of mosses of western distribution. However, in the comparison of the most common mosses there is a greater difference in the percentages from one area to the next. *Weissia microstoma* accounts for the 20% of eastern mosses reported from the Blue Hills. The presence of this moss in the Blue Hills and its rarity in the rest of Kansas are very intriguing. Especially noteworthy are the high percentage

Table 3. Percentage of the characteristic moss species of the seven physiographic areas with geographical distribution in both the eastern and the western United States, only in the eastern United States, and only in the Western United States.

	Eastern and Western	Eastern	Western
Smoky Hills	100	0	0
Blue Hills	60	20	20
Red Hills	80	0	20
High Plains	40	0	60
Wellington Lowland	100	0	0
Great Bend Lowland	100	0	0
Finney Lowland	67	0	33

of mosses of both eastern and western affinity in the Smoky Hills, the Wellington Lowland, and the Great Bend Lowland and the high percentage of western species in the High Plains.

Table 4 is a compilation of the most common or characteristic mosses of each of the seven physiographic areas. Although there are common elements from area to area, each assemblage of mosses is unique to its physiographic area. The Smoky Hills is notable for the relatively large number of mosses commonly found. The other areas have comparatively few common mosses, but with the exception of the Great Bend Lowland these floras cannot be considered an impoverished Smoky Hills flora because of the presence of mosses not characteristic of the Smoky Hills. *Weissia microstoma* is characteristic of only the Blue Hills; *Grimmia rauei* and *G. wrightii,* of only the High Plains, and *Pterigoneurum subsessile,* of only the Finney Lowland. Three of the characteristic species of the Red Hills are common species in the Smoky Hills, while the other two species are common in the High Plains. The Wellington Lowland shares three species in common with the Smoky Hills and one species with the High Plains. The Smoky Hills and the High Plains have only one characteristic species in common, *Bryum caespiticium.* Thus, it can be seen that each physiographic area provides unique microhabitats which select a characteristic assemblage of mosses.

TABLE 4. The characeristic mosses of the seven physiographic areas.

Smoky Hills	*Astomum muhlenbergianum* *Bryum argenteum* *B. caespiticium* *Campylium chrysophyllum* *Chamberlainia salebrosa*	*Desmatodon obtusifolius* *Grimmia laevigata* *Phascum cuspidatum* var. *americanum* *Physcomitrium pyriforme* *Weissia controversa*
Blue Hills	*Astomum muhlenbergianum* *Barbula unguiculata*	*Didymodon rigidulus* *Bryum caespiticium* *Weissia microstoma*
Red Hills	*Astomum muhlenbergianum* *Barbula unguiculata*	*Campylium chrysophyllum* *Weissia controversa* *Didymodon rigidulus*
High Plains	*Grimmia rauei* *G. wrightii*	*Didymodon rigidulus* *Barbula unguiculata* *Bryum caespiticium*
Wellington Lowland	*Astomum muhlenbergianum* *Barbula unguiculata*	*Bryum argenteum* *Phascum cuspidatum* var. *americanum*
Great Bend Lowland	*Astomum muhlenbergianum* *Bryum argenteum*	*Bryum caespiticium* *Physcomitrium pyriforme*
Finney Lowland	*Bryum argenteum*	*Bryum caespiticium* *Pterigoneurum subsessile*

It should be stated here that the mosses of the Great Plains and Arkansas River Lowlands are still imperfectly known. This area, of great geographical extent and geologic diversity, requires much more investigation before the knowledge of the mosses is complete. The mosses of the McPherson and Wellington Lowlands are only poorly known. The Cedar Hills Sandstone and the Whitehorse Sandstone of the Red Hills are promising areas that have not been collected from. Further investigation should not overlook the Laverne and Rexroad formations exposed in Seward County in the High Plains. The mosses of the Smoky Hill Chalk Member of the Niobrara Formation may need to be treated as a separate unit, rather than as a subordinate unit in the High Plains. However, this study should establish without doubt that the Great Plains and Arkansas River Lowlands of Kansas are areas of great bryological interest.

DISCUSSION OF INDIVIDUAL SPECIES

Each taxon is listed and its geographical range in the United States and in the Great Plains and Arkansas River Lowlands is stated. Geographical ranges are based on information in Grout (1928-1940) and on reports in volumes 18 to 60 *The Bryologist,* McGregor (1950), and McGregor and Hartman (1956). Morphological features of special interest are also discussed. Starred taxa were previously unknown from Kansas or were without voucher specimen. A total of 117 species and varieties are reported with 23 new records. Unless otherwise noted, all taxa are on file in the herbarium at the University of Kansas, Lawrence, Kansas.

Acaulon rufescens Jaeg. Known from the eastern United States and also reported from Arizona, this species is rare and was found on soil in Cloud, Clay, Ottawa, and Ellsworth counties in the Smoky Hills, in Barber County in the Red Hills, in Reno County in the Great Bend Lowland, and on Pleistocene terraces in Kingman County in the High Plains.

**Acaulon schimperianum* Sull. Formerly known only from Arizona, Texas, and Iowa this species has been collected once in Kansas. The plant was growing beneath a round, white, quartz pebble on a Pleistocene terrace in Reno County in the Great Bend Lowland.

Acaulon triquetrum (Spruce) C. M. Known from the eastern United States, this moss has been reported by Cridland (1960) on a Pleistocene terrace in Reno County in the High Plains. Specimens are not on file in the herbarium at the University of Kansas.

Aloina brevirostris (Hook. & Grev.) Kindb. Distributed in Montana and the Rocky Mountains, this moss has been reported by Cridland (1960) on silty calcareous soil in Meade County in the High Plains. The specimen, sterile and tentatively assigned to this taxon, is not on file in the herbarium at the University of Kansas.

**Aloina rigida* (Hedw. ex Schultz) Kindb. This moss has been reported from California, the Rocky Mountains, Arizona, Iowa, and Illinois. In Kansas this rare species grows on soil in Cheyenne, Stanton, and Clark counties in the High Plains, and in Clark and Barber counties in the Red Hills. The Kansas material is sterile and is referred to this taxon because the leaves are curled-in when dry and spreading when moist.

**Amblystegiella subtilis* (Hedw.) Loeske. This species, distributed in the eastern United States, is known in Kansas from one locality in Cheyenne County in the High Plains. The habitat was bark and rocks.

Amblystegium americanum Grout. This moss has been reported by McGregor (1950) on moist soil near a spring in Scott County in the High Plains. Known from Wisconsin, Iowa, and North and South Dakota, this taxon is considered by Conard (1959) to be a variety or form of *A. compactum,* which is distributed across the United States.

Amblystegium juratzkanum Schimp. Widely distributed throughout the United States, this is a rare moss, growing on bark, soil, and rocks in the Smoky Hills, the Red Hills, the Blue Hills, and the High Plains.

Amblystegium serpens (Hedw.) Bry. Eur. This moss, widespread in the United States except for the West Coast States, is a rare species growing on bark, soil, and rocks in the Smoky Hills, the Blue Hills, the Red Hills, the Great Bend Lowland, and the High Plains.

Amblystegium varium (Hedw.) Lindb. This widely distributed species of the United States, is rare in Kansas and is found on rocks, bark, and soil in the Smoky Hills.

Amblystegium varium (Hedw.) Lindb. var. *ovatum* Grout. Known from Pennsylvania, Missouri, and Iowa, this variety has been reported by McGregor (1950) on moist soil in Ottawa County in the Smoky Hills.

Aphanorhegma serratum (Hook. & Wils.) Sull. This moss, known from the eastern one-half of the United States, has been reported by McGregor (1950) from Decatur County in the High Plains.

**Archidium ohioense* Schimp. This moss has been reported from New York, North Carolina, Florida, Texas, and Minnesota. In Kansas this rare moss has been found on Pleistocene alluvium in Harper County in the Red Hills, on sand dunes in Harvey County in the Great Bend Lowland, and on Pleistocene terraces in Kingman County in the High Plains.

Aschisma kansanum Andrews. This moss is presently known only from Kansas. It was described by Andrews (1915) from material collected by E. Hall on the prairies of western Kansas. Type material is in the herbarium of the New York Botanical Garden and the Sullivant and James herbarium. Cridland (1959, 1960) reported this moss from Barber, Reno, and Pratt counties. A persistent protonema develops beneath rounded, relatively translucent, quartz pebbles with diameters of one to five cm. The pebbles, with protonema growing beneath them, are a milky-white color; dark pebbles are apparently too opaque to support growth of the protonema. Gametophores are produced around the edge of the pebble near the surface of the soil and occasionally even beneath the pebble itself. This moss was found fruiting profusely on April 28, 1962, in section 28, R. 32 S., T. 14 W., in Barber County in the Red Hills. Pebbles with *Aschisma kansanum* have also been found in Kiowa County in the Red Hills and in Clark County in the High Plains.

Cridland (1959) reported *Acaulon* sp. from Reno County and *Weissia* sp. from Pratt County in association with quartz pebbles. To these may be added *Acaulon schimperianum* from Reno County; *Astomum* sp. (sterile) from Cheyenne, Kingman, Phillips, Scott, and Wallace counties; *Barbula unguiculata* from Cheyene County; *Bryum argenteum* from Kingman and Scott counties; *B. caespiticium* from Kingman County; *Grimmia wrightii* from Scott County; *Phascum cuspidatum* var. *americanum* from Kingman County; and *Pterigoneurum subsessile* from Wallace County. As Cridland points out, no other taxa utilizes the habitat under the quartz pebble as successfully as *Aschisma kansanum*. Occasionally *Oscillatoria* sp. and *Nostoc* sp. grow with the protonema of the mosses.

**Astomum ludovicianum* Sull. This moss was formerly known only from West Virginia to Florida and Texas. The Kansas plants extend the range of this taxon much farther inland. The species is common in the Smoky Hills and especially abundant on soil at Rock City near Minneapolis in Ottawa County. It has been found also in Sumner County in the Wellington Lowland and in Kingman County in the High Plains.

Astomum muhlenbergianum (Sw.) Grout. This moss is distributed throughout the United States except for the West Coast States. It is an important species on soil in the Smoky Hills, the Red Hills, the Blue Hills, the Wellington Lowland, and the Great Bend Lowland. It is rare in the High Plains and presently unknown in the Finney Lowland.

**Astomum phascoides* (Hook.) Grout. This moss was formerly known only from North Carolina, Ohio, Minnesota, Texas, and Arizona. It is rare in Kansas, known on soil only in Smith County in the Blue Hills and Sumner County in the Wellington Lowland.

Atrichum angustatum (Brid.) Bry. Eur. This moss, widely distributed in the eastern United States, is common on soil and rocks in the Smoky Hills and is rare in the Great Bend Lowland.

Atrichum undulatum (Hedw.) Beauv. Widely distributed in the United States, this moss has been reported by McGregor (1950) on soil in Washington County in the Smoky Hills.

Atrichum undulatum (Hedw.) Beauv. var. *minus* (Lam. & De Cand.) Web. & Mohr. Known from Pennsylvania, Iowa, Kansas, Texas, and Washington, this variety has been reported by McGregor (1950) on soil in Washington County in the Smoky Hills.

Barbula cruegeri Sond. Known from North Carolina to Kansas and southward, this moss has been reported by McGregor (1950) on soil in Republic County in the Blue Hills. No gemmae were found but the stems and midribs of leaves were red.

Barbula fallax Hedw. This moss, reported from the United States, except from the West Coast States, is a rare species, growing on rocks and soil in the High Plains, the Red Hills, the Blue Hills, and the Smoky Hills. McGregor (1950) has reported it on Pleistocene terraces in the Wellington Lowland.

Barbula unguiculata Hedw. Known throughout the United States but rare in the West Coast States, this is an important species on soil and rocks in the High Plains, the Red Hills, the Blue Hills, and the Wellington Lowland. It is common in the Smoky Hills but rare in the Great Bend Lowland. McGregor (1950) has reported it from the Finney Lowland.

Bruchia sullivanti Aust. This moss of the eastern United States has been found in the study area at one locality in sand dunes of Harvey County in the Great Bend Lowland.

Bryum argenteum Hedw. This moss, widely distributed throughout the United States, is an important moss on soil and rocks in the Smoky Hills, the Wellington Lowland, the Great Bend Lowland, and the Finney Lowland. It is fairly common in the High Plains but is rare in the Red Hills and the Blue Hills except on sandy substrates.

Bryum bicolor Dicks. Distributed throughout the United States, this is a rare moss in Kansas, growing on soil in Ottawa County in the Smoky Hills and on sand dunes in Harvey County in the Great Bend Lowland. It has been reported by McGregor (1950) from the Blue Hills, the Red Hills, and the High Plains.

Bryum caespiticium Hedw. This moss is widely distributed in the United States and is an important species on soil in the Smoky Hills, the Blue Hills, the High Plains, the Great Bend Lowland, and the Finney Lowland. It is rare in the Wellington Lowland and the Red Hills except on sandy substrates.

Bryum cuspidatum (Bry. Eur.) Schimp. This species, known from the United States except for the West Coast States, is rarely found on soil in the Smoky Hills, the Blue Hills, the Red Hills, and the High Plains.

Bryum gemmiparum DeNot. This species is distributed throughout the United States and has been reported by McGregor (1950) on moist soil and rocks at a spring in Scott County in the High Plains.

Bryum pendulum (Hornsch.) Schimp. This moss is found throughout the United States except for the West Coast States. It is a rare moss on soil and rocks in the Smoky Hills.

Bryum pseudotriquetrum (Hedw.) Schw. This species is rare in Kansas, growing on rocks in the Smoky Hills and on sand dunes in Reno County in the Great Bend Lowland. It is distributed throughout the United States.

Campylium chrysophyllum (Brid.) Bryhn. This species, known from the United States except from the West Coast States, is common on soil and rocks in the Smoky Hills and important but less common in the Red Hills. It is rare in the High Plains, the Blue Hills, and the Great Bend Lowland.

Campylium chrysophyllum (Brid.) Bryhn var. *brevifolium* (R. & C.) Grout. This moss, known from the eastern United States, is rare on soil and rocks in Ottawa and Ellsworth counties in the Smoky Hills.

Campylium hispidulum (Brid.) Mitt. This moss is fairly common on soil, bark, and rocks in the Smoky Hills and on soil at local areas of Ogallala and Smoky Hill Chalk outcrops in the High Plains. It is rare in the Blue Hills. The species is unknown from the West Coast.

Ceratodon purpureus (Hedw.) Brid. This moss, widely distributed in the United States, is fairly common on soil in the Smoky Hills but is rare in the Great Bend Lowland, the Red Hills, and the Blue Hills. The specimens reported by McGregor (1950) for Clark and Rawlins counties in the High Plains are *Didymodon rigidulus.*

Chamberlainia acuminata (Hedw.) Grout. Known from the eastern United States and Arizona, this rare moss grows on soil, rocks, and bark in the Smoky Hills, the Blue Hills, the Great Bend Lowland, and the High Plains.

Chamberlainia oxyclada (Brid.) Robins. *Brachythecium oxycladon* (Brid.) J. & S. Restricted to the eastern United States, this moss has been reported by McGregor (1950) on soil in the Smoky Hills, the Blue Hills, and the Wellington Lowland. Because the Kansas material is sterile and the vegetative characters of *C. oxyclada* and *C. salebrosa* are not completely distinct, the assignment of specimens to these two species is difficult. *Brachythecium oxycladon* var. *dentatum* (Lesq. & James) Grout has been reported by McGregor (1950) for Washington County. Robinson (1962) does not mention this variety. It is possible the variety should be suppressed.

Chamberlainia salebrosa (Web. & Mohr) Robins. *Brachythecium salebrosum* (Web. & Mohr) Bry. Eur. This widely distributed species is common on rocks and soil in the Smoky Hills but rare in the Blue Hills, the Wellington Lowland, and the High Plains. *Brachythecium flexicaule* R. & C., reported by McGregor (1950) for Cloud County, is referred to this taxon. According to Robinson (1962), Grout's concept of *B. flexicaule* was apparently based on material that was *C. salebrosa.* The Cloud County plants identified as *B. flexicaule* cannot be referred to *C. calcarea* (Kindb.) Robins., *B. calcareum* Kindb. and *B. flexicaule* R. & C. (correctly conceived) as synonyms, because the dry leaves are not secund.

**Chamberlainia velutina* (Hedw.) Robins. This moss, distributed throughout the United States, is presently known in Kansas from one locality in Rawlins County in the High Plains. It was found in a recess beneath an overhanging ledge of mortar beds in a ravine. Dried tumbleweeds had piled up in front of the recess.

Desmatodon obtusifolius (Schw.) Jur. This moss, known throughout the United States, is common on rocks in the Smoky Hills but rare in the High Plains and the Red Hills. It is also known from an isolated outcrop of the Dakota Formation in Barton County in the Great Bend Lowland (McGregor, 1950).

Desmatodon plinthobius Sull. & Lesq. This moss is fairly common on rocks in the High Plains and is present on sandstone concretions at Rock City in the Smoky Hills. It is also known from an isolated outcrop of the Dakota Formation in Barton County in the Great Bend Lowland. It is unknown from the West Coast but has been reported for most other parts of the United States. The specimen reported by McGregor (1950) for Sumner County is *Phascum cuspidatum* var. *americanum*.

**Dichodontium pellucidum* (Hedw.) Schimp. This moss, distributed in the United States except from the Southeast, is known in Kansas from one locality on sandy soil in McPherson County in the Smoky Hills.

Dicranella varia (Hedw.) Schimp. Widespread throughout the United States, this species has been reported by McGregor (1950) for Washington County in the Smoky Hills.

Didymodon rigidulus Hedw. This western species is known eastward to Texas, Kansas, South Dakota, Iowa, and Michigan. It grows on rocks and soil and is the most common moss in the High Plains. It is less common but still important in the floras of the Blue Hills and the Red Hills and is occasionally found in the Smoky Hills. Some plants produce smooth, spherical, 2 to 6-celled gemmae in the axils of the leaves. The cell contents of the gemmae are green and the cell walls are a reddish-brown color.

Didymodon tophaceus (Brid.) Jur. This moss, widely distributed in the United States, is rare on rocks and soil in Barber County in the Red Hills and in Cheyenne and Clark counties in the High Plains.

Ditrichum pallidum (Hedw.) Hampe. This moss is distributed in the eastern United States and is fairly common on soil and rocks in the Smoky Hills. It is rare in the Red Hills, the Blue Hills, and the Great Bend Lowland.

**Drepanocladus aduncus* (Hedw.) Warnst. Known across the United States, this moss is a rare species found growing in a moist ravine in Jewell County in the Blue Hills.

Drepanocladus aduncus (Hedw.) Warnst. var. *polycarpus* (Bland.) Warnst. This widely distributed species of the United States has been reported by McGregor (1950) on very moist sandy soil in Mitchell County in the Smoky Hills and in Trego County (specimen in the herbarium at Kansas State University, Manhattan, Kansas).

Entodon compressus (Hedw.) C. M. This moss of the eastern United States has been reported by McGregor (1950) on bark and soil in Ottawa and Washington counties in the Smoky Hills.

Entodon seductrix (Hedw.) C. M. Known from the eastern United States and Arizona, this species is fairly common on rocks, bark, and soil in the Smoky Hills.

Ephemerum cohaerens (Hedw.) Hampe. This species, distributed in the eastern one-half of the United States, is a rare moss, growing on sandy soil in Reno and Harvey counties in the Great Bend Lowland, in Sumner County in the Wellington Lowland, in Harper County in the Red Hills, and in Republic County in the Blue Hills.

Ephemerum crassinervium (Schw.) C. M. Known from the eastern one-half of the United States, this species is rare on dune sand in Reno County in the Great Bend Lowland.

**Ephemerum spinulosum* Schimp. This moss is distributed in the eastern one-half of the United States and is a rare moss, growing on soil in Ottawa and Ellsworth counties in the Smoky Hills and on sand dunes in Reno and Harvey counties in the Great Bend Lowland.

Eurhynchium hians (Hedw.) J. & S. This rare moss is known for the eastern United States and Arizona and grows on soil in the Smoky Hills.

Eurhynchium serrulatum (Hedw.) Kindb. This moss, known from the eastern United States, is a rare species, growing on soil, bark, and rocks in the Smoky Hills, the Blue Hills, and the High Plains.

Fabronia ciliaris (Brid.) Brid. Reported for the eastern United States, New Mexico, and Arizona, this species is known from one locality in the Great Plains of Kansas. It was found growing on oak bark in Barber County in the Red Hills.

**Fabronia imperfecta* Sharp. This moss has been previously reported only from Tennessee by Sharp (1933). The peristome is imperfect or lacking. The spore size of the Kansas plants ranges up to 20 microns, 5 microns larger than those of the Tennessee plants. This variation is not surprising in a genus which Conard (1956) has described as: "A whole series of intergrading forms as to shape of leaf, size of marginal teeth, size and shape of cells, size of spores." Conard adds: "Some combinations are named, others fortunately, are not." This taxon has been found growing on elm bark in Ellsworth County in the Smoky Hills and in Barber County in the Red Hills.

**Fissidens bryoides* Hedw. This moss, distributed widely in the United States, has been found in Kansas on soil in Washington County in the Smoky Hills and on rock in Rawlins County in the High Plains.

Fissidens minutulus Sull. Known from the eastern United States and Arizona, this is a rare moss which grows on soil in Jewell, Rooks, and Trego counties in the Blue Hills, in Barber County in the Red Hills, and in Rawlins County in the High Plains.

Fissidens obtusifolius Wils. This moss, known from the eastern United States, Colorado, and Arizona, is a rare species which grows on rock in the Smoky Hills.

Fissidens obtusifolius Wils. var. *kansanus* R. & C. This variety was described from material collected by Henry in Saline County (Grout, 1936). The type specimen is not in the herbarium at the University of Kansas. This variety has since been reported from Arizona.

**Fissidens osmundioides* Hedw. Reported from the eastern United States, Wyoming, and Idaho, this species has been collected once in Kansas on rock in Ellsworth County in the Smoky Hills.

Fissidens sublimbatus Grout. This moss has been reported from Arizona, New Mexico, Texas, and Missouri. It is a rare moss, growing on rocks and soil in Washington and Ellsworth counties in the Smoky Hills, in Barber County in the Red Hills, and in Decatur and Scott counties in the High Plains.

**Funaria americana* Lindb. This moss, known from the eastern United States and California, is a rare species on rocks and soil in Jewell and Ellsworth counties in the Smoky Hills.

Funaria flavicans Mx. Known from the eastern United States and Wyoming, this is a rare moss which grows on soil in McPherson County in the Smoky Hills and on sand dunes in Reno and Harvey counties in the Great Bend Lowland.

Funaria hygrometrica Hedw. This moss, widely distributed throughout the United States, is rare on soil in the Smoky Hills, the Great Bend Lowland, and the Blue Hills. McGregor (1950) has reported it from the Finney Lowland.

Grimmia apocarpa Hedw. Widely distributed throughout the United States, this moss is fairly common on rocks in the Smoky Hills and rare in the Blue Hills. It is excluded from the High Plains as reported by McGregor (1950).

Grimmia laevigata (Brid.) Brid. This moss, widely distributed in the United States, is common on dry wind-swept rocks in the Smoky Hills. It is also known on the Cheyenne Sandstone in Kiowa County in the Red Hills.

Grimmia plagiopodia Hedw. Known from the western United States except the West Coast States eastward to Iowa, this species has been reported from Kansas by McGregor (1950) on dry rocks in Rice County in the Smoky Hills.

Grimmia pulvinata (Hedw.) Sm. This moss is known from the western United States and eastward to Iowa and has been found on rocks in Ellsworth County in the Smoky Hills.

Grimmia rauei Aust. As treated in Grout (1940), *G. rauei* has leaves with entire apical margins and *G. wrightii* has leaves with denticulate apical margins. Because of the variability of denticulation, Sayre (1952) referred plants with ovate leaves to *G. rauei* and plants with obovate or oblong leaves to *G. wrightii*. The Kansas plants are classified according to Sayre's concept of the two species. Since the publication in 1952 of Sayre's key to the genus *Grimmia, G. rauei* has been reported in "The Bryologist" from South Dakota, Texas, and Arizona. Conard (1956) reports it from Minnesota to Texas and Arizona. *G. rauei* is common on the mortar beds in the High Plains and rare on the Cheyenne Sandstone in Comanche and Kiowa counties in the Red Hills.

Grimmia teretinervis Limpr. This moss has been reported by Kucyniak (1952) for North America from Quebec, Wisconsin, Minnesota, Missouri, and Kansas. McGregor and Hartman (1956) reported this species on sandstone rocks in Russell County in the Smoky Hills and on mortar beds in Norton and Scott counties in the High Plains. This moss has again been found on the mortar beds in Scott County. It is well known in the Alps of Europe (Kucyniak, 1952). The dry wind-swept cliffs in Kansas appear to resemble the alpine habitat with respect to the growth of this moss. McGregor (1956) states: "It *(Grimmia teretinervis)* appears to be an alpine, non-arctic species which can occur at low altitudes, even sea level, where conditions of wind and other climatic factors somewhat duplicate alpine conditions."

**Grimmia wrightii* Aust. Since the publication in 1952 of Sayre's key to the genus *Grimmia, G. wrightii* has been reported in "The Bryologist" from South Dakota and Texas. In Kansas it is an important species on dry windswept rocks in the High Plains. This taxon is also present on the sandstone concretions at Rock City in Ottawa County in the Smoky Hills.

Hedwigia ciliata Hedw. This widely distributed moss is fairly common on rocks in the Smoky Hills.

Homomallium adnatum (Hedw.) Broth. This moss, known from the eastern United States and Arizona, is fairly common on rocks and bark in the Smoky Hills.

**Homomallium mexicanum* Cardot. This species has previously been reported from Arizona, New Mexico, and Texas. The Kansas plants extend the range considerably northward. Presently this taxon is known in Kansas from only one locality on soil and gypsum rock in Barber County in the Red Hills.

Hygroamblystegium irriguum (Wils.) Loeske. Distributed throughout the United States, this is a rare moss which grows on rocks, soil, and bark in the Smoky Hills and the High Plains.

**Hypnum cupressiforme* Hedw. This moss, distributed in the United States except for the West Coast States, is known from one Kansas locality in Scott County in the High Plains where it was growing on soil and rocks.

Leptobryum pyriforme (Hedw.) Schimp. This widespread moss was found on soil in McPherson County in the Smoky Hills.

Leptodictyum riparium (Hedw.) Warnst. This widespread species was found on bark at a spring in Ellsworth County in the Smoky Hills. McGregor (1950) has reported it on moist soil in Meade County in the High Plains.

Leptodictyum trichopodium (Schultz) Warnst. This eastern species is rare on soil and bark in the Smoky Hills, the Blue Hills, and the High Plains as reported by McGregor (1950).

Leskea gracilescens Hedw. This moss, distributed in the eastern United States and westward to the Rocky Mountains, grows on bark in the Smoky Hills, the Blue Hills, the Red Hills, the Wellington Lowland, and the Great Bend Lowland.

Leskea obscura Hedw. Widely distributed east of the Rocky Mountains, this moss has been reported by McGregor (1950) on bark in Mitchell and Lincoln counties in the Smoky Hills.

Lindbergia brachyptera (Mitt.) Kindb. This moss is distributed in the eastern United States and Arizona (Crum, 1956). Crum has examined and verified the specimen collected by Henry from Saline County but did not specify the particular herbarium where the specimen is located.

Mnium cuspidatum Hedw. This widely distributed species is fairly common on rocks and soil in the Smoky Hills.

**Oreoweisia serrulata* (Funck) DeNot. This widespread moss has been found on rocks in Decatur, Rawlins, Scott, and Clark counties in the High Plains. The upper part of the leaves is partially monostratose and partially bistratose.

Orthotrichum diaphanum Brid. This moss has been reported from Arizona, New Mexico, Colorado, Texas, Oklahoma, and Kansas. Previously this taxon was known in Kansas only from Reno County as reported by McGregor (1950). This bark-inhabiting species is now known in Barton, Stafford, and Reno counties in the Great Bend Lowland, in Sumner County in the Wellington Lowland, in Barber County in the Red Hills, in Rooks County in the Blue Hills, and in Decatur County in the High Plains.

Orthotrichum pumilum Dicks. Distributed in the United States except from the West Coast States, this species grows on bark in the Smoky Hills, the Wellington Lowland, the Great Bend Lowland, the Red Hills, and the Blue Hills.

Orthotrichum pusillum Mitt. Distributed in the eastern United States, this moss has been reported from Reno County by McGregor (1950). The specimen, collected by Voth, is located in the herbarium at the Chicago Natural History Museum.

Orthotrichum strangulatum Schw. This moss, known from the eastern United States and Utah, has been found on rocks in the Smoky Hills in Ellsworth County and in Mitchell County as reported by McGregor (1950).

Phascum cuspidatum Hedw. var. *americanum* R. & C. Known in the eastern United States and Arizona, this is an important species on soil in the Smoky Hills and the Wellington Lowland. It is rare in the Great Bend Lowland, the Red Hills, and the High Plains.

Philonotis longiseta (Rich.) E. G. B. This moss, known from the eastern one-half of the United States, has been collected on a sandy creek bank in Washington County in the Smoky Hills.

Physcomitrium hookeri Hampe. This species is known from the central United States, New York, and Utah, and has been collected on soil in McPherson County in the Smoky Hills. McGregor (1950) has reported it on soil at the edge of a swamp in Meade County in the High Plains.

Physcomitrium pyriforme Brid. This widely distributed moss is common on soil in the Smoky Hills and rare on sand dunes in the Great Bend Lowland.

Physcomitrium pyriforme Brid. var. *serratum* (R. & C.) Crum and Anderson. (*P. kellermani* Britt. and *P. drummondii* Britt. as synonyms). This variety is limited to an area roughly corresponding to the Great Plains from Louisiana and Texas to North Dakota (Crum and Anderson, 1955). It is a rare moss on soil in Washington and Clay counties in the Smoky Hills, in Sumner County in the Wellington Lowland, in Harper County in the Red Hills, in Jewell and Ellis counties in the Blue Hills, and on sand dunes in Reno and Stafford counties in the Great Bend Lowland and in Phillips County in the High Plains. The spores of the Kansas plants showed no tendency to adhere in diads, triads, and tetrads as reported for most specimens by Crum and Anderson.

Plagiothecium geophilum (Aust.) Grout. This moss, distributed in the eastern United States, New Mexico, and Arizona, is a rare species which grows on rocks in Ellsworth County in the Smoky Hills.

Platygyrium repens (Brid.) Byr. Eur. This moss, distributed east of the Rocky Mountains, has been reported by McGregor (1950) on bark in Mitchell County in the Smoky Hills.

Pleuridium subulatum (Hedw.) Lindb. This rare species is known from the eastern United States and California and grows on soil in Washington and Ellsworth counties in the Smoky Hills, on sand dunes in Harvey County in the Great Bend Lowland, and on Pleistocene terraces in Kingman County in the High Plains.

Pohlia nutans (Hedw.) Lindb. This widely distributed moss is fairly common on soil and rocks in the Smoky Hills and rare on sand dunes in the Great Bend Lowland.

Pohlia wahlenbergii (W. & M.) Andr. Widely distributed in the United States, this species has been reported by McGregor (1950) on rocks and soil in the Smoky Hills.

Polytrichum juniperinum Hedw. This widely distributed species is rare in the Great Plains of Kansas. It is presently known on rocks only in Ellsworth County in the Smoky Hills.

Polytrichum piliferum Hedw. This widely distributed moss has been reported by McGregor and Hartman (1956) from a sandy hillside in Ellsworth County in the Smoky Hills.

**Pottia arizonica* Wareham. This species has been reported from Arizona and southern California. The Kansas plants were found growing on sandy Pleistocene alluvium in Clark County in the Red Hills.

**Pterigoneurum ovatum* (Hedw.) Dixon. This moss has previously been reported from Washington, Idaho, Utah, Wyoming, North Dakota, Arizona, New Mexico, and Texas. The Kansas plants are known from one locality on soil where the Cockrum Sandstone outcrops in Stanton County in the High Plains.

Pterigoneurum subsessile (Brid.) Jur. This moss has been reported from Arizona, Texas, North Dakota, Kansas, and Illinois. This taxon is important on sand dunes in the Finney Lowland and the High Plains. It is fairly common in the remainder of the High Plains and rare in the Red Hills, the Blue Hills, and the Wellington Lowland.

Pterigoneurum subsessile (Brid.) Jur. var. *henricii* (Rau) Wareham. The type specimen, collected by Henry in Saline County, is in the herbarium at the New York Botanical Garden (Grout, 1939). Grout considered it possible that the variety should be suppressed. Plants resembling this variety have been reported from Texas.

Ptychomitrium incurvum (Muhl.) Sull. Known from the eastern one-half of the United States, this species is fairly common on rocks in the Smoky Hills.

Pylaisia selwynii Kindb. This moss, known from the eastern United States and Arizona, is a rare species which grows on bark in the Great Bend Lowland, the Blue Hills, the Red Hills, and the Smoky Hills as reported by McGregor (1950).

Pyramidula tetragona (Brid.) Brid. This moss has been reported from Colorado, Texas, Oklahoma, Kansas, Nebraska, Iowa, Minnesota, and Indiana. It is rare on soil in the Smoky Hills and the Wellington Lowland.

Thuidium virginianum (Brid.) Lindb. This moss, known from the eastern United States and Arizona, is a rare moss on soil in the Smoky Hills.

Timmia megapolitana Hedw. This widely distributed species has been reported by McGregor (1950) on sandy soil in Mitchell County in the Smoky Hills.

Tortella humilis (Hedw.) Jenn. Known from the eastern United States and Arizona, this species has been found on bark at base of a honey locust tree in Reno County in the Great Bend Lowland.

Tortula pagorum (Milde) DeNot. Distributed throughout the United States, this moss grows on bark in the Smoky Hills, the Red Hills, and the Wellington Lowland.

**Tortula ruralis* (Hedw.) Smith. This widely distributed species is fairly common on rocks and soil in the High Plains. It is rare in the Red Hills and the Smoky Hills.

Weissia controversa Hedw. Widely distributed, this common moss grows on soil and rocks in the Smoky Hills. It is a rare moss in the Blue Hills, the Red Hills, the High Plains, the Wellington Lowland, and the Great Bend Lowland.

**Weissia glauca* Bartr. This moss has been previously reported from Arizona and Texas. It is rare in the Great Plains on rocks and soil on Ogallala outcrops in Cheyenne, Rawlins, Wallace, and Scott counties and on Cockrum Sandstone outcrops in Stanton County.

**Weissia microstoma* (Hedw.) C. M. This moss has been reported from Massachusetts, New Jersey, Ohio, and Texas. It is most abundant on limestone outcrops in the Blue Hills. It has also been found on Smoky Hill Chalk outcrops in Phillips County in the High Plains, on Ogallala outcrops in Clark County in the High Plains, and on Flowerport Shale outcrops in Barber County in the Red Hills.

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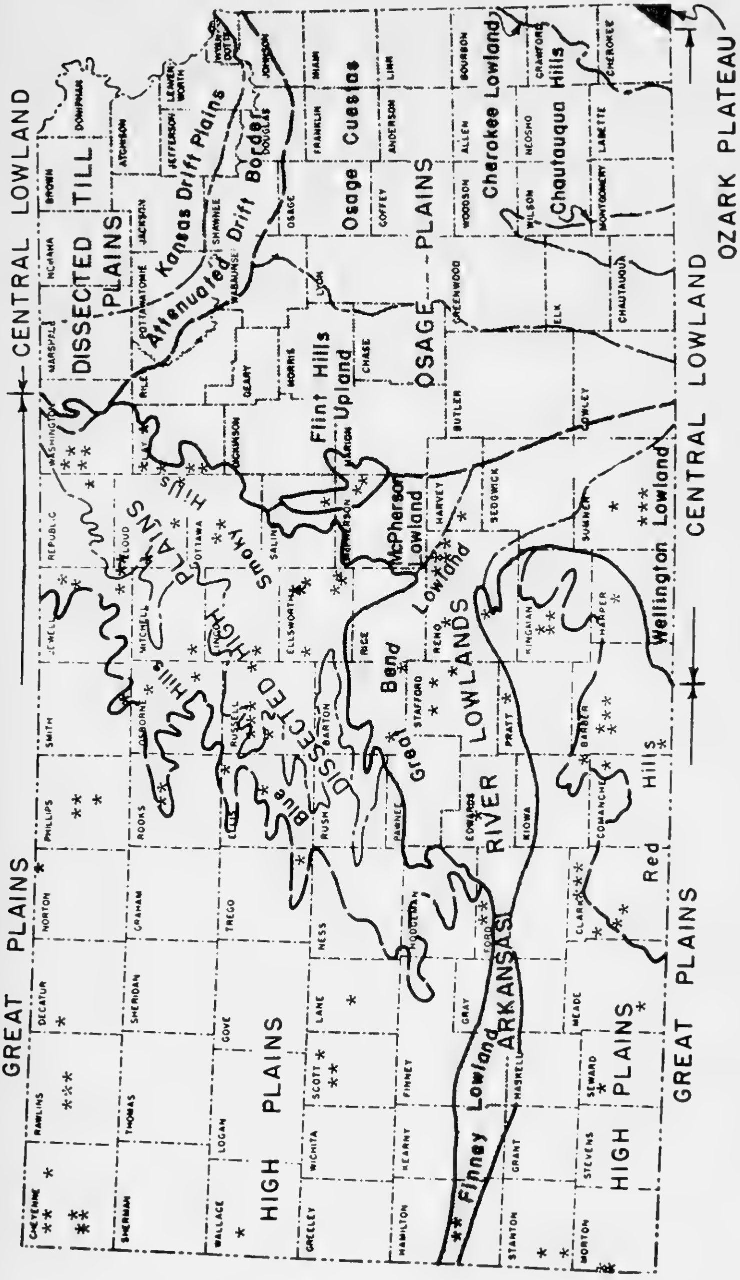

FIG. 1. Physiographic Map of Kansas. Used by permission of Dr. Walter H. Schoewe. (From Schoewe, 1949.) Each asterisk represents a locality where mosses have been collected by the author.

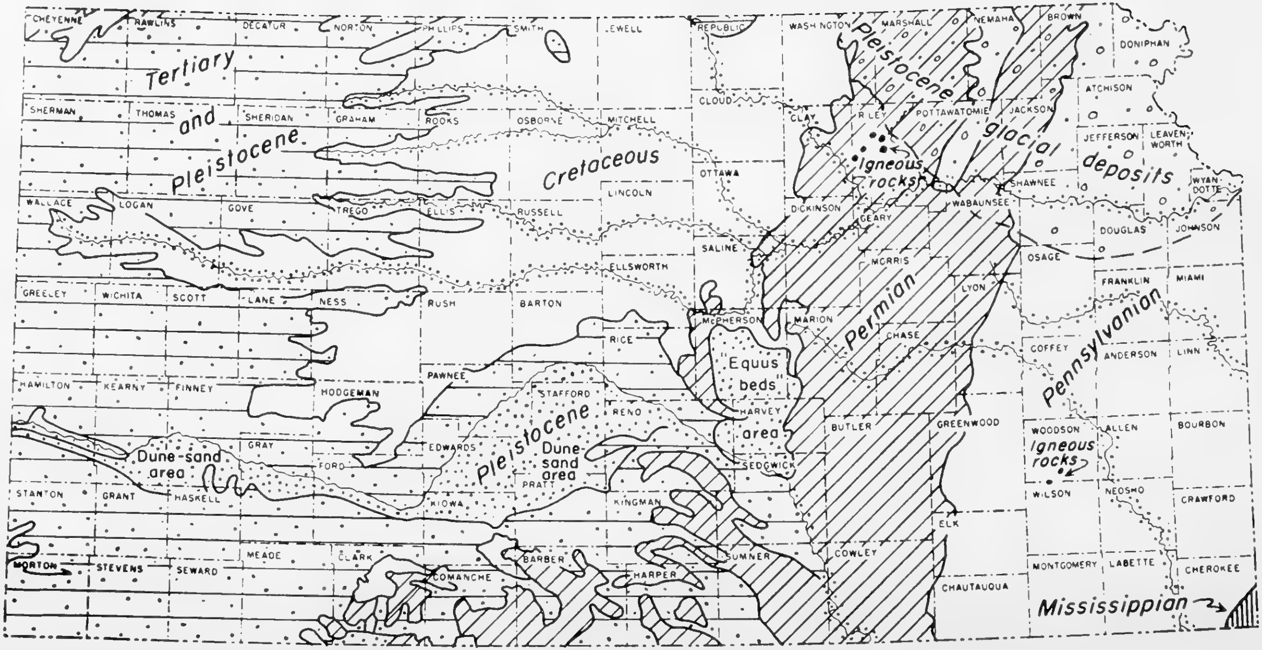

FIG. 2. Generalized Geologic Map of Kansas. Used by permission of the authors. (From Tolsted and Swineford, 1959.)

THE UNIVERSITY OF KANSAS
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SOME INTERSECTIONAL HYBRIDS AND RELATIONSHIPS IN HAPLOPAPPUS

By

R. C. Jackson

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Some Intersectional Hybrids and Relationships in Haplopappus[1]

By

R. C. JACKSON

INTRODUCTION

Over the past several years, morphological, cytological and hybridization data have been accumulated for several distantly related species of the genus *Haplopappus* as circumscribed by Hall (1928). These data support parts of Hall's treatment but point up some basic errors in others, particularly in his scheme of phylogenctic relationships based on certain "primitive" types in section *Blepharodon*. Section *Prionopsis*, certain disruptive elements of section *Blepharodon*, and one proposed new section are dealt with here. Most of the species discussed have been described in detail by Hall and only pertinent or general morphological data are presented.

The cytological and hybridization techniques used in this study have been described in detail elsewhere (Jackson, 1962, 1965). Voucher specimens of the intersectional hybrids and of the species with chromosome counts reported for the first time are in the University of Kansas Herbarium. Collection data for the chromosome counts are as follows: *Haplopappus brickellioides* Blake, Clark Co., Nevada, east of Mercury in the southern part of the Spotted Range, Oct. 1963, *Johnson 2117*; *Haplopappus phyllocephalus* subsp. *primitivus* Hall (=*Machaeranthera*), State of Mexico, about 15 miles southeast of Queretaro border along hyw. 57, Aug. 9, 1964, *Jackson 5157*; *Haplopappus aureus* Gray, Harris Co., Texas, jctn. of hyw. 290 and West 39th St., Houston, Oct. 7, 1964, *R. C. Jackson 5242*.

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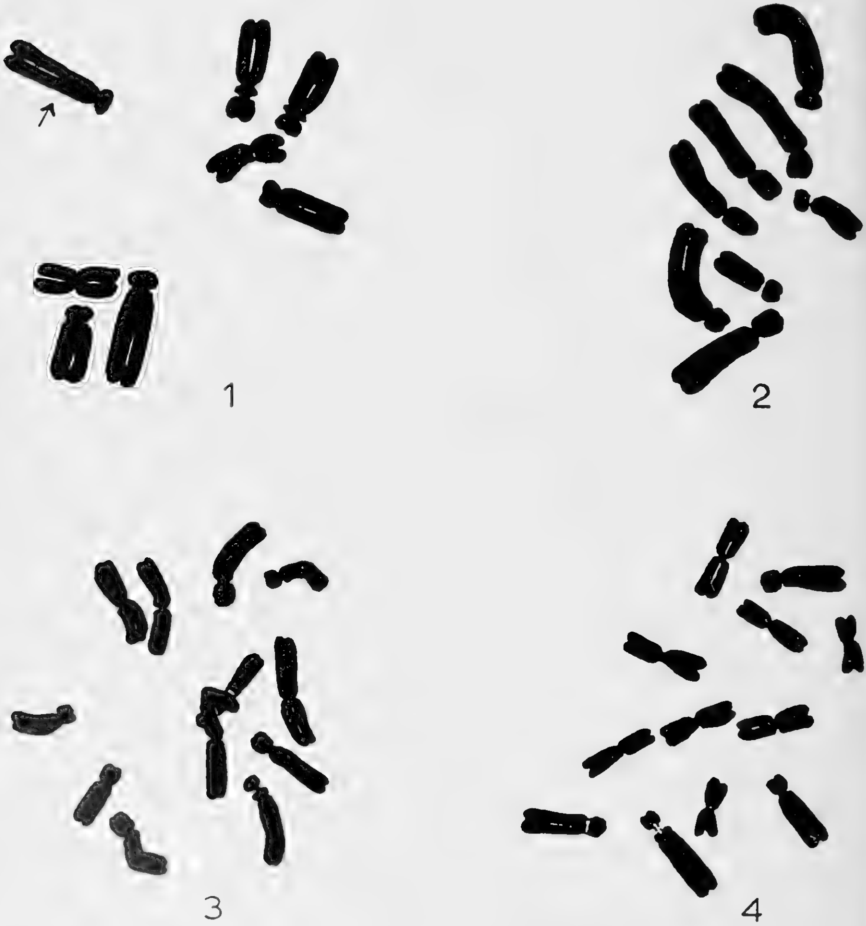
[1] This study has been supported by NSF Grant GB-3071.

GENERAL RELATIONSHIPS OF THE SECTIONS

Blepharodon, as delimited by Hall, is perhaps taxonomically the most difficult of the North American sections of *Haplopappus*. Field and morphological studies and cytogenetic analyses of F_1 hybrids have served to clarify and define certain diagnostic characters which delimit the section. The basic chromosome number is $X=4$ (Jackson, 1962). The basic karyotype appears to be stable in both the diploids and tetraploids studied so far, and it is quite distinct from those of several taxa previously included in the section (Fig. 1-4). The section has one chromosomally polymorphic species, *H. gracilis*



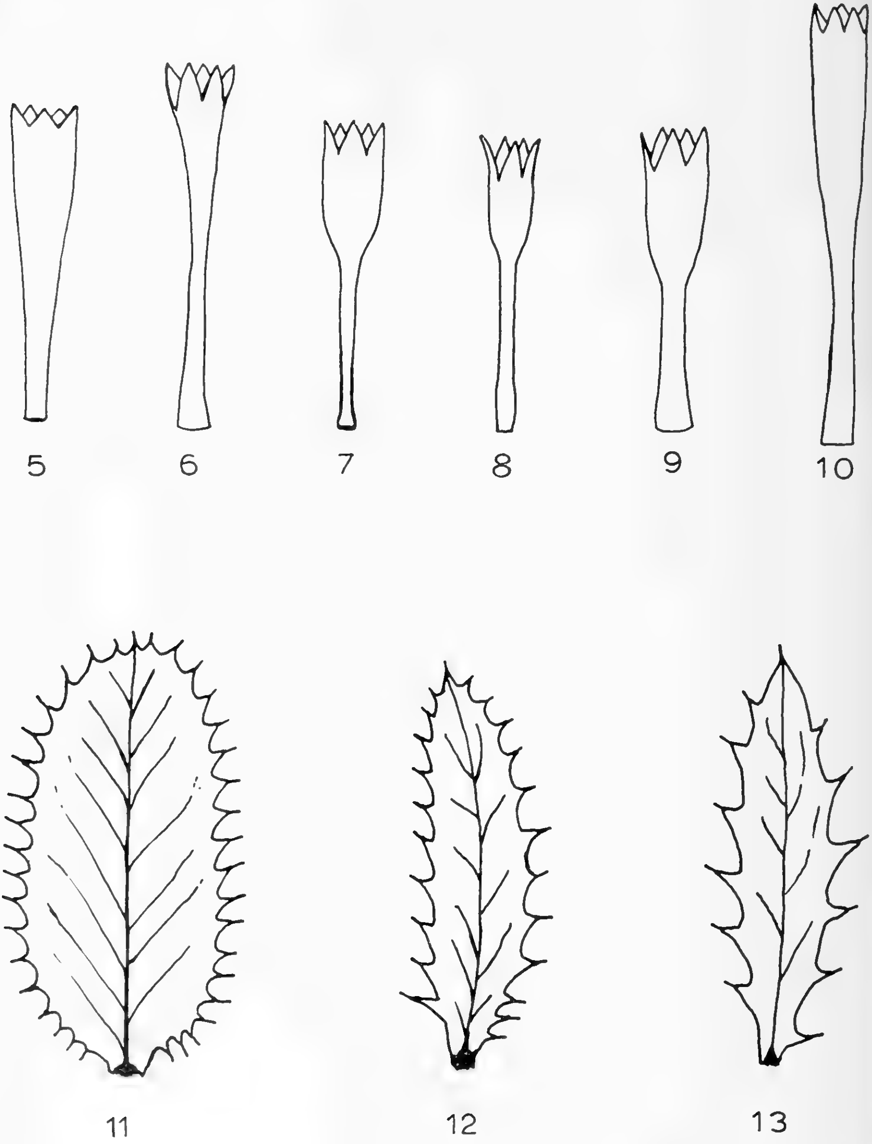
FIGS. 1-4. Root tip chromosomes. FIG. 1. *Haplopappus spinulosus* (Pursh) DC. (sect. *Blepharodon*). The arrow at upper left designates a chromosome ca. 5μ in length. Figures 3 and 4 are at a somewhat larger scale. FIG. 2. *H. havardii* (sect. *Havardia*). Fig. 3. *H. annuus* (sect. *Isocoma*). FIG. 4. *H. ciliatus* (sect. *Prionopsis*).

(Nutt.) Gray, which has races with $n=2$ and $n=3$ (Jackson, 1965). Supernumerary chromosomes have been found in most of the diploid and aneuploid taxa (Jackson, 1960; Raven *et al.*, 1960; Jackson & Li, 1961; Jackson, unpubl.).

In contrast to Hall's (1928) treatment, Cronquist and Keck (1957) agreed with Shinners' (1950) transfer of *Haplopappus gymnocephalus* DC. and *H. nuttallii* Torr. & Gray from section *Blepharodon* to the genus *Machaeranthera.* My own study of the type of *Haplopappus phyllocephalus* subsp. *primitivus* Hall ($n=4$) and living material at the type locality leave no doubt that it too is a *Machaeranthera*, probably *M. gymnocephala.* As the name *primitivus* indicates, Hall considered this subspecies as the ancestral type of several annual taxa of section *Blepharodon.*

The other subspecies of *H. phyllocephallus* (*sensu* Hall) are being retained in *Haplopappus* and have been studied in some detail. *Haplopappus phyllocephalus DC.* subsp. *phyllocephalus* and *H. p.* subsp. *megacephalus* (Nash) Hall are merged under *H. phyllocephalus. H. p.* subsp. *annuus* is considered as a distinct species, *H. annuus* (Rydb.) Cory. Crosses between *H. annuus* and *H. phyllocephalus* have demonstrated a sterility barrier in the F_1 hybrid, and I have not found that *H. phyllocephalus* passes insensibly into *H. annuus* as stated by Hall. These two species and the shorter, endemic *H. aureus* Gray are annuals with a chromosome number of $n=6$ (Jackson, 1960). In addition to chromosome number, there are several morphological differences that set these three species apart from all other taxa that Hall included in section *Blepharodon.* All of these differences need not be dealt with here, but the one of disc corolla shape is most striking and suggestive of certain relationships (Fig. 5-10). In the three species listed above the disc corolla is a slender tube that is abruptly dilated above the middle (Fig. 8). All other species of section *Blepharodon* have a disc corolla that gradually tapers and is funnelform (Fig. 5). This character difference is most striking in living plants and is easily discernible in dried material. Shinners (1950, p. 39) apparently did not notice this character when he merged section *Blepharodon* (*sensu* Hall) with *Machaeranthera*, stating that the two differ in no important technical feature of florets, achenes, or pappus, but only in the trivial one of ray color.

The disc corolla shape in *H. phyllocephalus*, *H. annuus*, and *H. aureus* is indistinguishable from that found among various taxa of section *Isocoma* (Fig. 7). Moreover, this section has a basic chromosome number of $X=6$, and the somatic and meiotic chromosomes show staining reactions similar to those of these three species. As generally recognized, section *Isocoma* is characterized by discoid heads with turbinate to narrowly campanulate involucres compared with radiate heads and broadly campanulate involucres of the three species listed above. However, vestigial rays have appeared in at least one species of section *Isocoma* that I have in cultivation so this qualitative difference is no longer absolute for separating the two groups.



FIGS. 5-13. Disc florets (×9) and median leaves (×1) of *Haplopappus* species and hybrids. FIG. 5. *H. spinulosus* (Pursh) DC. (sect. *Blepharodon*). FIG. 6. *H. havardii* (sect. *Havardia*). FIG. 7. *H. venetus* (sect. *Isocoma*). FIG. 8. *H. annuus* (sect. *Isocoma*). FIG. 9. *H. ciliatus* × *H. annuus*. FIG. 10. *H. ciliatus* (sect. *Prionopsis*). FIG. 11. *H. ciliatus*. FIG. 12. *H. ciliatus* × *H. annuus*. FIG. 13. *H. annuus*.

In view of the data presented, *H. phyllocephalus*, *H. annuus*, and *H. aureus* are tentatively assigned to section *Isocoma*. The origin of these annuals is almost certainly centered in this primarily perennial section, and they may have derived from certain broad-leaved, campanulate involucral forms of the Central Mexican Highlands comprising *H. venetus* (H.B.K.) Blake subsp. *venetus* and perhaps some undescribed taxa.

Another disruptive element in section *Blepharodon* is *H. brickellioides* Blake. This is a rarely collected species of Death Valley and adjacent regions of California and Nevada with a chromosome number of $n=6$. In leaf, involucre, and flower shape, it is closely related to species of section *Hazardia* and probably should be included in this group. Contrary to Hall's description, the species does have ray flowers although they are small.

Haplopappus havardii was described by Waterfall (1943) as allied to the *H. phyllocephalus* complex. In annual habit, leaf shape, and overall size, it is similar to *H. phyllocephalus* and related species. However, in disc flower shape (Fig. 6), chromosome number ($n=4$; Jackson, 1960), and karyotype (Fig. 2) it is quite distinct from these taxa. Furthermore, its fusiform achenes are different from any of the species of section *Blepharodon* (as delimited here) and *Isocoma*. Although a genetic relationship has been demonstrated with *H. annuus*, it is sufficiently distant so that taken together with its morphological and chromosomal divergence from other species, *H. havardii* must be considered as representing a separate section, and such is proposed here.

Haplopappus section *Havardia* R. C. Jackson, sect. nov.

Planta erecta rigida foliosa glandulose annua. *H. annuo* affinis, a quo differt glandulis confertioribus; foliis numerosis minoribus obtusis breviter dentatis; capitulis minoribus ramulos conspicue foliosos terminantibus; acheniis fusiformis.

Type and only known species: *Haplopappus havardii* Waterfall

Haplopappus section *Prionopsis* has but one species, *H. ciliatus* (Nutt.) DC. Originally described as a distinct genus, the section was doubtfully placed in *Haplopappus* by Hall (1928) who remarked on its similarity to *Grindelia*. The chromosome number of *H. ciliatus* is $n=6$ (Jackson, 1959) as is that of several species of *Grindelia*, but attempts to cross the two genera have thus far been unsuccessful. The general similarity in leaves, pappus, and resinous-vicid involucres of the two taxa may be the result of paralleled evolution or it may be indicative of a real but distant genetic affinity.

During mitosis and meiosis, the chromosomes of *H. ciliatus* are similar in size and staining reaction to those of *H. phyllocephalus* and *H. annuus*. The karyotype of *H. ciliatus* is, however, quite different from these species (Fig. 1-4). Although a genetic relationship can be demonstrated with *H. annuus*, *H. ciliatus* is morphologically and cytologically distinct from any other species of *Haplopappus*. In doubtfully including the species in *Haplopappus*, Hall suggested that even if a closer relationship of *H. (Prionopsis) ciliatus* to *Grindelia* could be demonstrated, this would scarcely bring the two genera together. In my opinion, *H. ciliatus* should be retained in *Haplopappus* as a monotypic section because of the demonstrated genetic relationship with *H. annuus* and indirectly with other taxa by way of this species.

INTERSECTIONAL HYBRIDIZATION

Haplopappus (Prionopsis) ciliatus ($n=6$) × *H. (Isocoma) annuus* ($n=6$).

Hybrids of this combination were produced in 1961 and again in 1964. They were generally intermediate for leaf and flower characters of the parents (Fig. 8-13). However, their growth and maturation were somewhat slower than *H. annuus* and more closely resembled *H. ciliatus.* Several heads were fixed for cytological analyses and others were used for backcrossing to *H. ciliatus.*

Meiotic prophase stages beginning with early pachytene were studied in as much detail as possible. Details of synapsis at pachytene were difficult to analyze because most of the chromosome ends seemed to be involved in more complex arrangements than bivalents. However, deletion or duplication configurations were noted in several cells (Fig. 14), and what appeared to be a combination of a translocation and inversion configuration involving at least four chromosomes (Fig. 15) was observed in one cell. The latter configuration may result in a plant heterozygous for an inversion with a translocation distal to it.

In a few cells at an early diplotene, all 12 chromosomes appeared to be connected in a branched, complex chain (Fig. 16). At later diplotene (Fig. 17), ten chromosomes were involved in a branched chain in at least five cells. By diakinesis, terminalization had broken down the long chains to smaller ones (Fig. 18). Table 1 gives the kinds of configurations and their frequencies at late diplotene and diakinesis.

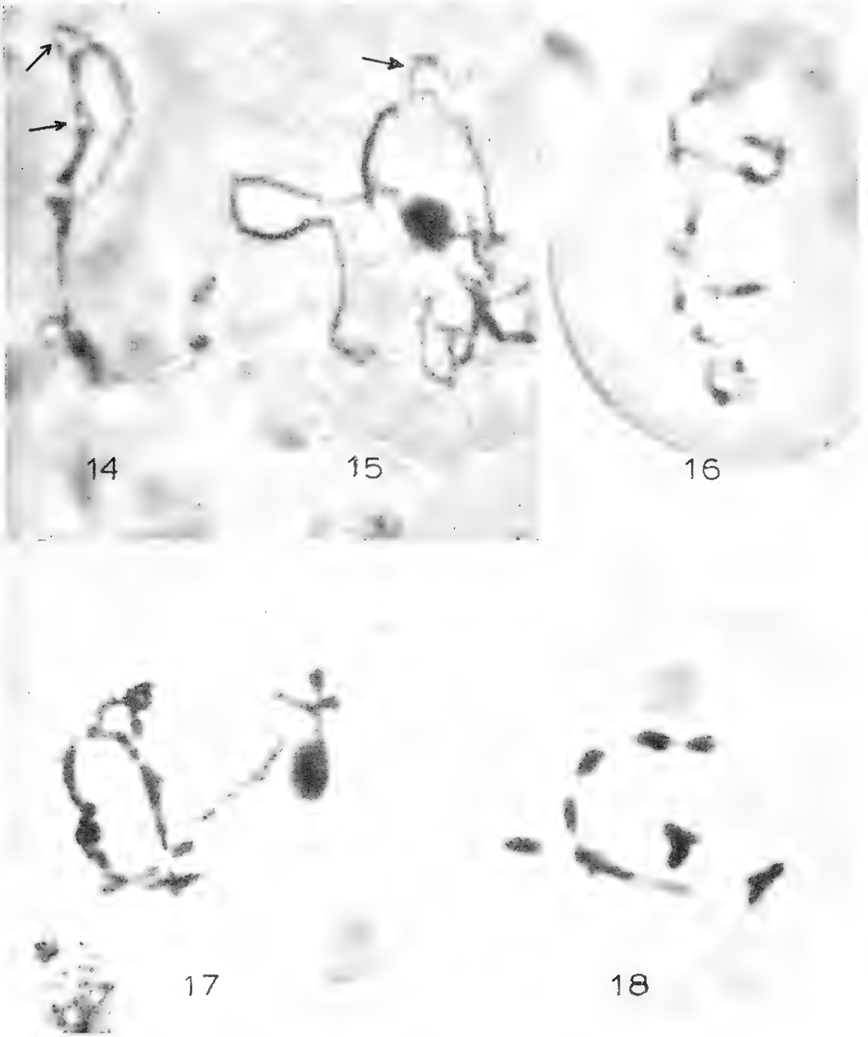
Metaphase I was usually characterized by two short chains, bivalents, and univalents but this and later stages were not analyzed in detail. The second meiotic division showed lagging chromosomes and occasional bridges at anaphase II. At telophase II, there were several to many micronuclei which yielded many abnormally small microspores.

In contrast to the 96-99% pollen fertility of the parental species, the F_1 had one stainable pollen grain out of the 1012 examined (0.09%), and it apparently resulted from an unreduced microsporocyte.

Repeated backcrossing of the F_1 to *H. ciliatus* produced no viable seed from either parent.

Haplopappus (Isocoma) annuus ($n=6$) × *H. (Havardia) havardii* ($n=4$).

Numerous attempts have been made to cross these species. A number of seed had small, aborted embryos, and one F_1 seedling was obtained several years ago. This plant grew very slowly to a height of about three cm. Leaves



Figs. 14-18. Meiotic stages in *H. ciliatus* × *H. annuus*. Fig. 14. Segments of pachytene chromosomes showing loops (arrows) which are characteristic of either duplications or deletions in paired chromosomes. Fig. 15. Arrow indicates an inversion configuration involving three or more chromosomes. Fig. 16. Early diplotene showing a branched chain of 12 chromosomes. Fig. 17. Mid-to late diplotene with a complex chain of ten chromosomes. Possibly the chain was torn away from an association with the nucleolar organizing bivalent. Fig. 18. A chain of seven chromosomes, two bivalents, and an univalent at diakinesis.

TABLE 1. Pairing configurations and minimum chiasmata at late diplotene and diakinesis in the F_1 hybrid of *Haplopappus ciliatus* (n=6) × *H. annuus* (n=6).

No. cells	Chain(s)	Pair(s)	Univalent(s)	Minimum chiasmata
5	10	1	..	10
1	10	..	2	9
1	9, 3	..	..	10
1	9	1	1	9
1	8, 4	..	..	10
1	8, 3	..	1	9
2	8	2	..	9
2	8	1	2	8
3	7, 3	..	2	8
2	7	2	1	8
3	7	1	3	6
1	6, 3	1	2	7
1	5, 4	1	2	7
1	5, 3, 3	..	1	8
1	5, 3	2	..	8
1	5	3	1	7
2	5	2	3	6
2	4, 4	2	..	8
3	4, 3	2	1	7
1	4, 3	1	3	6
3	3, 3	2	2	6
1	3	4	1	6
Total 39				305
				$\bar{X}=7.8$

and stems showed irregular patches of tissue that closely resembled "sectoring" in irradiated plants. Toward the end of its growth, the F_1 produced many small heads two to three mm in diameter, but mature flowers were not formed. Since meiotic material was not available for analyses, somatic chromosomes and nuclei of some young leaf tissue were studied. Ten chromosomes (Fig. 19, 20) were found in one cell and these corresponded in size and structure to those of the parental species. Several anaphase stages had a chromosome bridge, and in some cells it appeared that fragmentation of chromosomes had occurred. Several late telophase nuclei were connected by a chromatin bridge (Fig. 21).

DISCUSSION

The morphological hiatus between *Haplopappus (Prionopsis) ciliatus* and *H. (Isocoma) annuus* is accompanied by an equally great change in karyotype. *Haplopappus ciliatus* has four sets of metacentric and two sets of acrocentric chromosomes (Fig. 3), whereas *H. annuus* has four sets of acrocentric and two sets of metacentrics (Fig. 4).

The difference between the two species in relative position of centromeres may have been caused by pericentric inversions, unequal reciprocal translocations, or a combination of both. However, analyses of pairing in the F_1 hybrid of the two species indicate that the primary changes have been translocations. The complex, branched chains of chromosomes observed at early diplotene suggest that all of the chromosomes were involved in the configuration. Cells at late diplotene and diakinesis seemed to bear this out when chains of up to ten chromosomes were observed. Branching of the chromosome chains is probably the result of interstitial and/or multiple translocations in which one chromosome may be made up of segments of several different chromosomes in comparison to the ancestral condition.

Six chiasmata is the minimum number needed to hold the six parental bivalents together until metaphase I. The mean minimum chiasma frequency per cell was 7.5 in *H. annuus* and 8.2 in *H. ciliatus.* The means were derived from a study of 20 cells for each species. The F_1 had a mean of 7.8 chiasmata per cell. Despite the large number of translocations and the probable reduction in chiasmata caused by them, these data indicate that a high degree of homology still exists among the chromosome segments of the parental species.

The arrangement of the F_1 chromosomes at metaphase I indicated that anaphase I segregation involved short chains, some bivalents, and univalents. This would probably yield a lower pollen fertility than the expected 1.56% from a translocation heterozygote with six independent translocations, as-

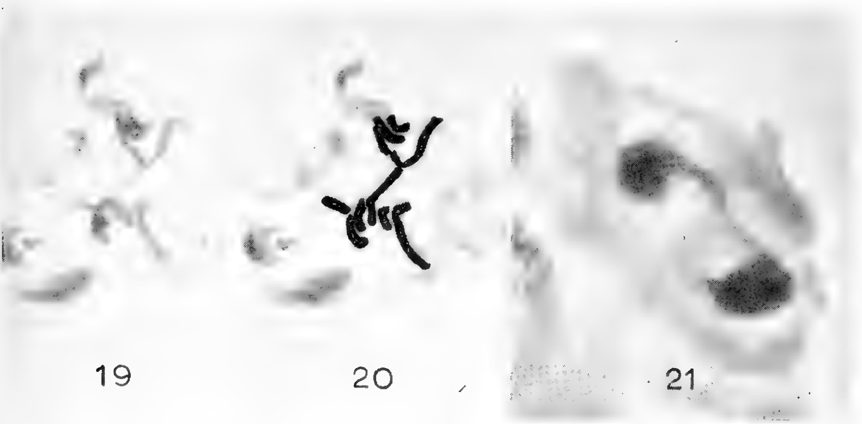


Fig. 19-21. Leaf squashes of *Haplopappus annuus* × *H. havardii.* Figs. 19, 20. Photograph and tracing of same showing ten chromosomes at late prophase of mitosis. Note difference in size of chromosomes. Fig. 21. Chromatin bridge connecting leaf cell nuclei at late telophase.

suming that a single translocation causes 50% sterility. The relatively high chiasma frequency of the F_1 may have contributed to the sterility if the deletion or duplication loops noted at pachytene were the result of inversions and re-inversions. Estimations of sterility based on the translocations and other aberrations indicate that the sterility barrier separating *H. annuus* and *H. ciliatus* is largely due to structural repatterning of the chromosomes of one or both parental species.

In gross morphology *H. havardii* ($n=4$) closely resembles *H. phyllocephalus* and *H. annuus* ($n=6$) more than any other species of the genus, even though it differs from these species in chromosome number and disc corolla shape. Furthermore, genetic relationship, as demonstrated by the production of an F_1 hybrid, is only with *H. annuus* and indirectly with *H. phyllocephalus* because the latter crosses readily with *H. annuus*. Attempts at crossing *H. havardii* to species of other sections have failed repeatedly.

Since the hybrid between *H. annuus* and *H. havardii* is the first in the genus between a four- and six-paired species, it is unfortunate that meiotic material was not available for analysis. The chromosomes of *H. havardii* are larger than those of *H. annuus* in parental plants and in the F_1. In view of the morphological similarity and demonstrated genetic link of the two species, and the relationship of *H. annuus* to section *Isocoma* ($X=6$), I suggest that $n=6$ is more primitive in this case than $n=4$. The origin of $n=4$ from $n=6$ probably resulted from unequal reciprocal translocations and loss of centromeres as previously shown for another species of *Haplopappus* (Jackson, 1962). This is not to say, however, that one species is older than the other; the inference is simply that both species had their origin in an ancestral group with $X=6$.

The hybridizations among the three species discussed here verify a genetic relationship which was previously assumed because of morphological similarity. Other than this, the lineage or true phylogenetic relationships among them are unknown and will probably remain so because connecting morphological forms are no longer extant. They are well isolated by internal barriers (Stebbins, 1950) in the hybrids. In the case of *H. annuus* × *H. ciliatus* there is chromosomal sterility. *Haplopappus annuus* and *H. havardii* are separated by hybrid weakness and failure of flowering, and, if meiotic stages had been produced, there would surely have been chromosomal sterility.

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Embryology of *Haplopappus Gracilis* (Nutt.) Gray[1]

By

S. Venugopalan[2]

INTRODUCTION

The genus *Haplopappus,* monographed by Hall (1928), is of late receiving much attention by experimental taxonomists. Interspecific hybridization among various species of the section *Blepharodon* and related cytogenetic studies have been done in this genus (Jackson, 1959, 1962, 1963, 1964; Li and Jackson, 1961). With the report of the diploid chromosome number as four for *Haplopappus gracilis* by Jackson (1957), this species has become a handy tool for radiation cytologists (Kamra & Kamra, 1962), plant physiologists (Blakely & Steward, 1964), and studies on growth and development by tissue culture methods. Harling (1951) described briefly the embryology of two species of this genus, *H. croceus* and *H. lyallii,* in a comparative study of the tribe Astereae. Except for this, little is known of the embryology of the genus. Since embryological characters are known to be of value in the elucidation of taxonomic problems at various levels and of phylogeny as well (Maheshwari, 1950, 1963), the present work was undertaken as a preliminary to a comparative embryological study of the different sections of *Haplopappus* (*sensu* Hall, 1928).

MATERIALS AND METHODS

The materials were collected from plants growing in the greenhouse. Carnoy's fluid and formalin-acetic-alcohol were used as fixatives. Dehydration

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was performed with ethanol and tissue mat was used for embedding. Sections were cut at 10-18μ and stained with Heidenhain's Iron-alum haematoxylin and counterstained with Fast green or Orange G.

OBSERVATIONS

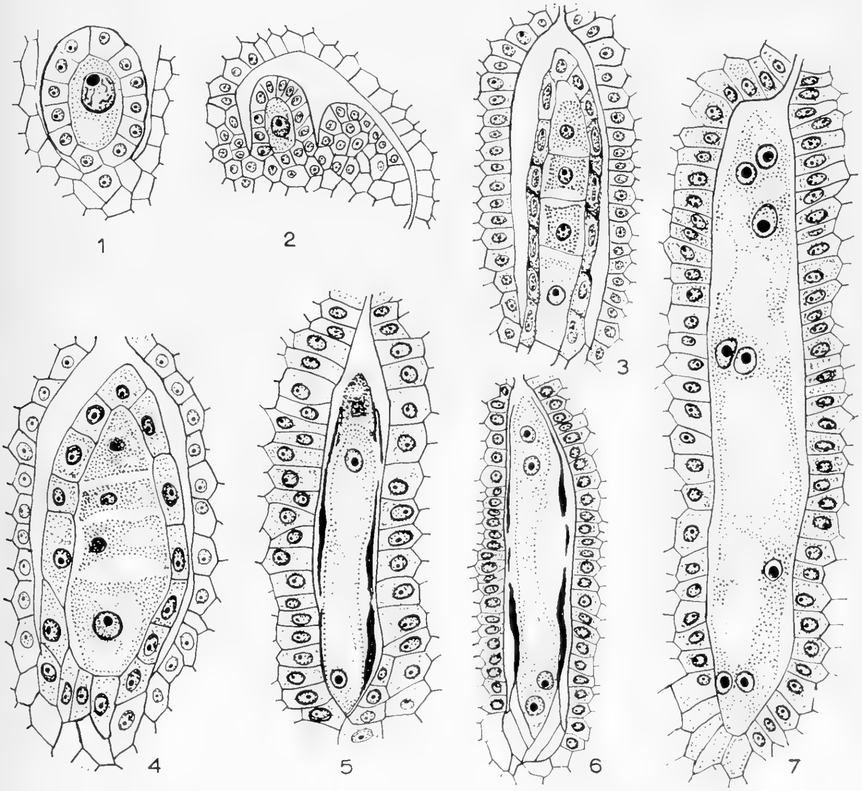
Ovule. The primordium of the ovule develops as a ventral protuberance from the floor of the ovary and eventually assumes an anatropous position. The ovule is monotegmic. Even as the archesporium is being differentiated, the primordium of the integument stands out on the side away from the raphe. In a well developed ovule the integument is a massive structure of several cells in thickness. The micropyle appears to be a uniformly narrow canal leading to the nucellus which can be hardly distinguished. From its inception the nucellus is a poorly developed tissue represented by a layer of cells surrounding the megaspore mother cell. By the time the functional megaspore begins to elongate, the nucellar cells disorganize and appear as darkly stained patches. The integumentary cells adjoining the nucellus become differentiated into a distinct endothelium. Its cells remain uninucleate throughout, although they divide to cope with the elongating embryo sac and the ovule.

Megasporogenesis. The archesporium consists of a hypodermal cell both in *H. gracilis* and *H. spinulosus,* and it functions directly as the megaspore mother cell (Fig. 1, 2). The two successive divisions of the mother cell result in a linear tetrad of megaspores (Fig. 3). The chalazal megaspore functions while the remaining ones degenerate (Fig. 4). The functional megaspore elongates toward the micropyle and forms the embryo sac. In *H. croceus,* Harling (1951) reported that the chalazal as well as the micropylar megaspores appear to enlarge.

Embryo Sac. Some of the representative stages in the development of the embryo sac are illustrated in Figs. 5 to 8. The degeneration of the nucellar cells brings the embryo sac close to the integument. The embryo sac shows eight nuclei, resulting from three mitotic divisions of the nucleus of the functional megaspore (Fig. 8). Three of these organize into the egg apparatus with two pyriform synergids and an egg cell, all of which lie in the same plane. The polar nuclei frequently lie near the egg (Fig. 8).

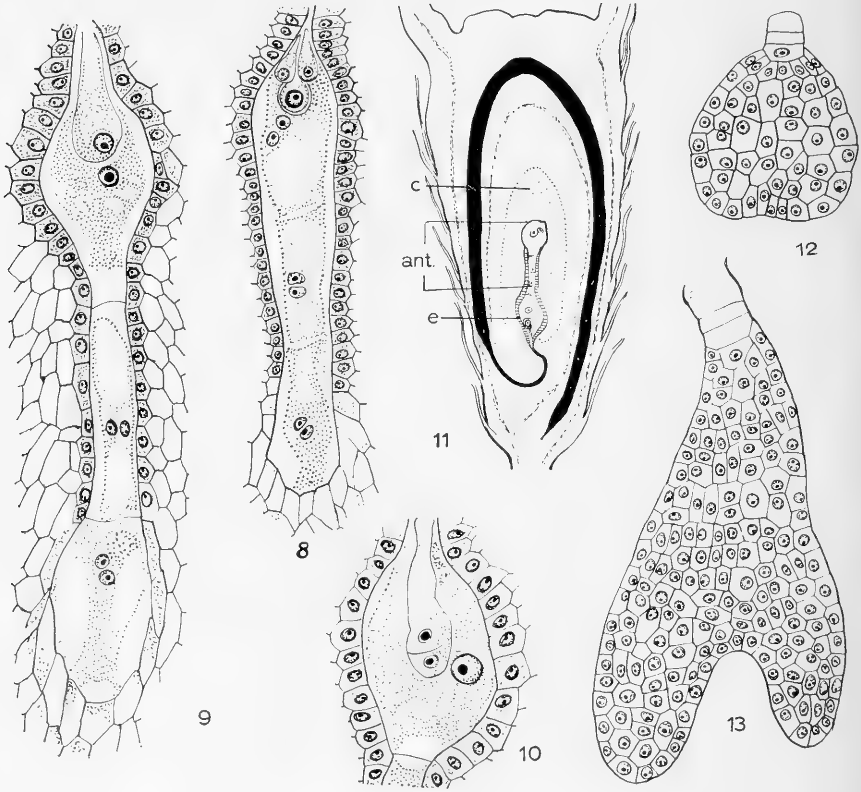
The three antipodal nuclei in the eight-nucleate embryo sac do not remain together as is the case in other angiosperms. One of them lies in the middle of the embryo sac while the other two are farther towards the chalazal end. The sister nucleus of the lower polar nucleus divides while near the middle of the embryo sac. Each set of antipodal nuclei is embedded in a separate mass of cytoplasm, but there is no evidence of wall formation before fertilization. The mature embryo sac thus consists of nine nuclei at the time of fertilization (Fig. 8). However, following fertilization the embryo sac is partitioned into three chambers (Fig. 9): the micropylar chamber with the zygote and the primary endosperm nucleus, the middle chamber with a binucleate antipodal cell, and the chalazal chamber, rather hypertrophied and uninvested by endothelial cells. The nuclei in the middle chamber unite to form a larger nucleus with many nucleoli. The nuclei at the chalazal pocket also tend to fuse. Similar nuclear fusions in antipodal cells have been reported for *Tridax procumbens* (Maheshwari & Roy, 1952) and *T. trilobata* (Kapil & Bala Sethi, 1962). But in the above two cases the antipodal cells persist as elongated tubular processes whereas they are vesicular and ephemeral in *Haplopappus gracilis*. There is no division of the primary antipodal cells as has been reported by Harling (1951) for *H. lyallii*.

Endosperm and Embryo. The division of the zygote is transverse and it precedes that of the endosperm nucleus (Fig. 10). Subsequent divisions of



FIGURES 1, 3-15. *Haplopappus gracilis*. FIGURE 2. *H. spinulosus*.
FIGURES 1-7. FIG. 1. Megaspore mother cell, × 353. FIG. 2. Hypodermal archesporium with the primordium of the integument, × 193. FIG. 3. Linear tetrad, × 353. FIG. 4. Same with three degenerate megaspores. FIG. 5. Two nucleate embryo sac, × 193. FIG. 6. Four nucleate embryo sac, × 193. FIG. 7. Eight nucleate embryo sac, × 353.

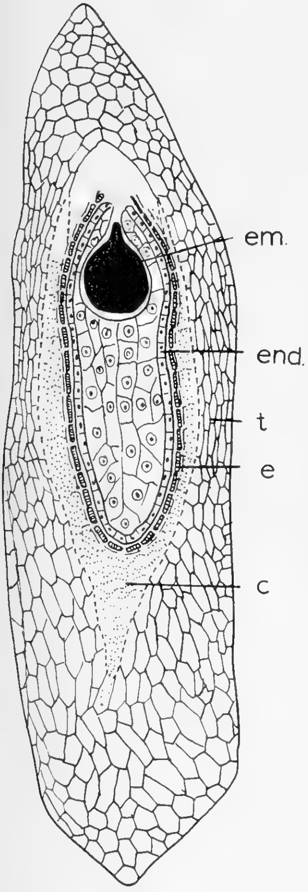
the proembryonal cells could not be followed for want of adequate preparations. The primary endosperm nucleus first divides vertically but there is no wall formation. Further divisions of these two free nuclei result in the formation of cellular endosperm. The development of endosperm is strictly confined to the micropylar chamber during the early stages. But soon, with the haustorial action of the antipodal cells and enlargement of the embryo sac, formation of endosperm extends to the chalazal region. Digestion of the endosperm cells does not begin until the heart-shaped stage of the embryo (Fig. 14). In the mature seed, however, all but the outermost layer of endosperm disappears. The endothelial cells degenerate as does also the integumentary tissue adjoining them. The early heart-shaped stage of the embryo



FIGURES 8-13. FIG. 8. Mature embryo sac; note the four antipodal nuclei, × 193. FIG. 9. Fertilized embryo sac; The primary endosperm nucleus lies close to the zygote and the antipodal cells are binculeate, × 353. FIG .10. Bicelled proembryo and endosperm nucleus, × 353. FIG. 11. L. s. ovule showing the two binucleate antipodal cells and their haustorial action on the chalazal ovular tissue: ant = antipodal cells; c = chalazal tissue affected by haustorial action of antipodals; e = endothelium; t = testa; × 36. FIG. 12. Early heart-shaped embryo, × 193. FIG. 13. Early dicotyledonous embryo, × 193.

(Fig. 12), the mature embryo with cotyledons, and a three celled suspensor are shown in Figs. 12 and 13.

Seed Coat. Of the fourteen or more layers of cells making up the integument in a mature ovule, all but four or five layers degenerate under the haustorial action of the enlarging chalazal antipodal chamber. The integument in a mature seed consists of rectangular and uninucleate flattened cells (Fig. 15). The pericarp external to the testa consists of four layers of flattened cells and some remnants of vascular tissue. Long epidermal hairs are seen on the surface of the pericarp. No special thickenings were observed on the testa or the pericarp.



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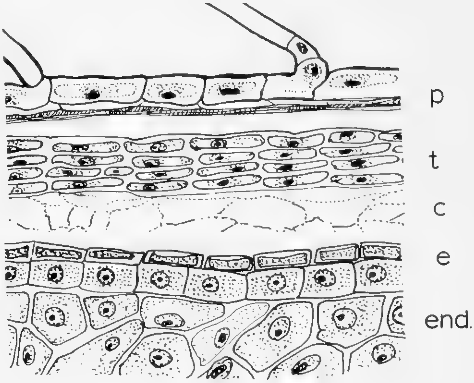

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FIGURES 14-15. FIG. 14. L. s. developing ovule showing the various parts: c = tissue of the integument showing haustorial action of antipodals; em = embryo; end = endosperm; e = endothelial cells; t = testa; × 36. FIG. 15. L. s. portion of fruit: t = testa; p = pericarp; e = endothelial cells; c = disorganized integumentary cells, × 139.

SUMMARY AND CONCLUSIONS

The present study on *Haplopappus gracilis* reveals that the archesporium of the ovule is unicellular and hypodermal and that the development of the female gametophyte is monosporic and of the polygonum type. This is in agreement with the findings of Harling (1951) for *H. lyallii.* However, these two species seem to differ in some details regarding the character of antipodal cells. In *H. gracilis,* the female gametophyte has nine nuclei, constituted into three uninucleate cells of the egg apparatus, two polar nuclei, and four antipodal nuclei. The increase in number of antipodal nuclei from three to four is due to secondary division of one of the nuclei of the chalazal quartet. Further, the formation of cell walls surrounding these nuclei takes place only after fertilization, and two binucleate primary antipodal cells are formed as a result. Of these, the chalazal one enlarges considerably and the nuclei in this cell as well as the other antipodal cells may fuse to form a large multinucleolate nucleus. In some, one nucleus divides and thus a multinucleate cell may result. Such endomitotic, heteroploid, primary antipodal cells are reminiscent of the microsporangial tapetum. Primary antipodal cells of this nature are known to occur in many of the embryologically studied species in the tribe Heliantheae (cf. Schnarf, 1931). Two other genera, *Grindelia* and *Aphanostephus,* both belonging to the tribe Astereae, are reported by Harling to exhibit enlarged primary antipodal cells.

In contrast with this is a secondary antipodal complex reported by Harling (1951) for *H. lyallii.* In this species the two primary antipodal cells keep on dividing to form 12 to 15 cells. The nuclear divisions are not always followed by cell divisions, thus resulting in small multinucleate secondary antipodal cells. These regions persist, restricting the endosperm formation to the micropylar region. Such a secondary antipodal complex has been held by Harling to be prevalent in the great majority of species showing monosporic development of the female gametophyte in the tribe Astereae, with the exception of *Erigeron, Vittidinia,* and *Aster* section of *Macranthera. Grangea maderaspatana* (Mitra, 1947) and *Solidago altissima* (Beaudry, 1958) also form secondary antipodal cells.

The prevalence of enlarged antipodal cells in *Grindelia* and *Aphanostephus* has been taken by Harling as indicative of the connection of these two genera with Heliantheae. Further, he has stated "it is perhaps no mere chance that *Grindelia squarrosa* exhibits a connection to the said tribe also in respect of chromosome number (n=6). The number six and multiples of this are in fact common in the Heliantheae but they have not been met with in the Astereae apart from *Grindelia.*"

Two points deserve mention here: (1) Heliantheae has haploid numbers ranging from four to 19 and six is not the common number of all these. (2) In Astereae there are some species of *Haplopappus* with n=6, besides

Grindelia and other genera, so it will be but proper to consider the correlation between embryological characters and chromosome number in *Grindelia* as fortuitous. Additional information on the embryology of the species of *Haplopappus* with a haploid number of six will be necessary before any valid conclusions can be drawn in this regard. In any case, secondary antipodal tissue in *H. lyallii* and species of *Solidago* suggest the latent ability of the female gametophyte to organize a nutritive mechanism independent of double fertilization.

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INTRODUCTION

During middle and late Tertiary time extensive sedimentary deposits were laid down over the mid-continental High Plains region, an area extending 400 miles eastward from the Rocky Mountain erosional front, stretching from Texas to South Dakota. These fluviatile sediments are preserved as erosion remnants of the originally broad layers of sediments. The most extensive of these broad sheets, known as the Ogallala Formation of late Miocene and Pliocene (Neogene) age forms ". . . relatively thin sheet of deposits, in part fine-grained, but containing lenses of coarser gravels carried eastward from the Rocky Mountains in the channels of withering streams. In many places its layers are peculiarly cemented by *caliche* as a result of soil-forming processes in an arid climate, so that they are resistant to erosion and create the *cap rock* of the plain." (King, 1959).

The Ogallala Formation has been famous for the numerous mammals contained in its sediments. Fossil plants, chiefly representatives of the family Gramineae, are also quite well-known. It is the purpose of this work to present a taxonomic revision of the genus *Biorbia* (Boraginaceae) which is the most abundant fossil found in the Ogallala Formation of the Great Plains region.

Though the Ogallala Formation is widely distributed, much of it is unavailable for study due to a covering of Quaternary deposits. In many areas, extensive searching must be done over almost featureless terrain in order to locate an exposed outcrop. The Ogallala Formation in western Kansas, in many cases of quite limited exposure, readily yielded thousands of specimens, while several extensive exposures in western Oklahoma and Texas were non-productive, the exception being a locality in Garza Co., Texas. Several other fossiliferous sites have been reported from northwest Texas by Frye and Leonard (1957), who established the rather extensive distribution of *Biorbia papillosa* Leonard in Texas.

The author has collected thousands of specimens of *Biorbia* fruits from various outcrops of the Ogallala Formation over the past two years (see the following list of collection sites and distributional map, Fig. 1). Fossils from all of these sites are permanently housed in the Paleobotanical Collection of the Department of Botany, University of Kansas, Lawrence.

The following is a list of collection sites of *Biorbia* from outcrops of the Ogallala Formation. The number of nutlets of *Biorbia fossilis* and *B. glabrum* collected are given in parentheses for at least one representative locality of each county in which collections were made.

KANSAS. Cheyenne Co.: about 2 mi. north of St. Francis along Hwy. 27, *Segal 121,* 26 Aug. 1964, *Biorbia fossilis* (1002), *Biorbia glabrum* (412). Clark Co.: SE½ Sec. 36, T. 30 S., R. 25 W., *McGregor 17214,* 24 June 1962, *Biorbia fossilis* (654), *Biorbia glabrum* (309); Clark Co. State Lake, *Segal 112,* 12 Oct. 1963, *Biorbia fossilis* (580), *Biorbia glabrum* (166). Hodgeman Co.: SW¼ SE¼ Sec. 30, T. 23 S., R. 25 W., *McGregor 17203,* 23 June 1962, *Biorbia fossilis* (333), *Biorbia glabrum* (58). Logan Co.: N½ SW¼ Sec. 24, T. 12 S., R. 32 W., *Segal 105,* 6 Sept. 1963, *Biorbia fossilis* (13), *Biorbia glabrum* (16). Meade Co.: 4 mi. south, 2 mi. west of Meade, *Beamer,* 16 Aug. 1945, *Biorbia fossilis* (186), *Biorbia glabrum* (37). Phillips Co.: NW¼ NW¼ Sec. 12, T. 2 S., R. 20 W., *Segal 90,* 4 Sept. 1963, *Biorbia fossilis* (272), *Biorbia glabrum* (38). Rawlins Co.: NW¼ SW¼ Sec. 12, T. 3 S., R. 33 W., *McGregor 17418,* 29 July 1962, *Biorbia fossilis* (256), *Biorbia glabrum* (668). Scott Co.: SE¼ SE¼ Sec. 2, T. 16 S., R. 33 W., *McGregor 17229,* 25 June 1962, *Biorbia fossilis* (102), *Biorbia glabrum* (161). Sheridan Co.: Sheridan Co. State Lake, *Segal 120,* 24 Aug. 1964, *Biorbia fossilis* var. *parvulus* (1637), *Biorbia glabrum* var. *minimum* (287). Smith Co.: center west line of SW¼ Sec. 32, T. 1 S., R. 14 W., *Segal 89,* 4 Sept. 1963, *Biorbia fossilis* (39), *Biorbia glabrum* (19). Wallace Co.: NW¼ SW¼ Sec. 16, T. 14 S., R. 39 W., *Segal 99,* 6 Sept. 1963, *Biorbia fossilis* (113), *Biorbia glabrum* (197); center west line of Sec. 32, T. 11 S., R. 42 W., *Segal 117,* 11 July 1964, *Biorbia fossilis* (3), *Biorbia glabrum* (129).

SOUTH DAKOTA. Bennett Co.: 5 mi. east of Vital, *McGregor 18803,* 11 Aug. 1964, *Biorbia fossilis* (151).

NEBRASKA. Keith Co.: Lake Ogallala State Recreation Area, *Segal 122,* 25 Aug. 1964, *Biorbia fossilis* (76), *Biorbia glabrum* (22).

TEXAS.[1] Garza Co.: 3.0 mi. west of the intersection of U. S. Hwys. 380 and 84 near Post, *Segal,* July, 1963. Briscoe Co.: 10½ mi. west of Briscoe-Hall Co. line and 6 mi. north of Briscoe-Floyd line. Floyd Co.: 1 mi. west of Floyd-Motley Co. line and 7 mi. north of U. S. Hwy. 70. Howard Co.: south wall of Wildhorse Creek valley, 5.2 mi. north of Coahoma. Randall Co.: 200 yards west of south end of Buffalo Lake dam.

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[1] The Texas collections, other than by Segal, were reported by Frye and Leonard (1957) and are included in the distribution map (Fig. 1), but specimens from these localities are not in the Paleobotanical Collection of the Department of Botany, University of Kansas.

SYSTEMATIC TREATMENT

Biorbia Elias, 1932, Kans. Univ. Sci. Bull. 20:350; pl. 29, figs. 2a-2e.

Type species: *Lithospermum fossilium* var. *rugosum* Berry 1928 (=*Biorbia fossilis* (Berry) Cockerell), Proc. U. S. Nat. Mus. 73:1-3, pl. 1, figs. 1-10.

Generic Diagnosis (emended):

Only nutlets known. Nutlets keeled, asymmetrically inflated, being more convex on the dorsal side. Surface rugose, covered with ridges arranged in honeycomblike net, or smooth and without network of ridges, or densely papillose and without prominent reticulate surface sculpture. Dorsal keel turns to right or left, spoiling the apparent bilateral symmetry of the nutlets. Probably four nutlets, two right and two left ones, constituted a complete fruit. Scar of attachment round, comparatively small and elevated, consists of a double ring and an elaiosome in the center. Distinct canal in the ventral part of the scar (Fig. 8). The slight emendment of Elias's original description of the genus *Biorbia* is necessary in order to accommodate the new species *B. levis* and the previously described species *B. papillosa* Leonard.

KEY TO THE SPECIES AND VARIETIES OF *BIORBIA*

A. Nutlet smooth	B
Nutlet rugose or papillose, not smooth	C
B. Nutlet 2. 3-3. 4 mm long	4. *B. levis*
Nutlet 1. 7-2. 3 mm long	5. *B. levis* var. *minimus*
C. Nutlet 1.7 mm long, sculptured by papillose excrescences	1. *B. papillosa*
Nutlet rugose, covered by reticulate sculpture	D
D. Nutlet 2. 3-3. 4 mm long	2. *B. fossilis*
Nutlet 1. 7-2. 2 mm long	3. *B. fossilis* var. *parvulus*

1. **Biorbia papillosa** Leonard, 1958, Univ. Kans. Sci. Bull. 38:1396, pl. 1, figs. 1-3.

Holotype: Museum of Natural History, University of Kansas; Catalogue No. 9917; collected by A. B. Leonard and John C. Frye, June 30, 1955.

Type locality: Partly cemented sand and gravel at the rim of the escarpment produced by resistant Pliocene deposits, 3.8 miles west of the intersection of U. S. Hwys. 380 and 84 near the center of Post, Garza Co., Texas.

Nutlet small, total length 1.7 mm, transverse diameter 1.3 mm, vertical diameter 1.3 mm; ovoid in shape, swollen near base, tapering toward cuspidate apex, but also compressed; ventral, bladelike ridge arising from base of style at anterior rim of scar of attachment, extending forward in midline over apex, thence backward along mid-dorsal axis of nutlet for a short distance before extending diagonally to the left, over side of the nutlet to reach scar of attachment; surface sculpture of closely spaced, conical, papillose excrescences, 0.2-0.3 mm high; in a few places along side of the nutlet, the papillae fused to form short ridges; scar of attachment circular in outline, depressed strongly in center, within outer rim a parallel groove, followed medially by a parallel row of six low, rounded papillae or bosses; a small cylindrical elevation (elaiosome) in center of scar of attachment, rising slightly above outer rim of scar; the style, situated on anterior rim of scar at point of origin of keel, elevated well above rim of scar, spatulate, possessing a large median vein and two smaller, parallel veins laterally (Fig. 5).

I found *Biorbia papillosa* at the type locality, but no new details can be added to the above account by Leonard. *B. papillosa* was also found by Leonard (1957) in several other exposures of the Ogallala Formation in northwest Texas.

Biorbia papillosa is a distinct species known only from the Pliocene of Texas; it has not been found associated with *Biorbia fossilis*. Since prolific quantities of *B. fossilis* were excavated from southwest Kansas (for instance, Clark Co.) an attempt was made to find fossil remains from the panhandle region of Oklahoma with the idea that *B. fossilis* or the new species *B. glabrum* might be found with *B. papillosa*. Such a discovery would be significant from both a geological and biologic view. However, no such fossiliferous exposures of the Ogallala Formation were discovered.

2. **Biorbia fossilis** (Berry) Cockerell, 1933, Torreya 33:15.

Lithospermum fossilium var. *rugosum* Berry, 1928, U. S. Nat. Mus., Proc. 73:1-3, pl. 1, figs. 1-10.
Celtis microendocarpica Watt, 1928, Penn. Acad. Sci., Proc. 2:54.
Celtis microendocarpica Brooks, 1928, Carnegie Mus. Ann. 18:299, pl. 17, fig. 1.
Celtis microendocarpica Brooks, 1929, Carnegie Mus., Ann. 19:135-137, 1 pl.
Biorbia rugosa (Berry) Elias, 1931, State Geol. Surv. Kansas, Bull. 18, vol. 32, no. 7, p. 150.
Biorbia rugosa (Berry) Elias, 1932, Univ. Kans. Sci. Bull. 20:350, pl. 29, figs. 2a-2e.
Biorbia fossilia (Berry) Elias, 1942, Geol. Soc. Amer., Spec. Paper 41, p. 106, pl. 15, fig. 12.

Isotypes: United States National Museum.

Type localities: Phillips Co., Kansas, and Kit Carson Co., Colorado.

Fossilized nutlets 2.2-3.4 mm long, 1.8-2.5 mm wide, hollow, walls exclusive of ridges ca. 0.08 mm thick, asymmetrically inflated, the dorsal side being more convex than the ventral. On the ventral side a keel extends from a cuspidate apex nearly or quite to the scar of attachment, unless lost on the way; surface rugose, covered with narrow and, when perfectly preserved, elevated ridges forming an irregular honeycomblike structure; scar of attachment round and elevated, about as high above the surface as the ridges of the exterior; scar consists of double ring, inside of which is prominent central elevation apparently corresponding to the elaiosome of living Boraginoideae-Anchuseae; a short and ventrally curved delicate pipe is ordinarily observed ventrally between the outer and inner rings of the scar, but when not preserved, a corresponding thin canal leading inside the nutlet can be seen (Fig. 4).

Frye, Leonard, and Swineford (1956) recognized that many seeds of *Biorbia fossilis* (Berry) Cockerell were smooth and lacked the reticulate sculpture of this, the rugose form, but they did not attempt to judge whether the smooth nutlets represented another species. Evidence will be presented to show that two species are probably represented, and the creation of the new species *Biorbia levis* is believed to truly delineate the biological diversity of the genus.

3. **Biorbia fossilis** var. **parvulus,** var. nov.

Biorbia fossilia var., Ellias, 1942, Geol. Soc. Amer., Spec. Paper 41, 106, pl. 15, fig. 10a.

Holotype: No. 120 (1a) from the type locality; *Segal 120,* Aug. 24, 1964. *Isotypes:* 1636 isotypic examples from the type locality; *Segal 120,* Aug. 24, 1964. *Type locality:* partly cemented sand and gravel deposit, Sheridan Co. State Lake, Sheridan Co., Kansas.

Nutlet small, asymmetrically inflated, 1.7-2.3 mm long, 1.3-1.8 mm wide; ovoid with swollen base; tapers to cuspidate apex; ventral keel arises from anterior rim of round and elevated scar of attachment which extends over cuspidate apex, turns to either left or right on the dorsal side and connects diagonally with the scar of attachment. Surface of the nutlet rugose with prominent reticulate surface sculpture, small papillae present between the reticulate ridges; scar of attachment a double ring enclosing central elaiosome, inner ring dentate; remnant of style at anterior rim of scar (Fig. 7).

This variety is easily distinguished from collections of *Biorbia fossilis* (Berry) Cockerell by its consistently smaller size as illustrated in Fig. 9.

Apparently this new variety is identical to that noted by Elias (1942) as a "small variety of *Biorbia*" from a locality near Sharon Springs, Wallace Co., Kansas, but he did not formally describe it.

Though we failed to find this variety at the locality specified by Elias, over 1600 specimens were located at the Sheridan Co. site. The difference in size in populations of *B. fossilis* and *B. fossilis* var. *parvulus* is quite striking and there is no difficulty in distinguishing these entities when populations are compared. Occasionally a small specimen or two is found in collections of *B. fossilis,* and in such instances one must assume this is an immature nutlet, or represents an abortive one. In living species of the Boraginaceae one or several nutlets frequently abort.

4. **Biorbia levis,** sp. nov.

Holotype: No. 17214(1) from the type locality; *McGregor 17214,* June 24, 1962. *Isotypes:* 308 isotypic examples from the type locality; *McGregor 17214,* June 28, 1962. *Type locality:* Consolidated coarse sand, SE¼ Sec. 36, T. 30 S., R. 25 W., Clark Co., Kansas.

Similar to *Biorbia fossilis* (Berry) Cockerell except that the nutlets are smooth with the keel representing the only surface ornamentation (Figs. 2, 3).

I believe that the recognition of these fossils as a distinct species is taxonomically correct and more adequately represents the biologic diversity within this genus.

At first I thought that the smooth and rugose nutlets were simply forms of the same species. It is known that various species of the Boraginaceae have heteromorphous fruits in which one of the four nutlets of each fruit may be distinguished by size or sculpture. Such a plant is *Cryptantha crassisepala* in which the fruit consists of one smooth and three granulate nutlets. This ratio is constant as determined from herbarium specimens, with the smooth being slightly larger than the granulate forms.

While the smooth fossil nutlets are generally also slightly larger than the rugose, the ratio of smooth to rugose nutlets is extremely variable. At the Bennett Co., South Dakota, exposure only rugose forms were found. At the Wallace Co., Kansas, localities the smooth forms were dominant, and at one site (center west line of Sec. 12, T. 11 S., R. 42 W.) rugose nutlets were rare. On the basis of the opposed ratios, I feel that the establishment of a new species is necessary.

5. **Biorbia levis** var. **minimus**, var. nov.

Holotype: No. 120(1) from the type locality; *Segal 120,* Aug. 24, 1964. *Isotypes:* 287 isotypic examples from the type locality; *Segal 120,* Aug. 24, 1964. *Type locality:* partly cemented sand and gravel deposit, Sheridan Co. State Lake, Sheridan Co., Kansas.

Similar to *Biorbia fossilis* var. *parvulus* except that the nutlets are smooth with the keel representing the only ornamentation (Fig. 6).

Again, as for *B. fossilis* var. *parvulus,* there is a sharp distinction in the size of the species and its variety. It is possible that if more information on the plants as a whole were available, the varietal forms would be elevated to species. In extant plants of the family, such differences in the form of the fruit are diagnostic of species (Fig. 10).

GENERAL DISCUSSION

The Pliocene strata of the Ogallala Formation of the High Plains is known to contain the following plant fruits:

Family GRAMINEAE
  Tribe Stipeae
    Genus *Stipidium*
      Stipidium aristatum (Berry) Elias
      S. asymmetricum Elias
      S. breve Elias
      S. coloradoense Elias
      S. commume Elias
      S. elongatum Elias
      S. grande Elias

- *S. intermedium* Elias
- *S. kansasense* Elias
- *S. minimum* Elias
- *S. nebraskense* Elias
- *S. novum* Elias
- *S. tubus* Elias
- *S. tubus* var. *leave* Elias
- *S. variegatum* Elias
- *S. hirsutum* Elias
- *S. schereri* Elias
- *S. ventricosum* Elias

Genus *Berriochloa* Elias
  - *Berriochloa amphoralis* Elias
  - *B. conica* Elias
  - *B. glabra* (Berry) Elias
  - *B. inflata* Elias
  - *B. maxima* Elias
  - *B. minuta* Elias
  - *B. primaeva* Elias
  - *B. tuberculata* Elias

Genus *Paleoeriocoma* Elias
  - *Paleoeriocoma hitchcocki* Elias

Genus *Nassella* Desvaus
  - *Nassella amphora* Elias

Tribe Paniceae
  Genus *Panicum* Linne
    Panicum elegans Elias
    P. eliasi Leonard
  Genus *Setaria* Beauvois
    Setaria chasea Elias
Tribe (?)
  Genus *Clementsiella* Elias
    Clementsiella laminarum (Cockerell) Elias
Family BORAGINACEAE
  Genus *Biorbia* Elias
    Biorbia fossilis (Berry) Cockerell
    B. fossilis var. *parvulus* Segal
    B. levis Segal
    B. levis var. *minimus* Segal
    B. papillosa Leonard
  Genus *Cryptantha* Lehman
    Cryptantha auriculata (Elias) Segal
    C. chaneyi (Elias) Segal
    C. coroniformis (Elias) Segal
  Genus *Prolithospermum* Elias
    Prolithospermum johnstoni Elias
Family COMPOSITAE
  Genus *Achaenites* Braun
    Achaenites kansanum Segal
Family ULMACEAE
  Genus *Celtis* Linne
    Celtis willistonii (Cockerell) Berry

With the exception of *Celtis willistonii,* all of these fossils represent the remains of grass and herbaceous fruits. Unlike the vast majority of late Cretaceous and Tertiary floras, the plant parts preserved in the Ogallala Formation represent the reproductive parts of the plant rather than the vegetative, a fact which facilitates their identification. Through all of the extensive collecting accomplished at the sites described above, only some rather sinuous fragments which resemble root or stem axes were found; no anatomical details were preserved.

The borages, represented prominently by the genus *Biorbia,* are without doubt the most abundant fossil in the Ogallala Formation. Though the large number of specimens collected attest to the fact that these remains are very prolific, sometimes rather diligent searching is required to find these fruits in the massive strata. The fossils usually occur in isolated clusters or pockets. I have found several thousand specimens of *Biorbia* in just a few cubic inches of sediment.

The fossil fruits appear to be buried approximately at the place of their growth. It seems likely that the fossils accumulated into clusters when small ephemeral pools of water dried up; these fruits could have survived very little transportation and still retain their detailed sculpture in water carrying coarse sediments in which the fossils are preserved.

The endocarps referred to as *Celtis willistonii* are the most wide-ranging petrifactions in the Ogallala Formation. They are of little stratigraphic significance in comparison to the various species of the grass and borage families which have been utilized in stratigraphic studies (Frye, Leonard, & Swineford, 1956).

It is an interesting facet of preservation that only fruits are so prominently found in the Ogallala Formation; and these, as shown for *Celtis willistonii*, are silicifications (Swineford & Franks, 1959). This is probably due to the fact that the fossil fruits, as some living borages and grasses, were so constituted that their naturally hard and indurated fruits were not readily susceptible to decay, and were gradually replaced by silica. Organs such as leaves, even of the borages, would not normally be expected to be preserved, particularly in the coarse sediments which compose the mass of the Ogallala Formation. Significant discoveries of leaves and other vegetative structures might be expected if fine-grained lake sediments could be located.

The absence of extensive arboreous vegetation is puzzling. In support of at least the presence of isolated elements of a woody flora, one can mention the Beaver County Flora (Chaney & Elias, 1936) and the Kilgore Flora of late Miocene or possibly early Pliocene age (MacGinitie, 1962). A study of these isolated floras reveals that arboreous vegetation, as *Populus, Salix, Ulmus,* and *Fraxinus* was present in the High Plains coexistent with the rich herbaceous vegetation emphasized by Elias (1942). This is especially significant since Wells (1965) has suggested that the development of the broad grasslands and the treeless landscape currently occupying much of the High Plains region is relatively recent.

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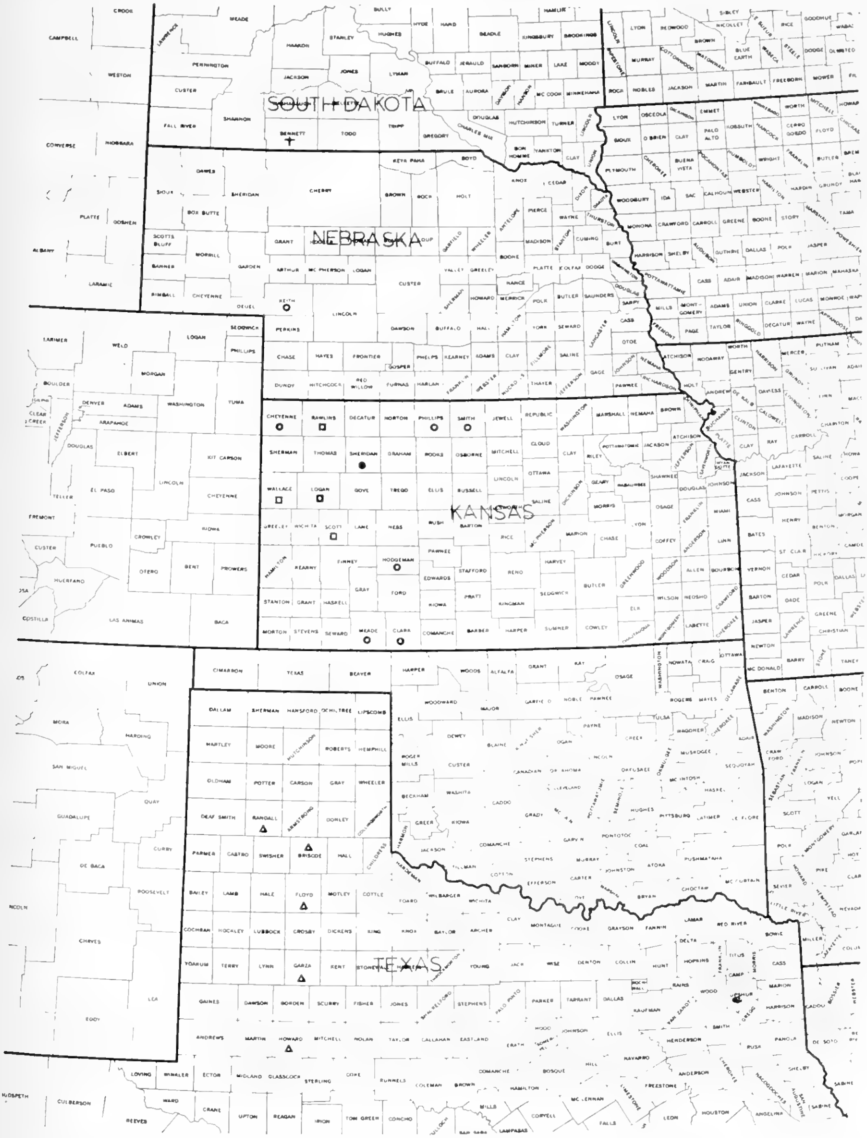

FIG. 1. Map showing distribution of the genus *Biorbia*. O=both *Biorbia fossilis* and *Biorbia levis* present, with *B. fossilis* dominant; △=*Biorbia papillosa* only; +=*Biorbia fossilis* only; □=both *Biorbia fossilis* and *Biorbia levis* present with *B. levis* dominant; ●=both *Biorbia fossilis* var. *parvulus* and *Biorbia levis* var. *minimus* with *B. fossilis* var. *parvulus* dominant.

FIG. 2. Drawing of *Biorbia levis*, new species, ca. 30×.

FIG. 3. Drawing of *Biorbia levis,* new species, ca. 30×.

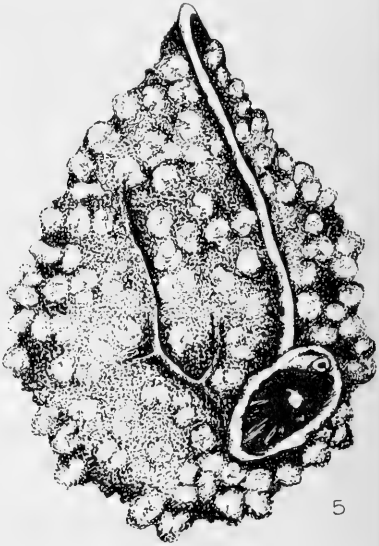

FIG. 4. Drawing of *Biorbia fossilis* (Berry) Cockerell, ca. 30×.

FIG. 5. Drawing of *Biorbia papillosa* Leonard, ca. 38×.

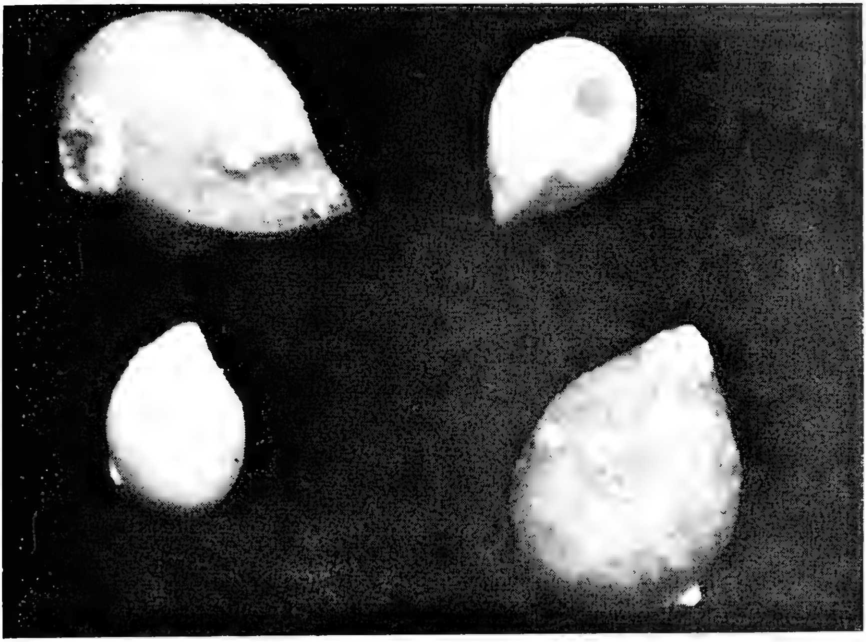

FIG. 6. Comparison of *Biorbia levis* (two large specimens), new species, and *Biorbia levis* var. *minimus* (two small specimens), new variety, ca. 13×.

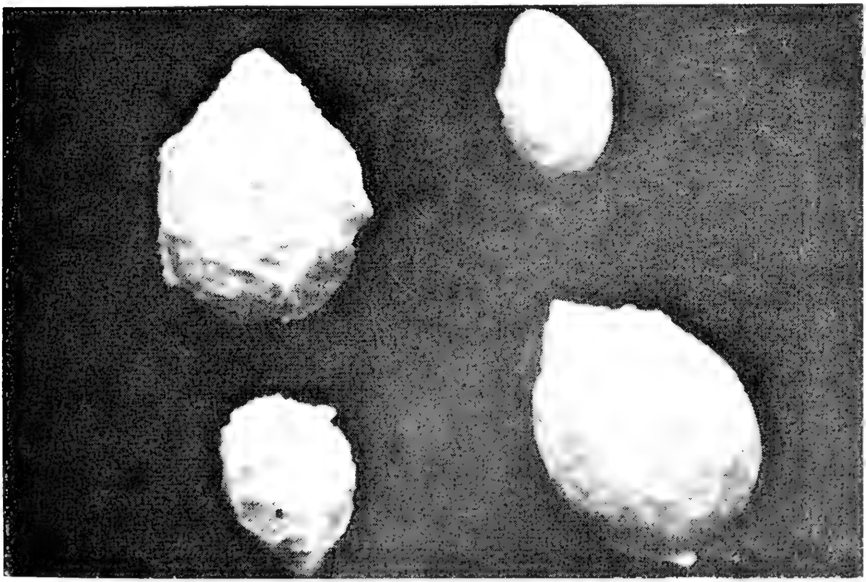

FIG. 7. Comparison of *Biorbia fossilis* (Berry) Cockerell (two large specimens), and *Biorbia fossilis* var. *parvulus* (two small specimens), new variety, ca. 13×.

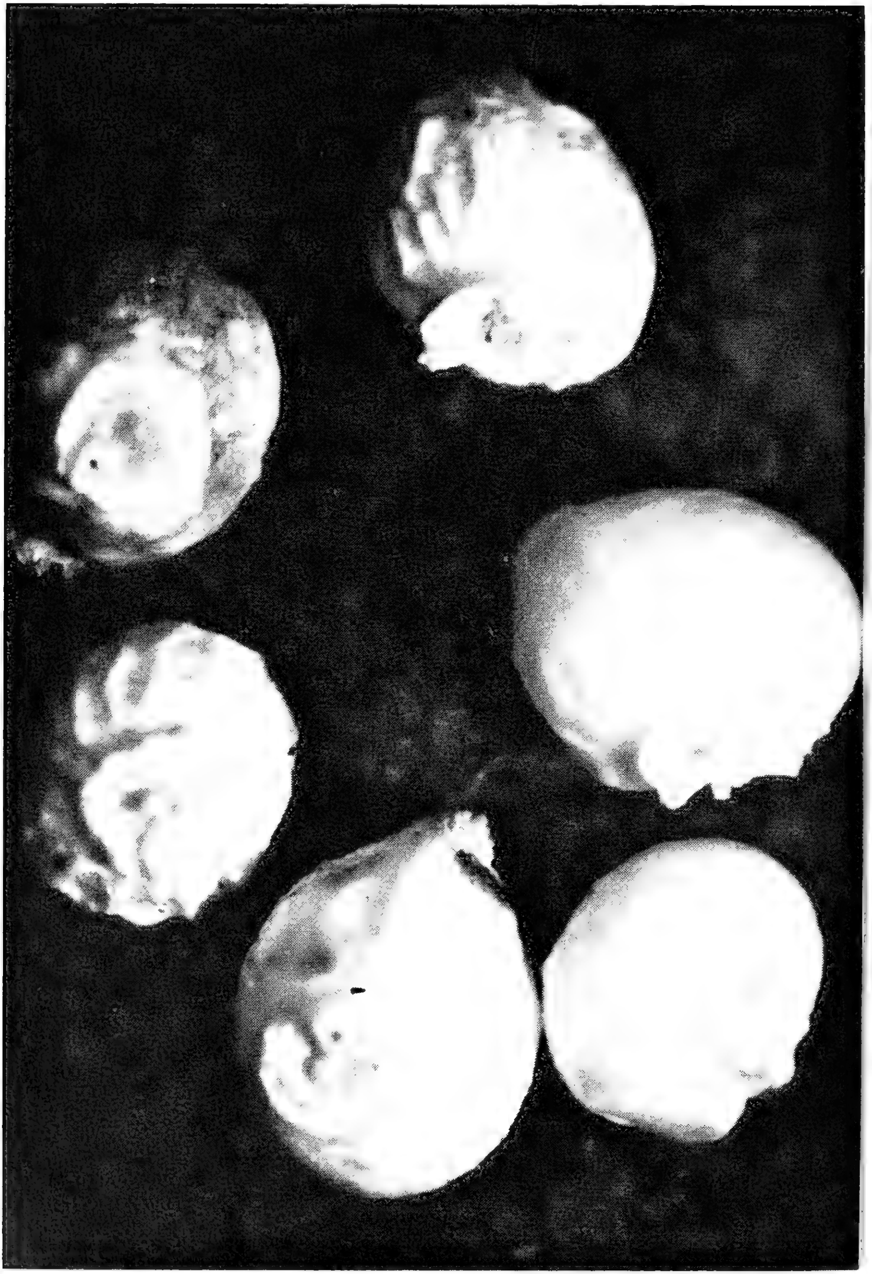

FIG. 8. Details of basal scar of attachment, ca. 20×.

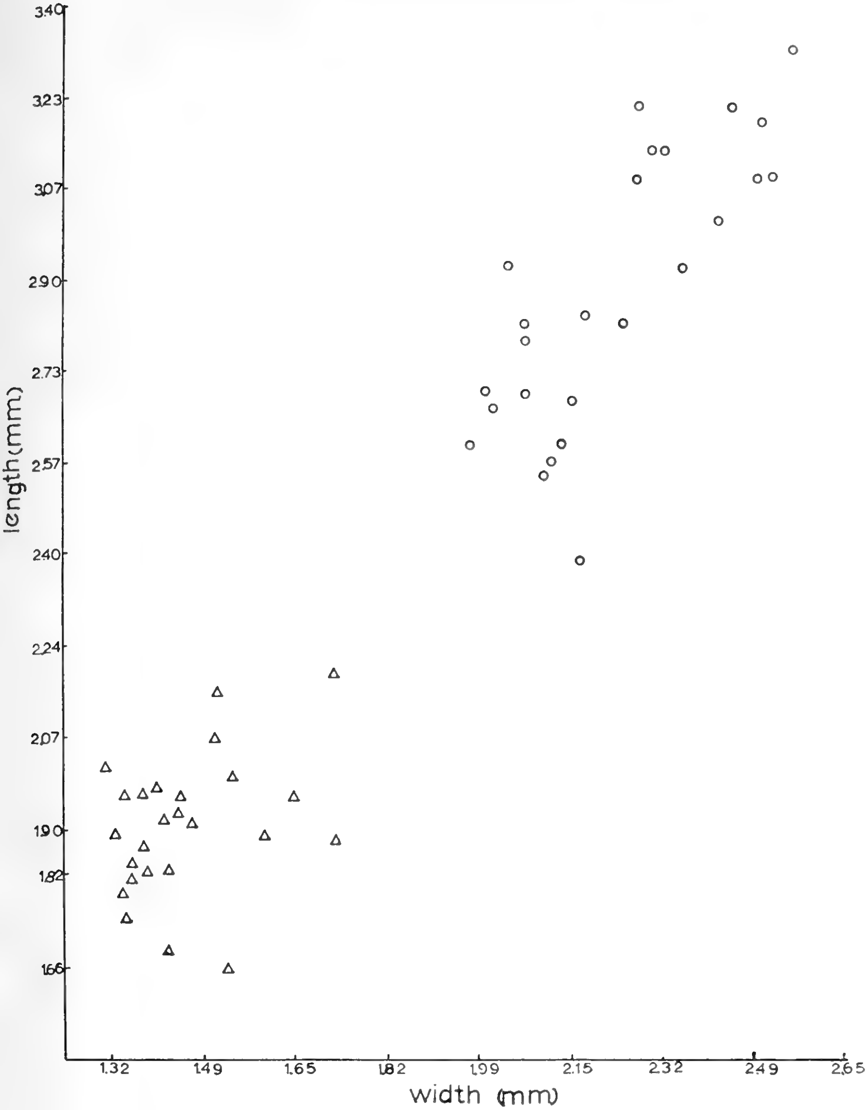

Fig. 9. Graph showing relative sizes of *Biorbia fossilis* and *Biorbia fossilis* var. *parvulus.* Data are based on the following collection sites: SE¼ Sec. 36, T. 30 S., R. 25 W., Clark Co., Kansas, for *Biorbia fossilis; McGregor 17214,* June 24, 1962. Sheridan Co., State Lake for *Biorbia fossilis* var. *parvulus; Segal 120,* Aug. 24, 1964. O=*B. fossilis*; △= *B. fossilis* var. *parvulus.*

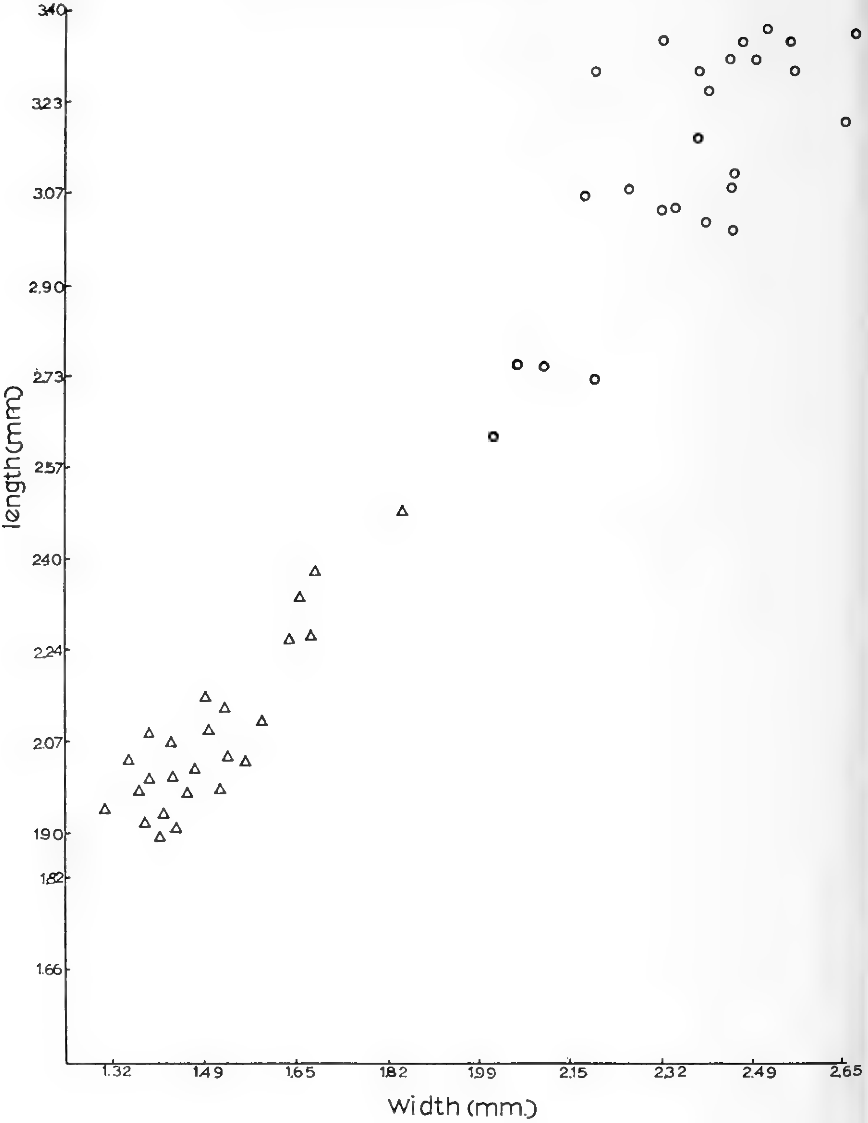

Fig. 10. Graph showing relative sizes of *Biorbia levis* and *Biorbia levis* var. *minimus*. Data are based on the following collection sites: SE½ Sec. 36, T. 30 S., R. 25 W., Clark Co., Kansas, for *Biorbia levis; McGregor 17214,* June 24, 1962. Sheridan Co. State Lake for *B. levis* var. *minimus*. O=*B. levis*; △=*B. levis* var. *minimus*.

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SYSTEMATICS OF THE GENUS *AUGOCHLORELLA* (Hymenoptera, Halictidae) NORTH OF MEXICO

By

Ellen Ordway

Vol. XLVI Pages 509-624 June 17, 1966 No. 16

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Systematics of the Genus *Augochlorella* (Hymenoptera, Halictidae) North of Mexico[1]

By

ELLEN ORDWAY[2]

ABSTRACT

In a revision of the bee genus *Augochlorella*, descriptions and keys are given for seven species occurring north of Mexico and one species and a subspecies from Mexico. One species from Texas, *A. bracteata* and the subspecies *A. neglectula maritima* from Mexico are new, and the male of *A. edentata* is described for the first time; *A. neglectula* is raised from synonymy, and *A. aurata* of recent authors has been divided so that most of the specimens from north of the Gulf Coast states are placed in *A. persimilis*. Other species treated are *A. pomoniella, A. gratiosa* and *A. striata*. Regional as well as individual variations are treated in detail since there is considerable morphological intergradation among females of some species.

INTRODUCTION

Although bees of the genus *Augochlorella* (Halictidae) are common over much of the United States, their interspecific relationships and biologies are little understood. This paper is a result of a study of interspecific relationships of the two species of *Augochlorella* occurring in the vicinity of Lawrence, Kansas. Females of the two species, *persimilis* and *striata*, could not be satisfactorily distinguished and preliminary biological observations indicated little or no difference between them. In order to understand the nature of the variations and intergradations occurring between these two, all species occurring within the United States were examined. They are redefined and illustrated, keys for their identification are provided, and variations within species analyzed.

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For those investigators who are interested chiefly in the species occurring in a certain area, primary use should be made of the Regional Account of the Species. Other sections to be consulted include the discussion of the genus, the section on terminology, the keys to the species and under the Species Accounts, parts on comparisons with other species and seasonal activity.

For those interested primarily in studies of variation, special attention should be given to sections on Specific and Other Characters, Terminology, Species Groups and under the Species Accounts, parts on comparisons and variation. The regional account should also be of value.

Augochlorella is a genus of bright metallic blue or green bees. As in most halictines, the species are morphologically variable and are in many cases difficult to distinguish. Therefore, special attention is given to the nature and extent of variations within and among species. Since other species, not being considered in this work, occur in Mexico, Central and South America, a complete analysis cannot be attempted until all species have been studied, preferably both biologically and morphologically. Eight species are treated here; seven occur north of Mexico, the other is from Mexico and Central America.

The more than 14,000 specimens examined in this study were obtained from a total of 50 private and institutional collections (Table 1). In addition to the pinned material, 414 specimens were examined from 134 nests excavated near Lawrence, Kansas, and the variation compared with that of populations throughout the country.

TABLE I. Collections studied.

Code No.	Collection
1	University of Arizona, Tucson.
2	University of Arkansas, Fayetteville.
3	California Academy of Sciences, San Francisco.
4	University of California, Berkeley.
5	Los Angeles County Museum, Los Angeles, California.
6	P. H. Timberlake Collection, Riverside, California.
7	University of Colorado Museum, Boulder.
8	Colorado State University, Ft. Collins.
9	United States National Museum, Washington, D.C.
10	State Department of Agriculture, Gainesville, Florida.
11	University of Georgia, Athens.
12	Fattig Collection, University of Georgia, Athens.
13	Chicago Natural History Museum, Chicago, Illinois.
14	Illinois Natural History Survey, Urbana.
15	Robertson Collection, Illinois Natural History Survey, Urbana.
16	Purdue University, Lafayette, Indiana.
17	Indiana University, Bloomington.
18	Iowa State University, Ames.
19	Kansas State University, Manhattan.
20	University of Kansas, Lawrence.

Code No.	Collection
21	Carl W. Rettenmeyer Collection, Kansas State University, Manhattan.
22	Museum of Comparative Zoology, Cambridge, Massachusetts.
23	University of Massachusetts, Amherst.
24	R. R. Dreisbach Collection, Michigan State University, East Lansing.
25	Michigan State University, East Lansing.
26	University of Minnesota, St. Paul.
27	University of Missouri, Columbia.
28	University of Nebraska, Lincoln.
29	David W. Ribble Collection, University of Nebraska, Lincoln.
30	Rutgers, The State University, New Brunswick, New Jersey.
31	Cornell University, Ithaca, New York.
32	American Museum of Natural History, New York City, New York.
33	North Carolina State, Raleigh.
34	North Dakota Agricultural College, Fargo.
35	University of North Dakota, Grand Forks.
36	Ohio State University, Columbus.
37	Oklahoma State University, Stillwater.
38	Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania.
39	Carnegie Museum, Pittsburgh, Pennsylvania.
40	South Dakota State College, Brookings.
41	University of Tennessee, Knoxville.
42	Alvin F. Shinn Collection, Oak Ridge, Tennessee.
43	Utah State University, Logan.
44	George E. Bohart Collection, Utah State University, Logan.
45	Brigham Young University, Provo, Utah.
46	Milwaukee Public Museum, Milwaukee, Wisconsin.
47	University of Wisconsin, Madison.
48	British Museum (Natural History), London.
49	Canadian National Collection, Ottawa.
50	Naturhistorisches Museum, Wien, Austria.

The genus *Augochlorella* was proposed (with the type species *Augochlora gratiosa* Smith) by Sandhouse (1937) in a revision of an assemblage of forms that had previously been included in the genus *Augochlora*. Prior to the revision by Sandhouse, all green halictines except *Agapostemon* were commonly referred to *Augochlora*, including forms now placed in *Augochlora*, *Augochloropsis* and *Augochlorella*. [For synonymies of these genera, see Sandhouse *(op. cit.)*.] I am not certain of the status of *Pereirapis* Moure, which was synonymized with *Augochlorella* by Michener (1954). Since the species included in *Pereirapis*, except for *edentata* (see Species Groups), are distinctly different from those of the north and are separated from each other by entirely different characters, I feel that they form a legitimate group which should perhaps be recognized at the subgeneric level.

Moure (personal communication, 1961) has included the following species in the *Pereirapis* group: *A. bidentata* Michener, *A. cerasis* (Vachal), *A. chrysaspis* (Vachal), *A. edentata* Michener, *A. phoenicis* (Vachal), *A.*

semiauratus (Spinola) [=*A. titania* (Smith), *A. hypixis* (Vachal)], *A. seminigra* (Cockerell) (=*P. rhysophila* Moure) and *A. simotes* (Vachal). He has also indicated that the following Central and South American species are to be placed in *Augochlorella* proper: *A. cladopyga* (Cockerell), *A. comis* (Vachal), *A. ephyra* (Schrottky) [=*A. traumatias* (Vachal), *A. ictis* (Vachal) and *Oxystoglossidia uraniella* Moure], *A. iopoecila* Moure, *A. iphigenia* (Holmberg), *A. michaelis* (Vachal) (=*Oxystoglossidia uranioides* Moure), *A. tredecim* (Vachal), *A. urania* (Smith).

SOME DIAGNOSTIC CHARACTERS

The genus can be distinguished from the other genera of green halictines occurring north of Mexico by the key below. A detailed description was given by Sandhouse (1937) and modified by Michener (1954). The following account, therefore, is brief and presents only the most diagnostic and readily visible characters by which *Augochlorella* can be distinguished from the other nearctic halictines of similar appearance.

HEAD: *The epistomal suture* (Fig. 2, *es.*) in *Augochlorella* and *Augochloropsis* extends ventrolaterally on each side of the clypeus to the level of the mandibular base where it angles abruptly laterally. In *Augochlora* and most *Agapostemon* it loops below the level of the mandibular base into the clypeal area, thus forming a lobate extension of the paraocular area (Fig. 1).

The *clypeus* is flattened in *Augochlorella* but with the apical half beveled or at a slight angle to the upper half. Females have the beveled portion brown or black with large, coarse, well separated punctures. The upper half is metallic green or blue with smaller punctures of varying sizes. In *Augochlora* the clypeus is flat, or the beveling is not noticeable since the entire surface is green except for a narrowly black apical edge. In *Augochloropsis* the clypeus is protuberant and rounded, sometimes slightly darkened medially at the apex. The clypeus of *Agapostemon* is similar to that of *Augochlorella* except for the ventrolateral or lobate extensions of the epistomal suture.

The vertex in *Augochlorella* is short, about equal to the oculo-ocellar distance, and abruptly angled or declivous between the posterior ocelli and the occipital carina (Fig. 5). In *Augochlora* this area is broadly rounded and longer than the oculo-ocellar distance (Fig. 3). In *Augochloropsis* the vertex is long and sharply angled so that the occipital carina is usually hidden from

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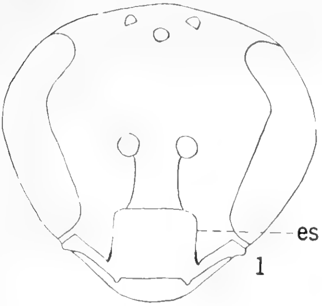
FIGS. 1-2. Front view of head. Fig. 1, *Augochlora*; Fig. 2, *Augochlorella*; *es:* epistomal suture.

FIGS. 3-5. Side view of head. Fig. 3, *Augochlora*; Fig. 4, *Augochloropsis*; Fig. 5, *Augochlorella*.

FIGS. 6-9. Forewings. Fig. 6, *Augochlorella*; Fig. 7, *Augochlora*; Fig. 8, *Augochloropsis*; Fig. 9, *Agapostemon*.

FIGS. 10-11. Body measurements. Fig. 10, a, width of head; b, length of clypeus; c, width of clypeus; Fig. 11, a, length of metanotum; b, length of propodeum.



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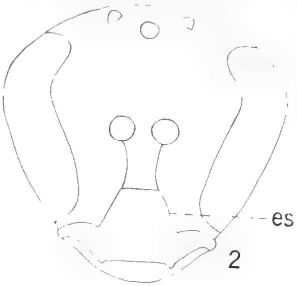

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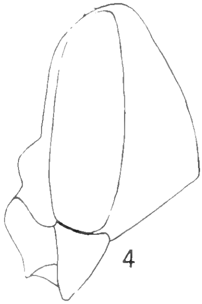

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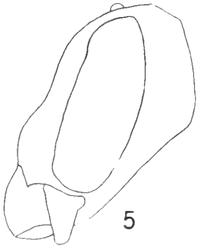

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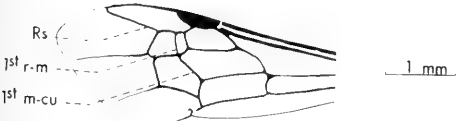

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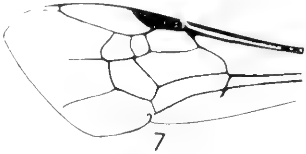

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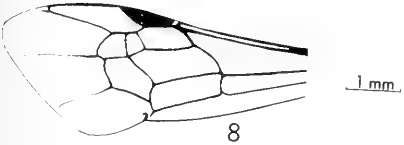

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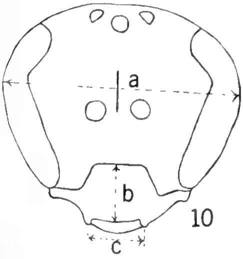

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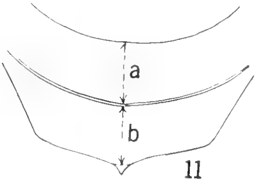

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above except when the head is strongly depressed (Fig. 4). In *Agapostemon* the vertex is similar to that of *Augochlorella*.

THORAX: The posterior vertical surface of the propodeum of *Agapostemon* may be distinguished from that of all the other genera by the key character given below.

The marginal cell of the forewing in *Augochlorella* is pointed at the wing margin (Fig. 6), whereas in the other three genera it is narrowly truncate at the tip or bent away from the margin of the wing. In *Augochlora* and some *Agapostemon* and *Augochloropsis* the lower vein of the marginal cell (*Rs*, Fig. 7) extends beyond the tip of the cell.

KEY TO GENERA OF GREEN HALICTINES OF THE UNITED STATES

1. Body surface strongly sclerotized with large, deep punctures, similar to that of chrysidids; female without scopa .... *Temnosoma*
— Body surface not as above; females with scopa on hind legs 2
2. Posterior vertical surface of propodeum enclosed by a strong carina; first recurrent vein (1st m-cu) basad of 1st r-m (Fig. 8) .... *Agapostemon*
— Posterior vertical face of propodeum not enclosed by a carina; first recurrent vein interstitial with 1st r-m (Fig. 6) 3
3. Epistomal suture forming deep loop into clypeal area, extending below level of base of mandible (Fig. 1) .... *Augochlora*
— Epistomal suture forming right angle, bending laterally at level of mandibular base (Fig. 2) 4
4. Marginal cell pointed on margin of wing (Fig. 6); inner hind tibial spur of female serrate; metasomal terga without fringe of long apical hair .... *Augochlorella*
— Marginal cell either truncate and appendiculate apically or pointed below margin of wing (Fig. 9); inner hind tibial spur of female pectinate 5
5. Tegula with inner posterior angle lobate; pronotum with dorsal edge carinate or lamellate; apical margins of metasomal terga green, usually with fringe of simple, apical hairs .... *Augochloropsis*
— Tegula oblong, not lobate posteriorly; pronotum with dorsal edge rounded or angulate; apical margins of metasomal terga black, without fringe of apical hairs .... *Pseudaugochloropsis*

TERMINOLOGY

Terminology for all morphological structures follows that of Michener (1944) unless otherwise stated. In the interests of simplicity and conservation of space, certain terms have been used in the descriptions and discussions of variation which may seem vague; they have been used, however, in precise ways as explained below:

The body *surface*: the integument of a sclerite in general or the areas between punctures, striations or other specifically mentioned conformations when present; its degree of shininess and roughening are often significant characters.

Shininess: *polished*, absolutely smooth at magnifications used and highly reflective; *shiny*, reflective but not brilliant and not necessarily smooth; *dull*, not shining although sometimes appearing smooth at magnifications used.

Roughness: *smooth*, without obvious irregularities or unevenness; *granular*, with very small, round pits, usually regularly distributed, giving the illusion of raised bumps as on fine sand paper; *rough* or roughened, with a slightly irregular or uneven surface but without any obvious pattern to the unevenness; *rugose*, deeply roughened or wrinkled, often forming a regular pattern with the elevations and ridges occupying an area as large as or larger than the depressions; *areolate*, deeply rugose, forming a network of ridges with depressions occupying greater areas than the elevations or ridges.

The degree of roughening or punctation is described by the following adverbs in sequence starting with the least amount of roughening: *minutely*, *weakly*, *finely* and *coarsely*. An adjective when used by itself (i.e., "rough") describes a condition between fine and coarse.

Punctures distinct: This expression is used if each puncture is separated from every other puncture, with the outlines easily discernible. Punctures may be very close together but nevertheless easily rcognizable as individual punctures.

Punctures indistinct: This expression is used if the punctures are not easily recognizable as distinct entities and may be either shallow or minute and vaguely defined or may merge together.

Disc refers to the dorsal area of the propodeum only. *The edge of the disc* refers to the angle formed between the dorsal and posterior surfaces of the propodeum. It grades from sharp or weakly carinate to gradually rounded. The *shape* or *outline of the disc* is the pattern formed by the edge of the disc when viewed from above.

Form refers only to particular variants in the species *striata*.

METHODS

Equipment. All specimens were examined under 40× magnification of a dissecting microscope. A 100 watt incandescent bulb was used when recording body sculpturing. A microscope light with blue filter was used to view the color of body and pubescence.

All photographs were taken at the same magnification and those appearing in any one plate are reproduced at the same magnification.

Measurements were made by means of an ocular micrometer at 40×

magnification. In all cases, the specimen was aligned so that both extremities of the structure being measured were in focus and a maximum measurement obtained of the distance between them.

Synonymies. In the synonymy of each species all known references are given, with annotations indicating the content as follows: descriptions or descriptive comparisons with other species (descr.), distributional records (distr.), flower records (fl.), keys (key), annotated or unannotated lists of species such as catalogues or regional compendia (list), and taxonomic treatments usually including keys, distributions, descriptions, etc. (tax.). Secondary references to synonymies in catalogues or taxonomic treatments are not included. Certain authors (Rau, 1922) have confused species of *Augochlorella* with *Augochlora pura*. References published under specific names of *Augochlorella* (e.g., *striata*) but known to refer to *Augochlora pura* are of course omitted from the synonymies.

Types. The type (holotype or lectotype) has been seen for each species unless otherwise noted.

Descriptions. With the exception of *persimilis* and *striata*, all specimens of a species were examined for all characters. During the course of the study all but those characters finally used in the descriptions were eliminated, usually because they were found to have little or no diagnostic value. The genitalia of about 50% of the males of each species, from localities throughout the range, were examined.

Because of the large number of specimens of *striata* and *persimilis*, the descriptions and detailed examinations of these species were made from a sample of about 50 specimens, mostly from one state. Samples from all other states were then compared with the description, and corrections and variations noted. Every specimen in both species, both male and female, was critically examined with regard to all propodeal characters and metasomal punctures and for the basitarsal hair of males. Other characters received attention commensurate with their diagnostic value. For variable characters in *persimilis*, enough specimens were examined to determine the extent of the variation and the distribution of the variants. For *striata*, variation was studied by recognizing several lettered "forms." The details are indicated in the discussion of that species.

Variations. An attempt has been made to indicate as closely as possible the range of variation of each character in each species. Whenever practical, particular specimens have been cited to illustrate certain variational features, or percentages are given if large numbers of individuals are involved. Particular specimens are identified by their label data followed by the code numbers, in parentheses, of the collections in which they are located (see Table 1).

In the section on regional variation all species occurring within each geographical area are compared.

Although much attention has been paid to the problem of variation in this group, this is not primarily a study of variation and at least in one species, *striata*, a considerable amount of work, both analytical and statistical, still needs to be done before a complete understanding can be achieved.

Distributions. Although a complete list of all label data has been made, and may be obtained from the author, localities are listed in this paper only by counties and are indicated on maps. Specific localities are given where the counties are large with widely varying habitats. Only those specimens that have been examined are recorded (unless otherwise specified). Records from the literature are omitted due to the unreliability of specific determinations.

For economy of space, listing of localities is omitted in whole or in part for certain common eastern species. Localities are shown approximately by the maps, and counties are listed by Ordway (1965).

Seasonal Activity. The data on this topic were obtained from pinned material unless otherwise noted. Dates given for seasonal activity are those on which collections were made and do not necessarily represent the entire season of the bees' activity.

Flower Records. Flower records were taken from the literature and from labels on pinned specimens but not from laboratory observations since host plant preferences in the laboratory are shown to have little correlation with those in the field under natural conditions (see Ordway, in press). The records listed under each species show the flowers on which bees were found without regard to the sex of the bee or to whether the bee was collecting pollen or nectar, since this information is usually not available. All flower names have been checked and the appropriate synonymies made according to the following references: Fernald (1950), Gould and Thomas (1962), Kearney and Peebles (1951), Munz (1959), Smith (1933) and Index Kewensis (1895-1955).

SPECIFIC CHARACTERS

Nearly all of the specific characters vary in a continuous manner, so that it is difficult to categorize the differences within and among species. Many of the characters are self explanatory but others require explanation and are discussed below. Some of these characters are of no value in distinguishing the North American species from one another but are of value in distinguishing certain neotropical species.

Body color. Coloration throughout the range of the species is extremely variable. The usual color is a bright green, but specimens may range from bronzy or yellowish green to a deep violet-blue. Blue specimens are found only in Florida. The part of the body with the greatest color variation is the metasoma where coloration is often incomplete, allowing various amounts of brown to show through, so that in some specimens this area looks brown with metallic reflections. Of the species considered in this paper, only the males of *edentata* have the metasoma consistently and naturally brown. It was found that in dried specimens, normally testaceous color (pale yellow-white) structures may in some specimens turn orange due to ageing or other factors. This condition has not been found in live or freshly killed bees.

The metallic color is structural and can be altered artificially by various environmental conditions or chemicals. Limited tests have shown that dried bright green bees turn blue-green to blue within five minutes in ethyl acetate (liquid) and that on drying, the bees stay blue-green. If they are then put into water the bright green color slowly returns. Bees preserved in alcohol or in Dietrich's or Carnoy's solutions remain green, but dry, bright green or yellow-green bees turn coppery-green to reddish in an atmosphere containing phenol (as in a relaxing chamber). Depending on the concentration and exposure time, the altered color may remain after the specimen has redried.

Chemicals may affect the coloration of insects found in collections. The color of live bees may be determined or influenced during the pupal stage by atmospheric or soil moisture. Specimens of *Augochlorella* found in Florida are uniformly darker green than they are to the north but it is not known whether the bright blue individuals, frequently found in collections from Florida, actually are this color in nature. Many of the blue specimens were collected by Graenicher. It is possible that he and some other collectors in Florida used acetate killing jars, thus changing the color of the bees. Some *persimilis* were reared in the laboratory in wet soil. Emerging females were usually a dark green but one blue individual was produced. The males produced were mostly the yellow-green color typical of both sexes of this species in Kansas. The blue reflections found on the frontal area of the head in some species appear to be a natural phenomenon with variation only in the intensity.

Size. Total body length, although inexact, gives a rough indication of the overall length and is given for comparison with species described by earlier workers. When a wide variation of lengths occurs the extremes are given. All measurements are made on individuals with bodies in extended positions. Width of the head is a more standard and reproducable measurement and has been shown (Michener and Lange, 1958), at least for *Lasioglossum rhytidophorum*, to be highly correlated with other body measurements such as wing length and thoracic size. Both in *A. striata* and *persimilis* a high correlation (r values significant at $< .01$) was also found between the width of the head and length of the wing with r values of .65 and .55 in *striata* and *persimilis* respectively (see Ordway, in press, a, for full discussion of variation). Head width was measured across the widest part of the face, at about the level of the ocular emargination (Fig. 10a). When available, at least 50 males and 100 females of each species were measured from throughout its geographic range, representing as wide a span of collecting dates as possible. An effort was made to include all size extremes. In *striata*, all "forms" were lumped together. Wing length was not used, as it is a difficult and unreliable measurement on dried material. The width-to-length relationship of the head is given as an indication of the shape of the face. Bees in which the length of the head is greater than the width have a face that appears long (Fig. 52); when the length is equal to the width (± 0.4 mm), it appears round (Fig. 53), and when the width is greater than the length, the face appears wide (Fig. 54). In some species the shape of the face is relatively constant; in others it is variable. The length of the face was measured from the apex of the clypeus to the vertex, with the head positioned so as to give a maximum measurement and with the distance being determined when both extremities were in focus. It is a poor measurement to use by itself, as it is frequently inexact or cannot be reproduced exactly on the same specimen. However, as a comparison with the width (greater than, equal to or less than), it is quite usable, and the same proportions may be obtained after multiple readings.

Clypeus. The clypeus in all species studied is largely green or similar in color to the rest of the head. In males, the apex is narrowly testaceous medially, slightly more extensively so at the lateral corners. In females the apex of the clypeus is nonmetallic brown or black, the extent of the nonmetallic area being variable within and among species. The length (Fig. 10b) is usually equal to or slightly greater than the width (Fig. 10c) in both sexes. The size and spacing of the punctures on the clypeus usually varies within species although some species have a more uniform pattern than others.

Supraclypeal area. This area is slightly convex and looks protuberant in all species except *edentata*. This protuberance is due more to depression of the epistomal suture and antennal sockets than to an elevation of the area itself. In *edentata* and some other neotropical species, there are scarcely any depressed areas so that the entire face looks broadly and evenly convex.

Tegula. The length to width ratio of the tegula differs among species. In all species unless otherwise noted, this structure is oval, shiny and smooth, transparent to pale yellowish anteriorly, becoming darker posteriorly and dark brown, usually with metallic reflections, along the proximal edge. The anterior part is usually minutely pilose.

Propodeum. The characters of the propodeum are highly variable. All variation is more or less continuous so that there are rarely distinct gaps separating species, and yet these characters are still the most diagnostic for distinguishing species, especially in the females. The length of the disc (the dorsal area) is measured along the median line from the anterior carina separating the metanotum and propodeum, to the posterior margin of the disc. When the posterior margin forms a sharp V medially, the posterior edge is assumed to be evenly rounded and the tip of the V is omitted from the measurement (Fig. 11b).

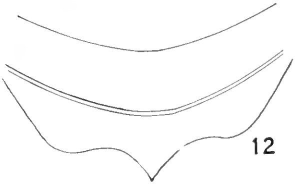
The outline or shape of the disc is classified into four categories, although all gradations occur among these. The "bracket" shape ({) is perhaps the most distinctive (Figs. 12-14, 57, 58) and is characteristic of *gratiosa*, *aurata* and some *striata*. The posterior edge comes to a point or V medially, slopes laterally to the posterolateral corners of the propodeum, then angles abruptly anterolaterally. The V-shape is similar but without the distinctive angulation at the posterolateral corners. The V may be deep, so that the length of the disc is considerably longer medially than at any other point, as in some *striata* B (Figs. 15, 63), or it may be shallow or "obtuse" with the length of the disc essentially equal throughout (Fig. 59). In addition, the posterior edge may be sharply pointed medially (Fig. 12) or blunt and rounded (Fig. 14), or may extend posteriorly in the plane of the rest of the disc or be depressed onto the posterior vertical propodeal surface (Fig. 63). The U-shape (Figs. 16, 62) lacks the medial V and is evenly rounded posteriorly. The length of the disc is greater medially than laterally. The semicircular shape is similar to the U-shape but is shorter in relation to its width, with shorter, more rounded posterolateral corners (Figs. 18, 64). Gradations among all shapes occur (Figs. 17, 65). Relationships of the different shapes are diagrammed in Figure 19.

The sharpness of the edge and the flatness of the disc is indicated by the profile type. In type 1 (Figs. 20, 21), the edge of the disc is weakly or sharply angulate to carinate and slightly elevated, giving the disc a concave appearance in profile. In type 2 (Fig. 22), the edge is abruptly rounded, not elevated, and distinct when viewed from the top. The surface of the disc is flat. In type 3 (Fig. 23), the edge is rounded but slightly prominent or thickened, so that although the edge is definite when viewed from above it is not as distinct as in type 2. Type 4 has a gradually and smoothly rounded edge (Fig. 24) without any demarcation between the dorsal and vertical surfaces. Type 5 (Fig. 25) includes only *pomoniella* and combines characteristics of types 3 and 4. The edge of the disc, although gradually and smoothly rounded, is at the same time prominent and somewhat elevated. The dorsal surface of the disc is therefore slightly concave, a feature that is evident both from the top and from the side.

FIGS. 12-18. Diagrams showing shapes of propodeal disc. Figs. 12-14, bracket-shaped; Fig. 12, *A. gratiosa*; Fig. 13, *striata* A; Fig. 14, aurata. Fig. 15, V-shaped, *striata* D. Fig. 16, U-shaped, *pomoniella*; Fig. 17, U-shaped, *edentata*. Fig. 18, semicircular, *bracteata*.

FIG. 19. Relationship of disc shapes: v, V-shaped; s, semicircular; u, U-shaped.

FIGS. 20-25. Diagrams showing profiles of thorax. Fig. 20, *A. striata* A, type 1; Fig. 21, *gratiosa*, type 1; Fig. 22, *aurata*, *persimilis*, *bracteata*, type 2; Fig. 23, *striata* B, D, *neglectula*, type 3; Fig. 24, *striata* C, *edentata*, type 4; Fig. 25, *pomoniella*, type 5.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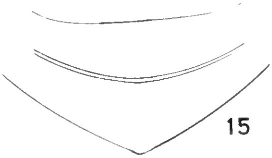
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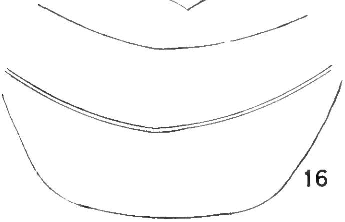
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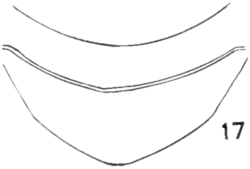
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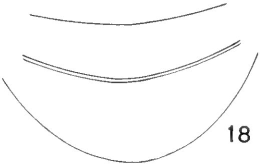
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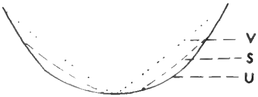

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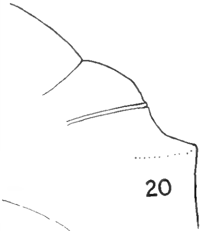
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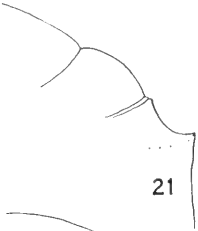
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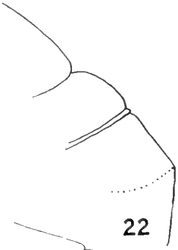
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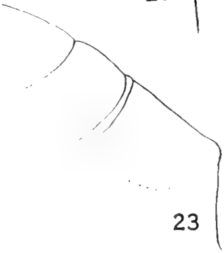
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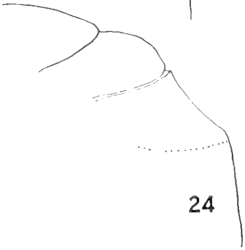
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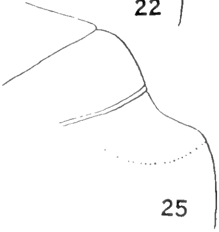
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When the striae do not reach the posterior edge of the disc or the edge is unclear as in profile type 4, the surface of the disc beyond the striae may be variously marked with granulations (Fig. 62), fine ridges (Fig. 66) or minute transverse lines or reticulations (Figs. 67, 69, 70); each type of surface is characteristic of certain species.

The posterior vertical surface of the propodeum is also variously sculptured in the different species, grading from smooth and shiny with minute punctures (Fig. 73) to smoothly granular (Fig. 74) to roughened and rugose (Fig. 75). There is some variation within species, particularly among the forms of *striata*, but in general each species is characterized by a certain type of sculpturing.

Metasoma. Because the first abdominal segment is incorporated into the thorax, segments of the apparent abdomen are numbered from one on and are called metasomal segments. Numbered terga and sterna always refer to these metasomal segments.

The size and density of punctures on the first and second tergum are variable within and among species in both males and females, sometimes varying geographically. The punctures may be distinct and regular or they may be indistinct, irregular or variable in size and spacing. The third and following terga in all species studied are densely and minutely punctured, with the punctures inconspicuous and blending together giving the surfaces of the terga a minutely reticulate appearance. The apices of the terga are narrowly margined with brown in all species. The sterna of both males and females are brown, with long hair on at least the apical halves. In females this hair is longer than in males and is frequently used by the bee as part of the scopa. In addition to color variations noted in a previous paragraph, the first and second terga may show dull, discolored areas on the dorsal median surface. This is due to a waxlike secretion from this area (Fig. 56) that leaves the otherwise shiny surface dull. The nature and function of this secretion is not known, but it occurs only in females of all species of *Augochlora* and *Augochlorella* examined. It is not found on fresh, young (entirely unworn) specimens but the discoloration, if not the waxlike substance itself, may be found on most older specimens.

Pubescence. Over most of the dorsal part of the body there are two types of pubescence, the long, simple or branched hairs usually referred to as the pubescence or hairs and exceedingly short, fine, highly plumose pubescence

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FIGS. 26-28. Male genital capsule of *Augochlorella striata.* Fig. 26, dorsal view; Fig. 27, ventral view (l_1: inner lobe of gonostylus; l_2: outer lobe of gonostylus; gn: gonostylus); Fig. 28, side view of genital capsule.

FIGS. 29-30. Male genital capsule of *Augochlorella seminigra.* Fig. 29, dorsal view; Fig. 30, ventral view.

FIGS. 31-36. Lobes of the gonostyli. Fig. 31, *A. bracteata*; Fig. 32, *striata*; Fig. 33, *persimilis*; Fig. 34, *gratiosa*; Fig. 35, *pomoniella*; Fig. 36, *edentata.*

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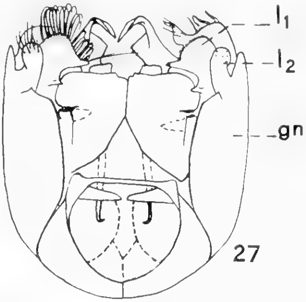

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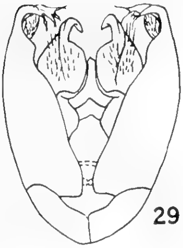

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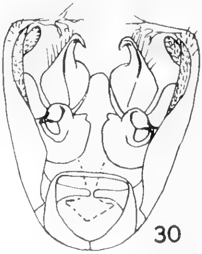

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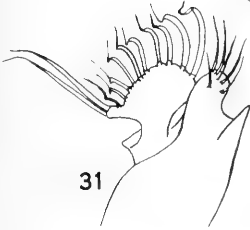

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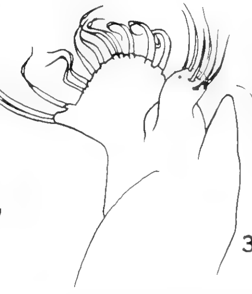

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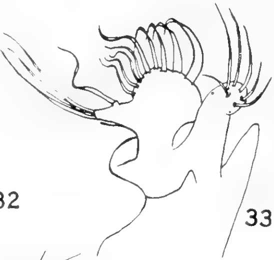

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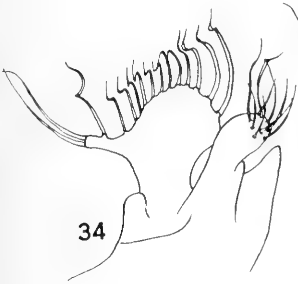

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not visible except when the longer hairs have been worn away and the surface is seen in profile. This latter pubescence is white in *Augochlorella* and may be rather dense in unworn specimens, especially on the head, posterior surface of the propodeum and metasoma. The longer hairs are white to golden-white, depending on the region of the body and on the individual specimen.

Male genitalia. The male genital capsule (Figs. 26-28) is basically similar for all Nearctic species but differs significantly in structure from that of *A. seminigra* of the *Pereirapis* group (Figs. 29-30). The only specifically variable structure on the capsule is the inner lobe of the gonostylus (l_1, Fig. 27). This lobe is essentially similar in all the eastern species (*aurata*, *striata*, *gratiosa*, *persimilis* and *bracteata*) (type 1, Figs. 31-34) but is distinctive for each of the remaining western and Mexican species (types 2-4, Figs. 35-39). In type 1, considerable variation occurs within species in the length of the attentuated, finger-like projection, the number of long setae, and the roundness and slope of the apical portion of the lobe. There are average differences in shape among the species, as seen in Figs. 31-36, but these differences are not constant and cannot be used as diagnostic characters. The number of setae is not constant but averages about 10 on the rounded portion of the lobe and 2 to 3 on the attenuation. The outer lobe (l_2, Fig. 27) is similar for all type 1 species and varies little except for the number of long, unbranched setae. The genitalia of the remaining (western and Mexican) species are described under those species.

Hidden sterna. Only three structural types are recognized among the eight species studied (Figs. 40-42), with all eastern species and *neglectula* belonging to type 1. Slight individual variations occur in type 1 (Fig. 40) that involve the degree of sclerotization, the shape of the apex, and the number and position of setae on the seventh sternum. The central thickening appears to be absent in *neglectula*. In *pomoniella* (Fig. 41), the sterna differs by the presence of a variably shaped knoblike median projection on the eighth sternum, by the minute setose projections on the distal arms, by the apparent lack of central thickening and the consistent lack of apical setae on the seventh sternum. In *edentata* (Fig. 42) the structure of the eighth sternum is similar to that of the eastern species, but the seventh sternum is elongate and truncated apically.

Eighth tergum. This tergum is hidden, mostly membranous, internal, usually closely adherent to the seventh tergum and attached by weakly sclerotized arms to the eighth sternum. There is a row of spiculate, finger-like pro-

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FIGS. 37-39. Lobes of the gonostylus of *A. neglectula*. Figs. 37-38, *n. neglectula*; Fig. 39, *n. maritima*.

FIGS. 40-42. Hidden metasomal sterna, a: sternum 7, b: sternum 8. Fig. 40, type 1, *A. striata*; Fig. 41, type 2, *pomoniella*; Fig. 42, type 3, *edentata*.

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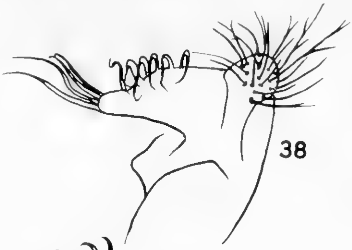

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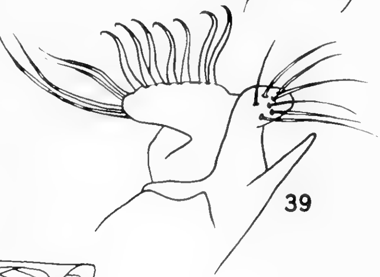

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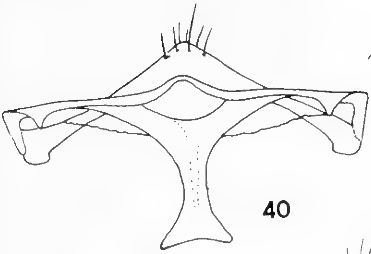

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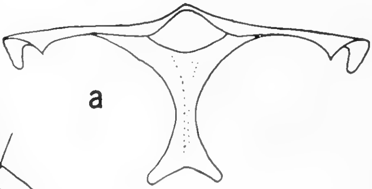

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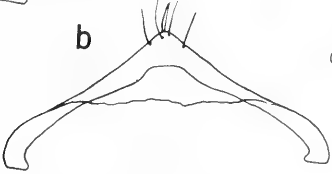

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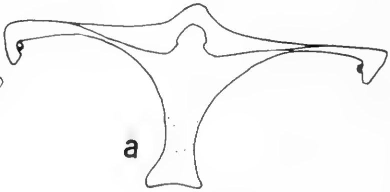

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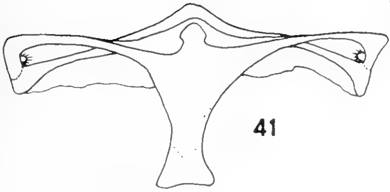

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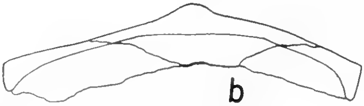

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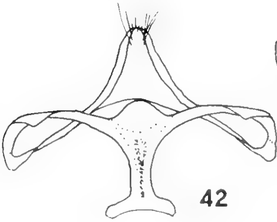

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jections along the anterior (inner) edge when the sclerite is in its normal inverted position (Fig. 43). However, this whole structure may be everted, in which case the projections extend posteriorly to the outside (Figs. 44, 45). There are differences among species in the number, shape and spacing of the finger-like projections. All the eastern species as well as *pomoniella* belong to type 1 (Fig. 43) characterized by 10 to 14 closely arranged, densely setose projections with the entire tergum minutely setose. The projections are sometimes branched at the tips in *gratiosa*. In *neglectula* (Fig. 46) there are 8 to 9 short, thin, widely separated, and sparsely, minutely and inconspicuously pubescent projections. The membrane appears finely pubescent laterally but bare medially. In *edentata* (Fig. 47) the projections number 12 to 14 are long, thin and very sparsely setose. The arms are minutely pubescent, but the transverse part appears bare. The differences noted here are easily observable under 200× magnification of a compound microscope. Differences in the shape of the tergum, length and shape of the lateral arms, presence and location of punctures and arrangement and pattern of the pubescence are not considered of diagnostic value because of the fragile nature and eversibility of the entire structure. The eighth tergum is most easily removed with the genital capsule and seventh and eighth sterna to which it is attached.

OTHER CHARACTERS

Other characters were studied and rejected because the characters were identical in all species, because they were too variable intraspecifically to have any meaning, or because the measurements or definitions were not precise or reproduceable. A total of 20 characters, most with multiple character states, were used in a factor analysis of differences between females of *persimilis* and *striata*. Although none of the characters was rejected on the basis of this study, it was shown that those characters deemed most useful in species recognition were indeed most highly correlated with the species (used in the analysis as one of the characters). These most useful characters were located in the propodeal area.

Characters studied but seldom or not found useful among the nearctic species are:

Head: Ratio of clypeal length to width; protuberance of clypeus and supraclypeal area, color and shape of labrum; degree of rugosity of frontal area; roughening of vertex; relations between upper interocular, the interocellar

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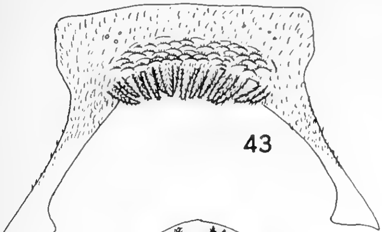
Figs. 43-47. Hidden eighth metasomal tergum. Fig. 43, *A. striata* (normal inverted position); Fig. 44, *gratiosa* (semi-everted); Fig. 45, *gratiosa* (everted position); Fig. 46, *neglectula*; Fig. 47, *edentata*.

Figs. 48-51. Male hind basitarsus, inner view. Fig. 48, *A. striata*; Fig. 49, *neglectula*; Fig. 50, *persimilis*; Fig. 51, *gratiosa*.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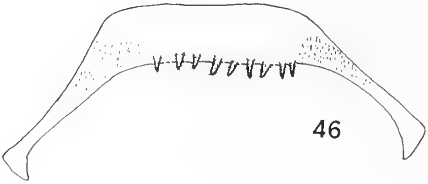
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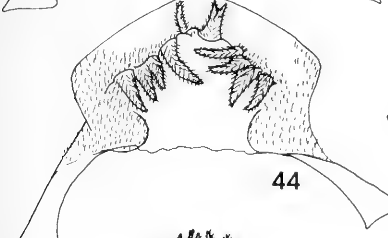
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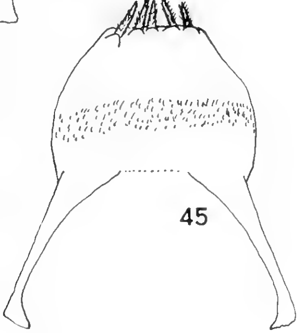
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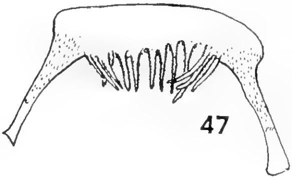
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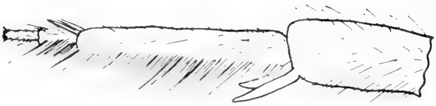
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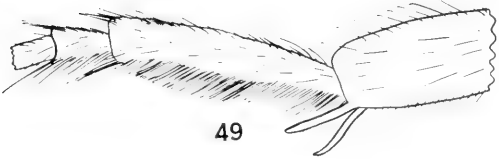
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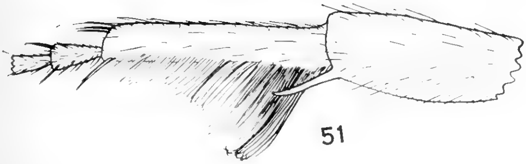
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and the ocellocular distances; smoothness, color and length of pubescence of genal area; antennal contrasts in color of different segments.

Thorax: The angle between the dorsum of the scutum and the slope of the propodeal disc; wing length; color, size, shape of the tegula; precise measurements and comparisons of size and spacing of punctures anteriorly, centrally, laterally and at anterolateral angles of the scutum; sculpture, color and smoothness of the scutellum; sculpture, color and smoothness of each part of the pleuron; size and spacing of the propodeal striations; ratio of dark to light areas on the femora and tibiae of the male; length to width ratios of the hind tibia and tarsal segments; color of the basitibial plate.

Metasoma: Detailed color variations of the terga; descriptions, measurements and comparisons of size and spacing of punctures and surface markings on all terga; punctures and lineations or other markings on the sterna; depth of the emargination of fourth sternum in males; comparisons of certain structures of the genital capsule of males—length of the attenuation of the inner lobe; roundness and height of the apex or crown of the inner lobe; spacing and number of setae on the inner lobe; shape, location and area of fusion of other lobes and processes on the gonostylus; comparison of profiles (side view) of the capsule.

SPECIES GROUPS

The Nearctic group of species (i.e., *Augochlorella s. str.*, not *Pereirapis*) includes both Neotropical and Nearctic species although only the Nearctic species are considered at this time. This group is divisible into eastern, western and southern subgroups, each showing certain distributional and morphological affinities. The only species included in this work from the southern subgroup is *edentata*, but there are undoubtedly other species to the south. The western or "*pomoniella* subgroup" contains *pomoniella* and *neglectula*. The eastern or "*striata* subgroup" consists of *aurata*, *striata*, *persimilis*, *gratiosa* and *bracteata*.

The *pomoniella* subgroup ranges from northern California southeast into Arizona and New Mexico in the United States and at least as far south as Costa Rica and Panama. The *striata* subgroup is found from south central and southeastern Canada through the eastern, midwestern and southern United States and as far west as Colorado and New Mexico. Except for *bracteata*, none of the included species ranges into Mexico.

Morphological characters separating the *striata* and *pomoniella* subgroups involve the shape of the fourth metasomal sternum of males (margin straight in *pomoniella* subgroup, emarginate in *striata* subgroup) and the shape of the inner lobe of the gonostylus of the male genital capsule. The degree of morphological variation occurring within the two groups is also significant.

These characters and their relationships among the species are discussed under each taxon. It is quite probable that significant biological differences may be found between the subgroups, but as yet, only the biologies of *persimilis* and *striata* are known (see Ordway, 1965a; in press).

The species of the eastern subgroup seem more closely related to each other than are the two species of the western subgroup. In the *striata* subgroup there is greater morphological variation and intergradation among the species and the male genitalia are all essentially alike. In the *pomoniella* subgroup the male genitalia differ, and there is comparatively little variation and virtually no intergradation between the two species.

The relationship of *edentata* to the northern *Augochlorella* and to the *Pereirapis* group is not clearly understood. The female appears to belong to *Pereirapis* and has been placed in that group by Moure. The male, however (previously undescribed), has clypeal and genitalic characteristics of the northern species but in other respects looks similar to *Pereirapis*.

SPECIES ACCOUNT

KEY TO THE SPECIES OF *Augochlorella*

This key must be used in conjunction with the regional keys and the section entitled Regional Discussion because of the wide variability within species and the continuous or intergrading nature of all characters. The key for females will not work for all specimens since intermediates are found among many of the species and forms. The term "disc" in all cases refers to the dorsal area of the propodeum.

FEMALES

1\. Striae of disc reaching edge posteriorly, i.e., with little or no unstriated area between ends of striae and edge of disc (Figs. 57-63) 2

— Striae of disc not reaching edge posteriorly, with distinct unstriated region between ends of striae and edge of disc (Figs. 64, 67, 69) 11

2\. Scutum coarsely punctate and strongly rugose anteriorly (Fig. 77) 3

— Scutum with small, distinctly separated punctures, finely roughened to weakly rugose anteriorly (Fig. 78) 9

3\. Striae of disc fine and close together; disc at least weakly bracket-shaped (Figs. 57, 58), length less than or only slightly longer than metanotum .... *aurata, gratiosa, striata* A (see regional keys)

— Striae of disc coarse, close together to widely separated; disc variably shaped, longer than metanotum .... *(striata)* 4

4\. Posterior edge of disc sharply angulate (Fig. 21) or abruptly rounded (Fig. 22); disc sharply pointed medially; length of disc less than 1.5 times that of metanotum (Fig. 60) .... *striata* A

— Posterior edge of disc gradually rounded or at most abruptly rounded, not sharply pointed medially, or if so, length more than 1.5 times as long as metanotum 5

5. Disc at least weakly bracket-shaped, length equal to or only slightly longer than metanotum (Fig. 71) .... *striata* D

— Disc V-shaped, U-shaped or semicircular (Figs. 16-19) 6

6. Disc obtusely and bluntly V-shaped (Figs. 15, 63), length 1.5 to 2 times that of metanotum .... *striata* B

— Disc U-shaped or semicircular, or if V-shaped then less than 1.5 times length of metanotum 7

7. Shape of disc semicircular or U-shaped; edge smoothly and gradually rounded posteriorly (Figs. 24, 62) without distinct difference in sculpture between dorsal and vertical surfaces .... *striata* C

— Shape of disc variable, posterior edge slightly raughened, abruptly angulate (Figs. 22, 23) or with distinct contrast in sculpture between dorsal and vertical surfaces 8

8. Disc roundly V-shaped with medial striae ending abruptly at posterior edge .... *striata* D

— Disc semicircular with striae ending gradually near posterior edge .... *striata* C

9. Shape of disc semicircular (Fig. 66); scutum with small, distinctly separated punctures, space between punctures smooth and shiny (Fig. 78) (Texas and Mexico only) .... *bracteata*

— Shape of disc at least weakly bracket-shaped (Figs. 57, 58); scutum with punctures irregular in size and shape, very close or contiguous with little or no smooth shiny space between (Fig. 81), giving scutum a slightly roughened appearance 10

10. Posterior vertical surface of propodeum finely and evenly granular or smooth (Fig. 74), length of disc equal to or slightly greater than length of metanotum .... *aurata*

— Posterior vertical surface of propodeum irregularly or coarsely granular with minute irregular ridges (Fig. 76), length of disc equal to or less than metanotum .... *gratiosa*

11. Scutum with small, distinct punctures, surface between punctures smooth, or minutely roughened and without distinct punctures (Figs. 78, 79) 12

— Scutum with surface rough, coarsely punctate or rugose, at least anteriorly .... *persimilis, striata* C, *neglectula, pomoniella* (see regional keys)

12. Antenna with yellow tip; scutum without distinct punctures (Fig. 79); propodeal disc more than 1.5 times as long as metanotum .... *edentata*

— Antenna with dark tip; scutum with close, distinct punctures (Figs. 78, 80); propodeal disc 1.5 times as long as metanotum or less 13

13. Striae occupying three-quarters the length of the disc or less as in Figure 69, with posterior edge of disc smooth and shiny .... *pomoniella*

— Striae occupying more than three-quarters the length of the disc, posterior edge roughened and dull 14

14\. Posterior vertical surface of propodeum finely and evenly granular or smooth; tegula shiny without distinct punctures .... *bracteata*

— Posterior vertical surface of propodeum roughened with horizontal rugae extending across posterolateral corners; tegula dull, with small but distinct punctures .... *neglectula maritima*

MALES

No attempt is made to separate males of *striata* into forms A to D, since only a few can be so classified. Differences among these forms, when present, are explained at the end of the description of *striata*.

1\. Fourth metasomal sternum with apical margin straight 2

— Fourth metasomal sternum with apical emargination 4

2\. Metasomal terga green or blue; first sternum with metallic reflections 3

— Metasomal terga brown; first sternum without metallic reflections .. *edentata*

3\. Posterolateral corner and lateral vertical surface of propodeum smooth, with punctures; frons without bluish reflections .... *pomoniella*

— Posterolateral corner and lateral vertical surface of propodeum rough or rugose, not punctate; frons with bluish reflections .... *neglectula*

4\. Hind basitarsus with erect hairs of two distinctly different lengths (exclusive of basal tuft), longest hairs at least twice as long as width of segment, usually curved at tips (Figs. 50-51) 5

— Hind basitarsus with erect hairs of similar lengths (exclusive of basal tuft), 1.5 times as long as width of segment or less; all hairs straight (Figs. 48-49) .... *aurata, striata, bracteata* (see regional keys)

5\. Basal third of hind basitarsus without long erect hairs; longest hairs on apical two-thirds about twice as long as width of segment (Fig. 50); last antennal segment similar in color to preceding segment, not entirely dark brown; fifth metasomal sternum without greenish reflections .... *persimilis*

— Basal third of hind basitarsus bearing long curved hairs, four times as long as width of segment (Fig. 51); least antennal segment entirely dark brown; fifth metasomal sternum with greenish reflections .... *gratiosa*

REGIONAL KEYS

If the user of the keys is directed to the Regional Keys by the main keys, he should select the region to which his specimens belong and continue keying at the appropriate couplet.

NORTHEAST (Canada, Maine, New Hampshire, Vermont, Massachusetts, Connecticut, Rhode Island, Pennsylvania, New York, New Jersey.)

FEMALES

From couplet 3: all specimens are *striata* A.

From couplet 11: all specimens are *striata* C.

Males

From couplet 4: all specimens are *striata.*

North Central (Ohio, Indiana, Michigan, Illinois, Kentucky, Kansas, Colorado, Wyoming, Nebraska, Iowa, Wisconsin, Minnesota, North Dakota, South Dakota, Montana.)

Females

From couplet 3: all specimens are *striata* A.

From couplet 11: intergrades occur throughout the region but particularly in Illinois, Indiana, Missouri, Nebraska and Kansas. Check regional discussion for description of variations.

Surface of disc beyond striae smooth; striae extending almost to posterior edge of disc (Fig. 68) .... *striata* c

Surface of disc beyond striae usually linearly roughened; striae extending about four-fifths or less the length of disc (Fig. 64) .... *persimilis*

Males

From couplet 4: all specimens are *striata.*

Southeast (Florida, Georgia, South Carolina, North Carolina, Virginia, West Virginia, Maryland, Delaware.)

Females

From couplet 3:

A. Posterior vertical surface of propodeum finely and evenly granular or smooth (Fig. 74); length of disc equal to or slightly greater than length of metanotum .... B

— Posterior vertical surface of propodeum irregularly or coarsely granular (Fig. 76); length of disc equal to or shorter than metanotum .... *gratiosa*

B. Striae of disc thick, regular, straight or slightly wavy (Fig. 60) .... *striata* A

— Striae of disc fine, close, irregular (Fig. 57) .... *aurata*

From couplet 11: nearly all specimens are *persimilis* from this area as *striata* c is not common and is usually large (more than 6 mm long) with characters not usually confused with those of *persimilis.* Neither one has been seen from Florida.

Striae of disc almost reaching posterior edge; surface beyond striae smooth and shiny or at most minutely reticulated (Fig. 68) .... *striata* c

Striae extending about three-fourths the length of disc medially, area beyond striae usually finely and linearly roughened parallel to edge of disc (Fig. 64) .... *persimilis*

Males

From couplet 4:

Striae of disc fine and close together (Fig. 57); scutum with small, distinct but crowded punctures, weakly rugose anteriorly .... *aurata*

Striae of disc coarse, widely or closely spaced (Figs. 59, 60, 63);

scutum smooth with large, widely spaced punctures or rough and coarsely punctate, coarsely rugose anteriorly .... *striata*

SOUTH CENTRAL (Texas, Louisiana, Mississippi, Alabama)

FEMALES

From couplet 3:

Posterior vertical surface of propodeum uniformly and finely granular (Fig. 74); length of disc equal to or longer than metanotum medially, striae straight or irregular and indistinct; apex of clypeus less than one-third brown; in Texas, first metasomal tergum strongly punctate (Fig. 82) .... *aurata*

Posterior vertical surface of propodeum roughly or irregularly granular (Fig. 76); length of propodeal disc equal to or shorter than metanotum, striae straight and regular (Fig. 58); clypeal apex more than or less than one-third brown; in Texas, first metasomal tergum finely punctate (Fig. 83) .... *gratiosa*

From couplet 11:

A. Posterior vertical surface of propodeum and posterolateral corners finely and transversely rugose; south-western Texas .... *neglectula*

— Posterior vertical surface of propodeum and posterolateral corners smooth and shiny or finely granular .... B

B. Striae extending almost to posterior edge of disc; surface beyond striae smooth or slightly irregular or roughened .... *striata* D

— Striae extending about three-fourths the length of disc; surface beyond striae usually linearly roughened .... *persimilis*

MALES

From couplet 4:

Scutum finely roughened anteriorly; posterolateral corners and lateral vertical face of propodeum punctate to weakly punctorugose .... *bracteata* (Texas only)

Scutum with anterior margin coarsely rugose to areolate; posterolateral corners and lateral vertical surface of propodeum rough to rugose .... *striata* (throughout the area)

WEST (California, Nevada, Utah, Arizona, New Mexico) and Mexico.

FEMALES

From couplet 3: none of these species range into this region.

From couplet 11:

A. Scutum with large, distinct, but close punctures; surface between punctures smooth; posterolateral corners of propodeum prominent, smooth and shiny (Fig. 69); posterior vertical surface of propodeum smooth, finely punctate (Fig. 73); striae of disc short, rarely extending more than two-thirds the length of the disc medially, surface beyond striae smooth and minutely reticulated (Fig. 69) .... *pomoniella*

— Scutum coarsely punctate; posterolateral corners of propodeum rough, dull, not prominent (Fig. 70); posterior vertical surface of propodeum finely roughened to weakly rugose (Fig. 75); striae of disc reaching about three-fourths the length of disc medially, surface beyond striae dull and granular .... B

B. Tegula shiny, oval, smooth, without distinct punctures .... *neglectula neglectula*

— Tegula dull, oblong, distinctly and roughly punctate (Mexico only) .... *neglectula maritima*

MALES

From couplet 4: all Mexican specimens are *bracteata;* all western specimens are *striata.*

Augochlorella pomoniella (Cockerell)

Augochlora pomoniella Cockerell, 1915, Pomona Jour. Ent. Zool. 7:232 (descr.); Cockerell, 1916, Pomona Jour. Ent. Zool. 8:51 (descr., distr.); Bray, 1917, Pomona Jour. Ent. Zool. 9:99 (list); Sandhouse and Cockerell, 1924, Proc. California Acad. Sci. (4)13:339 (distr., key); Cockerell, 1926, Ann. Mag. Nat. Hist. (9)18:624 (distr.); Cockerell, 1927, Pan-Pacific Ent. 3:162 (distr., descr.); Michener, 1936, Pan-Pacific Ent. 12:172 (distr.); Cockerell, 1937, Amer. Mus. Novitates 948:12 (distr.); Michener, 1937, Ann. Mag. Nat. Hist. (10)19:314 (descr.); Cockerell, 1939, Proc. California Acad. Sci. (4)23:429, 431 (distr., fl.); Cockerell, 1939, Bull. So. California Acad. Sci. 38:139 (distr.); Cockerell, 1941, Proc. 6th Pacific Sci. Congr. 4:289 (distr.); Linsley, MacSwain, Raven, 1963, Univ. California Pub. Ent. 33:44 (fl.).

Augochlora (Augochlorella) pomoniella pomoniella: Michener, 1951, *in* Muesebeck *et al.* U.S. Dept. Agr., Agr. Monogr. 2, p. 1125 (list).

Augochlorella pomoniella: Sandhouse, 1937, Jour. Washington Acad. Sci. 27:69, 71 (key, tax.); Michener, 1954, Bull. Amer. Mus. Nat. Hist. 104:55 (descr.); Linsley, 1962, Proc. 1st Internat. Sympos. on Pollination, Copenhagen 1960, p. 194 (fl.).

Augochlorella pomoniella pomoniella: Krombein, 1958, U.S. Dept. Agr., Agr. Monogr. 2, 1st suppl. p. 232 (list).

Augochlora utahensis Michener, 1937, Ann. Mag. Nat. Hist. (10)19:314 (descr.).

Augochlora (Augochlorella) pomoniella utahensis: Michener, 1951, *in* Muesebeck *et al.,* U.S. Dept. Agr., Agr. Monogr. 2, p. 1125 (list).

Types. Augochlora pomoniella, holotype female, from Aliso Canyon (2 miles from Laguna Beach) [Orange County], California (R. LaFollette) is in the collection of the U.S. National Museum. *Augochlora utahensis,* holotype female, from Rockville [Washington County], Utah, May 7, 1931 (I.

FIGS. 52-54. Shapes of heads of *Augochlorella.* Fig. 52, *neglectula,* longer than wide; Fig. 53, *persimilis,* as long as wide; Fig. 54, *pomoniella,* wider than long.

FIG. 55. Front view of head of *A. edentata.*

FIG. 56. First and second metasomal terga with waxlike exudate.


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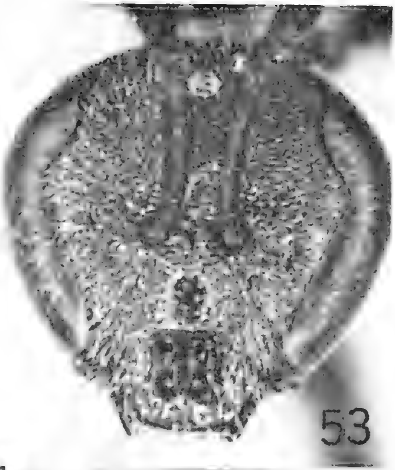
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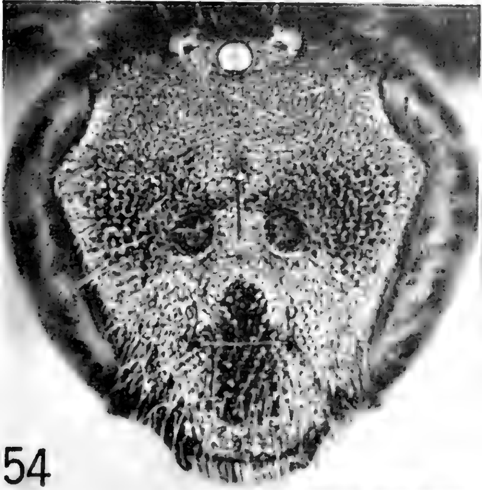
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FIG. 57. Propodeal disc of *A. aurata.*
FIG. 58. Propodeal disc of *A. gratiosa.*

FIG. 59. Propodeal disc of *A. striata* A from Florida.
FIG. 60. Propodeal disc of *A. striata* A from east coast (standard).

Fig. 61. Propodeal disc of *A. striata* c.
Fig. 62. Propodeal disc of *A. striata* c (standard).

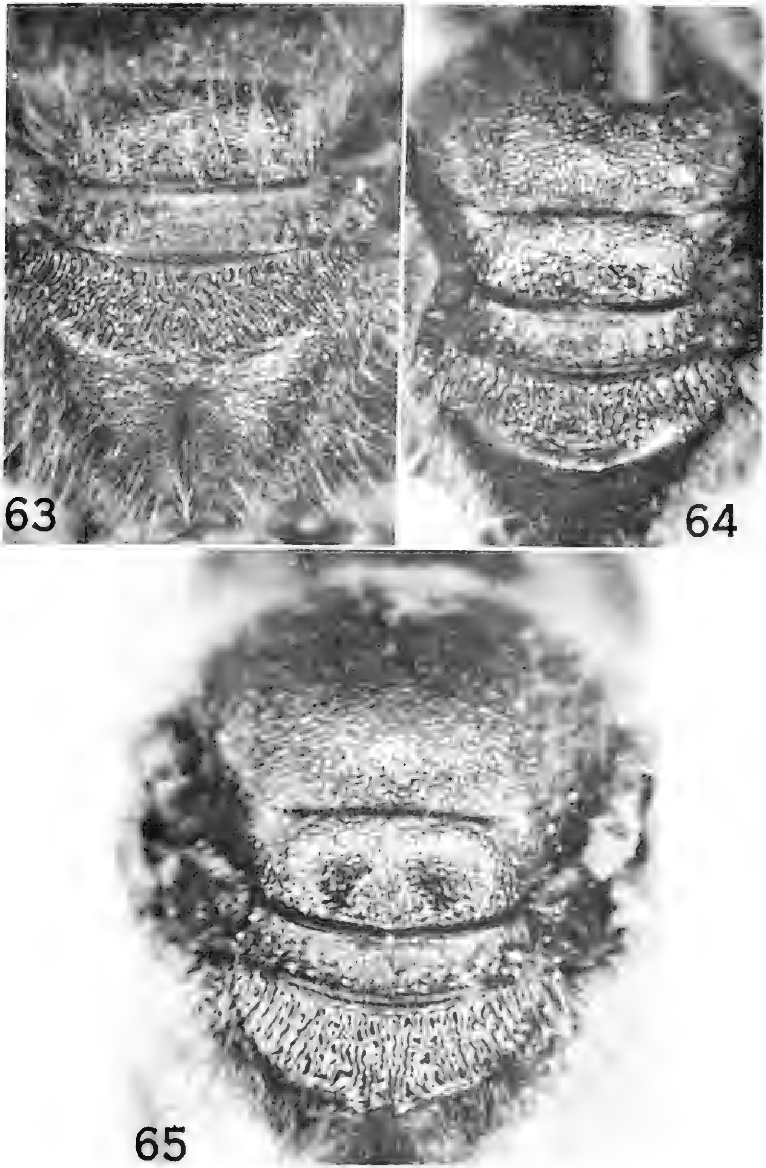


FIG. 63. Propodeal disc of *A. striata* B (standard).
FIG. 64. Propodeal disc of *A. persimilis*.
FIG. 65. Propodeal disc of *A. striata* B-C intermediate.

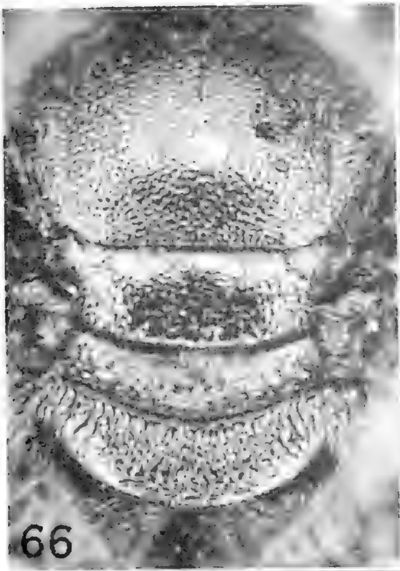


FIG. 66. Propodeal disc of *A. bracteata.*
FIG. 67. Propodeal disc of *A. edentata.*
FIG. 68. Propodeal disc of *A. striata* c-*persimilis* intermediate.

FIG. 69. Propodeal disc of *A. pomoniella.*
FIG. 70. Propodeal disc of *A. neglectula.*

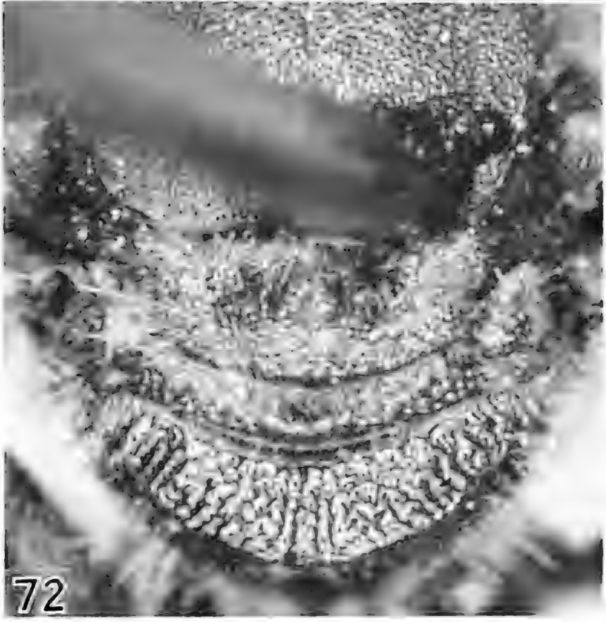
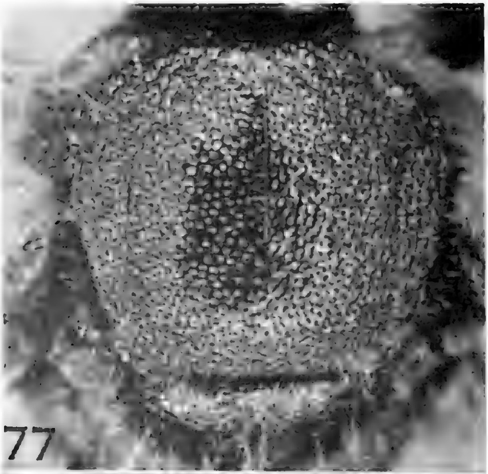


FIG. 71. Propodeal disc of *A. striata* D (standard).
FIG. 72. Propodeal disc of *A. striata* B-D intermediate.

FIG. 73. Posterior vertical surface of propodeum, *A. pomoniella*.
FIG. 74. Posterior vertical surface of propodeum, *A. persimilis*.
FIG. 75. Posterior vertical surface of propodeum, *A. neglectula*.
FIG. 76. Posterior vertical surface of propodeum, *A. gratiosa*.



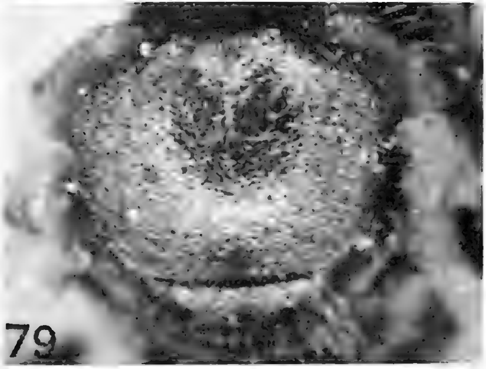


FIG. 77. Mesoscutum, *A. striata.*
FIG. 78. Mesoscutum, *A. bracteata.*
FIG. 79. Mesoscutum, *A. edentata.*

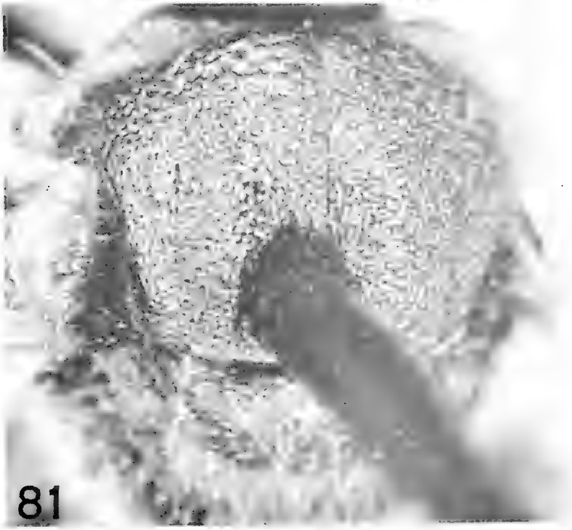


FIG. 80. Mesoscutum, *A. pomoniella*.
FIG. 81. Mesoscutum, *A. gratiosa*.

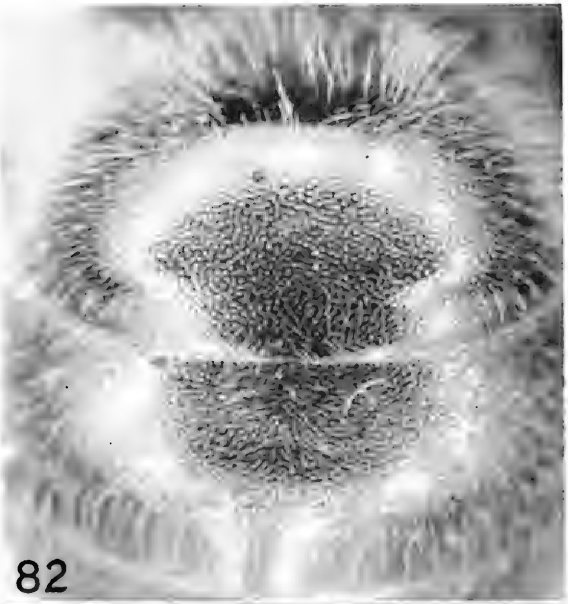


FIG. 82. Metasomal punctures, *A. aurata.*
FIG. 83. Metasomal punctures, *A. gratiosa.*

Wilson), on *Datura*, and one paratype female are in the Snow Entomological Museum, The University of Kansas.

Description. Female: (1) Length 7 to 9 mm; head width 1.8 to 2.6 mm, averaging 1.90 mm, usually wider than long (rarely as wide as long). (2) Color bright green to blue-green; frons often with slight bluish reflections; metasoma similar in color to head and thorax or darker or browner in Mexican specimens. (3) Mandible usually with basal half dark brown, lighter brown becoming ferruginous apically, with or without metallic reflections basally. (4) Clypeus about twice as wide as long; basal half green with large, widely spaced punctures, closer basally; apical half dark brown or black and slightly beveled, with large elongate punctures; surface between punctures usually smooth and shiny, sometimes minutely roughened. (5) Supraclypeal area shiny and irregularly punctured; surface smooth or sometimes minutely roughened. (6) Paraocular area punctorugose to finely rugose below level of antennae, more coarsely rugose above. (7) Antenna entirely dark brown; flagellum often slightly lighter below than above; pedicel as long as broad; first flagellar segment almost twice as wide as long. (8) Scutum regularly and densely punctate; punctures small, deep and close; anterior margin roughened medially, becoming weakly rugose at anterolateral angles. (9) Tegula less than twice as long as wide. (10) Scutellum with small, deep, close punctures. (11) Pleuron rugose, more coarsely so anteriorly. (12) Propodeum with disc 1.5 times as long as metanotum; outline of disc U-shaped, profile type 5, posterior edge abruptly rounded, shiny and smooth; disc extending slightly onto posterior surface of propodeum and particularly onto posterolateral corners; striae wavy, irregular, moderately coarse, extending about two-thirds the length of disc medially, usually attaining edge at extreme lateral corner; surface beyond striae minutely reticulate; posterior vertical surface smooth and shiny, sparsely and minutely punctured; posterolateral corners prominent, shiny, smooth, with few widely spaced punctures; lateral surface finely and linearly rugose anteriorly, weakly punctate toward posterior angles. (13) Legs brown, fore and hind coxae and trochanters with strong metallic reflections, femora usually with weak metallic reflections. (14) First metasomal tergum polished and brilliant, punctures fine and widely spaced anteriorly, smooth and shiny dorsally with punctures small, distinct, numerous, closely and regularly spaced; other terga with minute, often indistinct punctures close together; first sternum without metallic reflections. (15) Pubescence white on head, pale, golden to white on vertex, thorax, metasoma and legs; pubescence short and sparse on genal area, denser and coarser in Mexican specimens.

Male: (1) Length 9 mm; head with 1.75 to 2.25 mm, averaging 2.18 mm, width equal to length. (2) Color bright green to blue-green; frons without blue reflections on green specimens; metasoma dark green, usually darker than rest of body. (3) Mandible usually with metallic reflections basally. (4) Clypeus with punctures large, widely and irregularly spaced, surface between punctures usually smooth and shiny. (5) Supraclypeal area punctate to punctorugose below antennae, usually smooth, shiny and sparsely punctate basally. (6) Paraocular area with small distinct punctures below level of antennae, finely ruguose above. (7) Flagellum dark brown above, yellow-brown below; scape, pedicel and usually first flagellar segment dark brown in the United States and some Mexican specimens, last one or two flagellar segments often slightly darker than preceding segments; pedicel and first flagellar segment about equal in size, each about 1.5 times as wide as long. (8) Scutum shiny and smooth, uniformly punctured; punctures distinct, separated by less than a puncture width medially, more crowded at periphery than at center in specimens from areas outside of California; anterior margin roughened or finely rugose, becoming slightly more coarsely so at lateral angles. (9) Tegula twice as long as wide, entirely pale yellow in some Mexican specimens. (10) Scutellum shiny, roughened and punctate; punctations generally irregular in size and spacing. (11) Pleuron rugose to punctorugose, becoming areolate anteriorly. (12) Propodeum with disc 1.5 times as long as metanotum; outline of disc truncately to obtusely U-shaped; disc nearly horizontal and slightly concave, slightly lower at posterolateral corners than posteromedially; posterior edge abruptly rounded, smooth and shiny; striae rather coarse, distinct, wavy, extending about two-thirds length of disc medially or nearly to margin when median striae depressed, reaching edge laterally, often extending onto lateral surfaces of propodeum; surface of disc beyond striae shiny, smooth, minutely reticulate, smooth area extending onto posterior surface; posterior surface of propodeum shiny, usually slightly roughened with shallow, widely spaced punctures of variable size and density, distinct to indistinct; posterolateral corners closely and shallowly punctate; lateral surface regularly and distinctly punctate with surface between punctures smooth and shiny. (13) Legs brown, coxae, trochanters, femora and tibiae with metallic reflections; hind basitarsi with erect hairs of uniform length and density from base to apex, about as long as width of segment; basal tuft absent. (14) Metasomal terga dark green with apical margins slightly depressed, narrowly brown. First tergum polished anteriorly with numerous widely spaced punctures, smooth, usually dull dorsally, punctures small and close; second and third terga dull, punctures small and close; sterna light brown, minutely pubescent, hairs often longer and denser at apical margins than elsewhere, less so medially than laterally; first sternum usually with feeble metallic reflections; apical margins of all sterna straight or slightly convex. (15) Pubescence white. (16) Genital capsule as in Figures 26, 27, 35, type 2; inner lobe of gonostylus "fan-shaped," bearing variable number (usually about 8) of large heavy setae, inner portion divided to form finger-like section with two to five setae (usually 2 or 3); separation deep or shallow (so that "finger" may appear long or short, but always evident); sterna 7 and 8 without setae, variable in shape, 8 with broadly rounded basal edge medially, not truncate (Fig. 41b); 7 produced into knob-shaped lump medially, each arm with minute setose protuberance on distal inner angle (Fig. 41a); tergum 8 of type 1 (Fig. 43).

Comparisons. A. pomoniella is, perhaps, the most distinctive of all the North American *Augochlorella.* It is the largest (Fig. 86), smoothest and most brilliant of the species and the least variable. It seems most closely related to *neglectula,* although the male genitalia show closer affinities with those of the eastern species. Both male and female can be distinguished from *neglectula* by the more widely separated and larger scutal punctures and the generally smooth body surface, the greener legs, the polished posterior part of the propodeal disc and posterolateral corners, the smooth posterior propodeal surface, and in the males by the genitalia (distinguishable from all other North American species) and the sternal punctures and setae.

No *pomoniella* were found that would be confused with any other species.

Variation. Californian specimens, together with those from Nevada, both male and female, are the most morphologically stable of any species. Variability in size and color increases in Arizona and Mexico, where specimens tend to be smaller with the brown areas paler.

Specimens are larger in California (mean head width=2.33 mm) than in Mexico or Arizona (mean head width=2.07 mm) (Fig. 84) while females from Utah are about the same size as in California. Differences noted by Michener (1937) represent normal variations found not only among individuals from Utah but also in Californian material.

The metasoma of both males and females is noticeably darker in Mexican specimens than in specimens from the United States, with a greater tendency for the brown to dominate the green in males or brown to become black in females. Other brown structures, such as the mandibles, tarsi and tegulae, are paler in males from Mexico than in those from the United States, so that on the mandible, the dark brown area is restricted to the basal portion, and the tarsi of most specimens are lighter in color than other parts of the legs, contrasting with the uniformly dark brown legs of specimens from the United States. One series of nine specimens from Yucatan (13*) had both tibiae and tarsi pale although the tibiae were normal in the two other Yucatan males examined. All male specimens from Yucatan and Sonora had pale testaceous tegulae, although specimens from other parts of Mexico were normal. None of the females showed these variations in color.

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* See Table 1.

Thoracic punctation is uniform both in size and spacing in males from California, but in Arizona and Mexico the punctures are closer together and irregular in size at the periphery of the scutum. Females vary little in this respect.

The surfaces of the head and thorax are dull and finely roughened by minute reticulations in many female specimens from Mexico. This roughening is most apparent on the supraclypeal area, clypeus, scutum and scutellum. In addition, the clypeus is entirely brown or black or the brown area extends medially to the base. Such variants were not found in Baja California; only 1 of 28 specimens from Sonora showed such characters, but all 27 specimens from other Mexican states showed them in varying degrees.

As with other species of *Augochlorella*, the propodeal area shows the greatest amount of variation but even this is less than in other species and there is no geographical trend or seasonal pattern in the variation. The striae of the disc are distinct in all males but in females there are occasional individuals in which the striae are fine, weak, or barely recognizable. The striae normally extend half the length of the disc, although in about one-third of the specimens they are longer medially and almost attain the edge of the disc. Such length is more noticeable in the males where the median area is slightly depressed when this condition occurs.

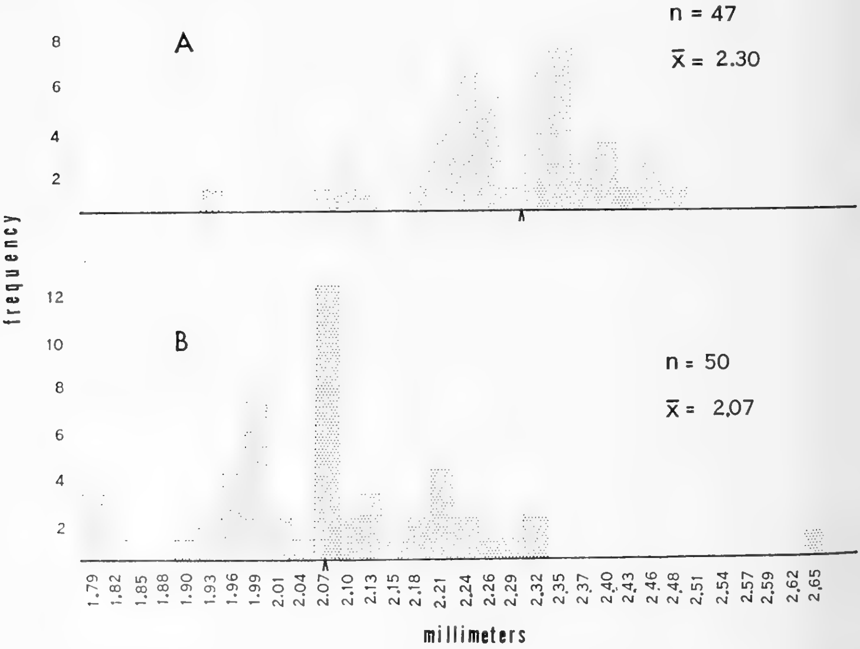

FIG. 84. Measurements of head widths of females of *A. pomoniella*. A. From California and Utah. B. From Arizona and Mexico.

Distribution. From northern California just north of San Francisco and western Nevada, southward through central and southern California; Washington Co., Utah, throughout the western half and southern part of Arizona; Baja, California, the west coast of Mexico to Chiapas and eastward to Yucatan, southward into Guatamala and Costa Rica (Map: Fig. 85).

A total of 118 males and 631 females have been seen. ARIZONA: *Cochise Co.*, 5 ♀ (Huachuca Mts.: Mouth of Carr Canyon; 7 mi. SW. Wilcox; Benson) (July, September); *Coconino Co.*, 2 ♂, 26 ♀ (Grand Canyon: Indian Garden ca. 3800 ft., Phantom Ranch ca. 2500 ft., South Rim 6800 ft.; Supai; Havaisu Canyon 3500 ft.) (June-August); *Maricopa Co.*, 1 ♂, 7 ♀ (Granite Reef Dam; 25 mi. E. Gila Bend; 20.7 mi. S. Gila Bend; Tempe) (March, July, September); *Mohave Co.*, 1 ♀ (Grand Canyon, mi. 179.2 at Lava Falls) (June); *Pima Co.*, 22 ♂, 78 ♀ (Tucson; Sta. Catalina Mts.: Pepper Sauce Canyon, Sabino Canyon, Sabino Basin 3800 ft., Ventana Canyon, Cape Canyon, Hitchcock Highway mile posts No. 5, 6, 8, 9, 5500 ft.; Saguaro Nat. Mon.; 18 mi. W. Sells; 5 mi. N. Tucson; 20 mi. E. Tucson; Lowell Ranger Sta. 2700 ft.; Sahuarita; Baboquivari Mts., Kits Peak Rincon; Sierritas 31° 51′ N. 111° 16′ W.; Black Dike Prspct. ca. 3750 ft.; Tanque Verde; Continental; Quitobaquito, Organ Pipe Nat. Pk.) (March-November); *Pinal Co.*, 4 ♂, 8 ♀ (Superior; 20 mi. W. Casa Grande; Florence Jct.; Coolidge; Río Aravaipa 2500 ft.) (February-March, June-July); *Santa Cruz Co.*, 3 ♀ (Coyote Mts. 31° 58′ N. 111° 29′ W., ca. 3500 ft.; Sonoita) (July-August); *Yavapai Co.*, 2 ♀ (Seligman; 3 mi. N. Rock Spr.) (July). CALIFORNIA: *Alameda Co.*, 5 ♀ (Tesla) (October); *Calaveras Co.*, 2 ♀ (Murphys 2500 ft.); *Contra Costa Co.*, 2 ♀ (Mt. Diablo) (July); *Fresno Co.*, 2 ♀ (Coalinga; Orange Cove) (April-May); *Inyo Co.*, 3 ♂, 63 ♀ (Lone Pine; Darwin Falls; Mazourka Canyon; Panamint Mts., Surprise Canyon; 7 mi. W. Westgard Pass; Death Valley; 5 mi. W. Lone Pine; Big Pine; Independence; Payson, 39° 19′ N. 118° 08′ W.; Inyo Mts. 7000-9000 ft.; Antelope Spr., 8 mi. SW. Deep Spr.) (April-August); *Kern Co.*, 5 ♀ (Arvin; Democrat Spr.; 6 mi. W. Inyokern, Short Canyon; Caliente) (March, June); *Kings Co.*, 2 ♀ (12 mi. SW. Avenal) (August); *Los Angeles Co.*, 13 ♂, 43 ♀ (Sta. Catalina Is.: Avalon, Cape Canyon, Pebbly Beach, Rancho Escondito; Newton; Clairmont; 5 mi. S. Pearblossum; Acton; Eagle Rock; Altadena; Whittier; 6 mi. W. Palmdale; Pasadina) (February-September, December); *Mariposa Co.*, 1 ♀ (1500 ft.) (May); *Mendocino Co.*, 1 ♀ (Ryan Cr.) (July); *Mono Co.*, 2 ♀ (Oasis) (May); *Monterey Co.*, 8 ♂, 15 ♀ (Paraiso Spr.; Jamesburg; Sta. Lucia Mts., Hastings Nat. Hist. Res. 1900-2700 ft.) (April-May, August-September, November); *Napa Co.*, 14 ♀ (Pope Valley; Mt. St. Helena; Conn Lake; Chiles) (March, May, September); *Orange Co.*, 3 ♀ (Newport Bay; Serra; Aliso Canyon nr. Laguna Beach; Laguna Beach) (July-August); *Riverside Co.*, 4 ♂, 32 ♀ (Palm

Spr.; Riverside; San Jacinto; San Jacinto Mts.: Idyllwild Keen Camp; 10 mi. W. Perris; Henshaw; The Gavilan; Whitewater; Corona; Palm Springs; Cathedral City; 2 mi. E. Anza; Elsinor; Murrieta; Andreas Canyon, Palm Spr.) (March-May, July, October); *San Bernardino Co.*, 1 ♂, 13 ♀ (Mill Cr.; Crestline; 5 mi. SE. Hesperia; 12 mi. SE. Ivanpah; E. Highlands; Morongo; Chino Canyon; Argus Range, Indian Joe Spr. 2600 ft.; Colton) (March-May, August-September); *San Diego Co.*, 3 ♂, 32 ♀ (Jacumba; Poway; Vista; Borego; 2 mi. N. Warner Spr.; 3 mi. S. Oak Grove; Barrett Spr.; El Cajon; San Diego; Campo; Descanso; Torry Pine Pk.; Warren) (March-April, July-September); *San Joaquin Co.*, 1 ♀ (Tracy) (July); *San Luis Obispo Co.*, 2 ♀ (Paso Robles; 2.5 mi. S. Creston) (April, September); *San Mateo Co.*, 1 ♀ (Jasper Ridge) (September); *Santa Barbara Co.*, 1 ♀ (Sta. Cruz Is.) (May); *Santa Clara Co.*, 2 ♂, 9 ♀ (Alum Rock Canyon; Stanford, Palo Alto; San Jose; Mt. Hamilton; Uvas Cr.) (July-August, October); *Sonoma Co.*, 5 ♀ (Guerneville; Preston) (May, July); *Stanislaus Co.*, 1 ♀ (del Puerto Canyon) (April); *Tulare Co.*, 1 ♂, 8 ♀ (Lindsay; Lemon Cove 500 ft.; 3-Rivers 600-800 ft.; Porterville; Kaweah) (June-July, November); *Tuolumne Co.*, 5 ♀ (Jamestown; 18 mi. SW. Sonora; 13 mi. SW. Sonora) (April, July); *Ventura Co.*, 54 ♀ (Quantal Canyon; 5 mi. S. Gorman, Hungary Valley) (May). NEVADA: *Douglas Co.*, 1 ♂, 1 ♀ (3 mi. S. Genoa) (August); *Washoe Co.*, 2 ♀ (Pyramid; Sutcliff) (June-July). NEW MEXICO: *Rio Arriba Co.*, 1 ♀ (Willow Creek) (August). UTAH: *Washington Co.*, 2 ♂, 66 ♀ (Zion Nat. Pk.; Toquerville; Leeds; St. George; Sta. Clara; La Verkin; Washington; Hurricane) (May-September).

BAJA CALIFORNIA: 16 ♀ (Cedros Is.: Bernstein Spr.; Isla Espíritu Santo; Coyote Cove, Conception Bay; Los Frailes; La Paz; 19 mi. E. Rosario; Canipol; 40 mi. S. El Arco Mine) (March, June, August, October). CHIAPAS: 1 ♀ (2 mi. N. Suchiapa) (July). GUERRERO: 19 ♂, 45 ♀ (17 mi. N. Chilpancingo 2250 ft.; Chilpancingo 3700 ft.; 5.2 mi. E. Chilpancingo 5700 ft.; 2 mi. S. Chilpancingo; 42 mi. N. Acapulco 1550 ft.; 9 mi. W. Acapulco; Acapulco; 42 mi. N. Acapulco 1550 ft.; Xalitla 1500 ft.) (March, August, December). MICHOACÁN: 1 ♂, 3 ♀ (11 mi. E. Apatzingan; 4 mi. E. Apatzingan; Apatzingan; 10 mi. N. Morelia 5900 ft.) (July-August). MORELOS: 1 ♂ (11 mi. S. Tlaltizapan) (August). NAYARIT: 2 ♂ (km. 78 Rte. 15) (September). OAXACA: 4 ♂, 6 ♀ (23 mi. S. Matías Romero 200 ft.; 4 mi. NW. Tehuantepec 700 ft.; 14 mi. NW. Tehuantepec 700 ft.; 6 mi. S. Tehuantepec 200 ft.; 10 mi. NE. Juchitán; 50 mi. N. La Ventosa) (June-July). SINALOA: 7 ♀ (6 mi. NE. Villa Unión 350 ft.; 3 mi. NW. Concha 50 ft.; 14 mi. SE. Elota; Los Moschis) (May, July). SONORA: 7 ♂, 18 ♀ (37 mi. N. Guaymas; 70 mi. N. Hermosillo; 4 mi. N. Guaymas;

Río Mayo; 20 mi. SE. Empalme) (April, September). YUCATÁN: 11 ♂, 1 ♀ (8 km. N. Muna; Mérida; Chichen Itza) (July). "San Carlos Bay" 1 ♀ (September); "San José de Guaymos" 4 ♂, 1 ♀ (April).

GUATEMALA: Retalhuleu, 2 ♀ (Champerico) (April).

COSTA RICA: Guanacaste, 3 ♂ (El Coco) (August).

A. pomoniella appears to be most abundant in California with smaller populations occurring from Baja California down the west coast of Mexico into Central America. Small and possibly isolated populations of *pomoniella* exist in Utah and possibly in New Mexico. The one specimen from New Mexico is without question *pomoniella* but does seem to be out of place. Whether this is due to mislabelling or to a lack of collecting cannot be determined from the available information. Specimens from the most southwestern county of Utah, Washington Co., are little different from those in California and seem to be a part of the main Californian stock. Specimens have been taken from near sea level to 7000 feet elevation in California and Arizona and from 200 to 6000 feet in Mexico. Specimens were found near sea level in Costa Rica.

The only species of *Augochlorella* with which *pomoniella* is in contact in the United States is *neglectula*, a species found chiefly on the Mexican Plateau and in the mountains of southern New Mexico and Arizona. Although the ranges of the two species broadly overlap in southern Arizona, they are apparently somewhat different ecologically, judging by random collections made in the Santa Catalina Mountains near Tucson, Arizona. These collections show *pomoniella* occurring from the Sonoran desert near Tucson, a saguaro-mesquite habitat at about 2800 feet near the base of the mountains, to about 5200 feet in oak-juniper association. *A. neglectula* has been collected at about 3800 feet and ranges well into the pines near the tops of the mountain at about 8100 feet elevation. *A. neglectula* has not been collected in the desert area around Tucson. This comparison is based only on the label data of 73 *pomoniella* and 64 *neglectula* from this one area.

Seasonal Activity. Females have been collected between February 28 and December 27 and males between May 3 and December 17, with little difference in dates throughout the range. Females were collected with pollen in their scopes from early March until the beginning of October in California, with similar dates being recorded from other areas as well. The wide variation in size (Fig. 84) is due to geographical differences rather than to seasonal or caste differences.

Flower Records. Acacia, Arctostaphylos, Argemone, Asclepias, Aster, Baileya, Bebbia, Brassica, Carnegia, Centaurea, Cercidum, Chrysothamnus, Cirsium, Cissus, Cleome, Cryptantha, Dalea, Encelia, Eriogonum, Eucnide, Fendlerella, Gossypium, Gutierrezia, Haplopappus, Helianthus, Heliotropi-

FIG. 85. Distribution of *A. pomoniella* (solid dots) and *bracteata* (rings).

um, Heterotheca, Hymenothrix, Isomeris, Kallstroemia, Melilotus, Oenothera, Opuntia, Penstemon, Peucephyllum, Rhus, Salix, Salvia, Senecio, Sisymbrium, Sphaeralcea, Tamarix.

Augochlorella neglectula neglectula (Cockerell)

Augochlora neglectula Cockerell, 1897, Bull. New Mexico Coll. Agr. Exper. Sta. 24:43 (descr.); Cockerell, 1898, Bull. Sci. Lab. Denison Univ. 11:47 (descr.); Cockerell, 1898, Zool. 2:80 (fl., distr.); Cockerell, 1899, Catalogo de las Abejas de Mexico p. 6 (list); Cockerell, 1899, Canad. Ent. 31:256 (fl., distr.); Cockerell 1900, Amer. Nat. 34:488 (fl., distr.); Cockerell, 1901, Ent. News 12:39 (fl.); Cockerell, 1902, Amer. Nat. 36:811 (fl.); Cockerell, 1903, Ann. Mag. Nat. Hist. (7)12:442 (descr.); Cockerell, 1906, Trans. Amer. Ent. Soc. 32:295

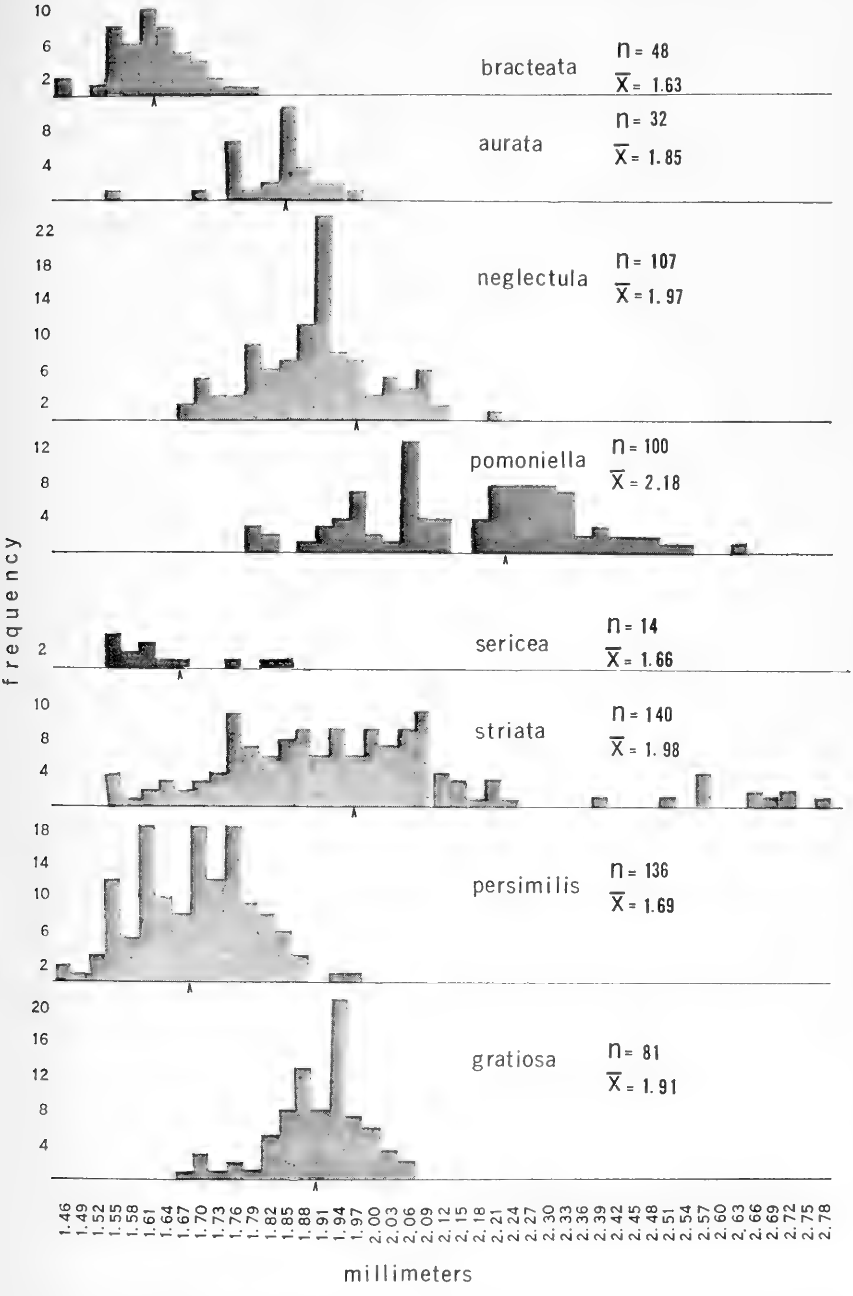

FIG. 86. Histograms showing head widths of field caught females throughout the range of each species, samples from throughout the season.

(distr.); Cockerell, 1915, Pomona Jour. Ent. Zool. 7:232 (descr.); Cockerell, 1927, Pan-Pacific Ent. 3:162 (descr.).

Augochlora dimissa Cockerell, 1923, Proc. U.S. Nat. Mus. 63:5 (descr.) (new synonymy).

Augochlora confusa: Cockerell, 1897, Bull. New Mexico Coll. Agr. Exp. Sta. 24:23, 25 (misidentification).

Augochlorella aurata: Sandhouse, 1937, Jour. Washington Acad. Sci. 27:71 (in part). (Since 1937, when Sandhouse erroneously synonymized *neglectula* with *aurata,* various authors have repeated this synonymy, but additional data pertaining to *neglectula* does not appear to have been given.)

Types. Augochlora neglectula, holotype male, from Filmore Canyon [Dona Ana Co.], New Mexico, August 29 (Townsend), in the collection of P. H. Timberlake, University of California at Riverside, California. Cotype (paratype) female, Filmore Canyon, New Mexico, August 24 (Townsend), No. 4345, in the collection of the U.S. National Museum. In 1906, Cockerell listed the type locality as Organ Mountains, New Mexico; probably Filmore Canyon is merely a more specific statement of the same locality. The species was recognized as new on the basis of male characters, and the holotype is well marked with "type" labels, although not in Cockerell's usual hand. *Augochlora dimissa*, holotype female, from Victoria [Tamaulipas], Mexico, March 16, is in the collection of the U.S. National Museum, No. 25582.

Description. Female: (1) Length 6 to 7 mm; head width 1.68 to 2.21 mm, averaging 1.97 mm; head usually wider than long. (2) Color bright green to dark blue; frons usually with blue reflections; metasoma often darker than head and thorax and suffused with brown. (3) Mandible with basal third dark brown, reddish brown centrally, rufous apically, without metallic reflections basally. (4) Clypeus slightly wider than long; basal half green with rather large punctures about a puncture width apart; apical half dark brown and slightly beveled, with about three to five large, often elongate punctures; surface between punctures smooth and shiny or finely reticulated at base and laterally. (5) Supraclypeal area irregularly punctate, sparsely so medially; surface between punctures usually shiny and smooth, sometimes minutely roughened and dull. (6) Paraocular area closely punctorugose below level of antennae, coarsely rugose above. (7) Antenna dark brown, flagellum slightly lighter below than above; pedicel as broad as long; first flagellar segment less than twice as wide as long. (8) Scutum with punctures variable in size and spacing, grading from distinctly and closely punctate to punctorugose, usually closer together laterally than medially; anterior margin finely roughened medially, becoming finely to coarsely rugose at anterolateral angles. (9) Tegula with length slightly greater than width, shiny, without conspicuous punctures. (10) Scutellum with small, close, irregular sized punctures, becoming indistinct in Mexican specimens. (11) Pleuron coarsely rugose, areolate anteriorly. (12) Propodeum with disc usually less than 1.5 times as long as metanotum; outline of disc broadly semicircular, profile type 3, posterior edge abruptly rounded medially, becoming gradually rounded laterally; striae variable, usually regular, fine and radiating from medial area, medially extending about three-fourths length of disc and ending gradually, laterally nearly reaching edge or extending onto vertical surface; surface beyond striae dull and granular to edge; posterior and lateral vertical surfaces finely roughened, usually with fine horizontal rugae extending from lateral to posterior surface across rounded posterolateral corners. (13) Legs brown; fore and hind coxae with strong metallic reflections; fore femur sometimes weakly metallic. (14) First metasomal tergum with anterior surface polished, sparsely and finely punctate, dull to shiny dorsally, with fine, distinct, close punctures; second tergum with fine, close punctures, surface between punctures smooth, shiny to dull; first sternum with or without metallic reflections. (15) Pubescence white on head and ventrally on thorax and metasoma, white to pale golden or dorsal parts of thorax and metasoma and on legs, golden on thorax of most Mexican specimens.

Male: (1) Length 7 to 8 mm; head width 1.66 to 2.04 mm, averaging 1.85 mm, greater than, equal to or less than length. (2) Color bright green to blue, frons with bluish reflections in all specimens; usually variably blue-green over entire body. (3) Mandible with or without metallic reflections basally. (4) Clypeus with punctures large, widely spaced, surface between punctures minutely roughened to smooth and shiny. (5) Supraclypeal area variably punctate, surface between punctures smooth and shiny or sometimes minutely reticulate and dull. (6) Paraocular area closely punctate to finely rugose. (7) Flagellum dark brown above, yellowish brown below; scape and pedicel entirely dark brown or black; last one or two flagellar segments usually slightly darker below than preceding segments; pedical as broad as long; first flagellar segment about twice as wide as long. (8) Scutum shiny with punctures distinct, variably spaced medially to parapsidal lines, closer laterally; becoming weakly rugose at lateral anterior margin. (9) Tegula less than 1.5 times as long as wide, shiny, with punctures inconspicuous or lacking. (10) Scutellum shiny, distinctly punctate, more densely so posteromedially than elsewhere. (11) Pleuron areolate anteriorly and laterally. (12) Propodeum with disc slightly longer than, to 1.5 times as long as metanotum; outline of disc semicircular, posterior edge abruptly rounded; striae coarse, irregular, wavy, not reaching edge medially, extending onto vertical surface laterally; surface of disc beyond striae narrowly smooth and shiny or slightly roughened; posterior vertical surface shiny, finely roughened or rugose; posterolateral corners with lineate, horizontal rugae extending from lateral to posterior surfaces; lateral vertical surface finely rugose with horizontal lineate rugae anteriorly. (13) Legs brown, fore and hind coxae and trochanters with strong metallic reflections; femora and fore tibia weakly metallic; middle and hind tibiae and all tarsi brown; hind basitarsus with straight, erect hairs of uniform length along entire segment; these hairs almost 1.5 times as long as width of segment; basal tuft reduced to inconspicuous. (14) Metasomal terga green with apical margins brown; first tergum polished with fine, widely scattered punctures anteriorly, smooth but less shiny dorsally with punctures small and close together; second tergum minutely to indistinctly punctate; sterna brown, occasionally suffused with black, pubescence short and fine, evenly distributed; first sternum with weak metallic reflections; second through sixth sterna with apical margins straight. (15) Pubescence white over entire body to golden in some Mexican specimens. (16) Genital capsule of type 4 (Figs. 37-38); inner lobe of gonostylus long and thin with blunt apex, bearing 3 to 5 stout setae; posterior edge of lobe with setae variable in size and number; setae on outer lobe (l_2 Fig. 27) usually branched; seventh tergum type 2 (Fig. 46); seventh and eighth sterna type 1 as figured (Fig. 40).

Comparisons. Most *neglectula* can be distinguished from all other North American species of *Augochlorella* by the fine radiating striae that extend only about three-quarters of the way across the propodeal disc, by the rugose nature of the posterior propodeal surface, by the blue areas on the frons, and by the shape of the inner lobe of the male gonostylus. In addition to these characters, it differs from *pomoniella* by the usually close, deep, often contiguous scutal punctures giving the scutum a rough or even rugose appearance. In *pomoniella* the scutum is smooth with distinct, widely spaced punctures. The legs, especially the trochanters and femora, are more uniformly brown in *neglectula* than in *pomoniella.* In most specimens there are no distinct posterolateral corners to the propodeum (Fig. 70) or if there are, they are weak. The corners are rarely polished and shiny as in *pomoniella* but usually are traversed by horizontal rugae extending from the lateral to posterior surfaces. This character will also distinguish *neglectula* from *striata* when the striae of the disc of *neglectula* become coarser and less strongly radiating than usual. Males can be easily distinguished from *striata* on the basis of the fourth sternum and genitalia.

A truer picture of the relationships of *neglectula* to the other North American species of *Augochlorella* must necessarily wait until a study is made of the Mexican, Central and South American species of the genus with which it is possibly more closely related. It has no close affinities with *Pereirapis* and among the species from the United States is most similar to *pomoniella. A. neglectula* and *pomoniella* may look similar in areas where their ranges overlap but there is no evidence of genic exchange since the features of each species are maintained. There is a similar resemblance in a few individuals to *striata* but in all such cases also, *neglectula* maintains its identity.

Variation. Populations of *neglectula* in Arizona show the greatest amount of variation, particularly in the degree of thoracic roughness. Females are more variable than males.

There is not much difference in size among individuals from different areas of the range although the mean head width of females is largest in Mexico (1.99 mm) and smallest in Texas (1.85 mm). The width of the head is less variable in males, but no trends can be described due to the meager samples available from most areas.

The supraclypeal area is shiny in most males and females from the United States but is rarely polished or brilliant. It may be entirely punctate or, more frequently, sparsely punctate medially, more densely so laterally. In many of the Mexican females, as in some Mexican *pomoniella*, the supraclypeal area is dull due to minute reticulations on the integumental surface. This dullness extends onto the basal area of the clypeus and over the scutum, and the brown color on the apex of the clypeus extends in a narrow medial line to the base of the clypeus. In no case is the clypeus entirely brown. But unlike *pomoniella*, other less dull or even shiny *neglectula* sometimes show this same variation of clypeal coloration. The dull specimens may be found throughout the range of Mexican *neglectula* from March to September. The supraclypeal area of the males is rarely dull even though it may be coarsely punctured. The minute fine reticulations were found on only three out of 42 males from Arizona (from Yuma, Cochise and Pima Counties) and on four out of 18 Mexican individuals (from Chihuahua, San Luis Potosí, Durango and Guerrero). Although the roughening may extend onto the clypeus, it does not appear on the scutum and the dullness is considerably less striking than on the females. The female holotype of *Augochlora dimissa* from Victoria, Mexico, shows this dull condition although in every other respect appears to be a normal Mexican *neglectula*. Since there is no apparent morphological difference associated with this condition and no geographical pattern or even distinct population of dull individuals, there is no basis for recognizing this variant either as a species or subspecies.

Although the blue patch on the frons is characteristic of this species, in many Mexican females the blue area is obscure and can only be found with difficulty. It is not found at all in the Mexican subspecies *maritima*.

The punctures of the scutum are distinct with their diameters about equal to the spaces between them in about half the males (40 specimens) from all parts of the range, but are close, deep, and contiguous or form a rugose surface in the other half (37 specimens). The scutum is coarsely and closely punctured in females (except for six females from Arizona which have the punctures more widely spaced).

There is considerable variation in the nature of the propodeal area, especially in specimens from Arizona. In the females, the Mexican specimens show the typical *neglectula* pattern with fine, straight, radiating striae on the disc, often reaching the posterior medial edge of the disc. The horizontal rugae are rarely present on the posterior and lateral surfaces of the propodeum but these surfaces are rough and dull. When the striae are larger or less fine the rugae are present posterolaterally. "Typical" *neglectula* are also found in Arizona but individuals occasionally may resemble either *pomoniella* or *striata*. Those similar to *pomoniella* [10 out of 57 specimens from the Santa Catalina Mts. (1*), and two out of five specimens from Globe (9)] have short striae that are finer than found on the usual *pomoniella*. The posterolateral corners are weak and the edge of the disc is shinier than usual, but the polished surface does not extend onto the vertical sides. All these specimens have horizontal rugae on the posterior surface. Those that resemble *striata* have coarser striae than normal, often reaching almost to the posterior margin of the disc, but in all cases the vertical surfaces are rough with well defined horizontal rugae. Such specimens were found commonly in New Mexico and Texas although the rugae are often less distinct in Texan specimens. None of the specimens from New Mexico or Texas resembles *pomoniella*.

In males, the striae of the disc are variable in thickness but generally rather coarse. In 10 of the 42 males from Arizona and 3 of the 18 Mexican males (Zacatecas, Chihuahua and "Guadalupe"), the propodeum resembled that of *pomoniella*, having shiny, smooth posterolateral corners and smoother vertical surfaces than is normal for *neglectula*, with the horizontal rugae indistinct or absent. Punctures on the propodeum were distinct although close and coarse so that the roughened character of *neglectula* is maintained in these specimens.

The inner lobe of the gonostylus of the male genitalia is rather constant in shape but variable in the number and character of the setae it bears on its outer edge. These setae may number two or three and be short, very thin and flaccid (Fig. 37), but may vary to long, thick, heavily sclerotized and up to 14 in number. When the larger number are present the series is continuous with the setae at the apex of the lobe, with one or two weaker setae between those on the posterior and apical margins (Fig. 39). If the setae are weak, there is usually a space between those of the two series (Fig. 38). As the setae become longer and thicker the lobe itself becomes shorter and broader. All intermediate conditions occur between the two extremes, and all forms apparently occur throughout the range. No correlation has been found between these genitalic differences and external morphological varia-

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* See Table 1.

tion. In no case does the inner lobe look similar to that of any other species here considered.

The outer lobe of the gonostylus bears long, fine, branched or unbranched setae. Branched hairs cannot be correlated with either locality or external morphological variation.

The Guatemalan and Panamian specimens look like those from Mexico.

Distribution. From the southern half of Arizona and southwestern New Mexico into the Big Bend area of Texas, southward through all of central Mexico, with specimens also from Guatemala and Panama (Map: Fig. 87).

A total of 79 males and 279 females have been seen: ARIZONA: *Apache Co.*, 1 ♀ (White Mts.) (June); *Cochise Co.*, 7 ♂, 23 ♀ (Huachuca Mts., Ramsey Canyon; Chiricahua Mts.: SW. Res. Sta. 5400 ft., Rustlers Park 8784 ft., Portal 5000 ft.; Douglas; 6 mi. NE. Douglas) (March-August); *Coconino Co.*, 1 ♀ (Oak Creek Canyon 3500 ft.) (August); *Gila Co.*, 7 ♀ (Bot Fly Canyon, Pinal Mts. 3500 ft.; Globe; Payson) (May, July, September); *Graham Co.*, 3 ♂, 2 ♀ (Graham Mts.: 6000-7000 ft., Wet Canyon) (July); *Maricopa Co.*, 1 ♀ (Reef); *Navajo Co.*, 1 ♀ (Carrizo Cr.) (June); *Pima Co.*, 24 ♂, 72 ♀ (Santa Catalina Mts.: mile posts Nos. 9, 10, 23 Hitchcock Highway, Pepper & Sauce Canyon, Sabino Canyon, Sabino Basin ca. 3800 ft., Ventana Canyon, Catalina Springs, Molino Basin; Santa Rita Mts. 4000-8000 ft.; Baboquivari Mts.: Kits Peak Rincon ca. 1050 ft., Brown's Canyon) (February, April-November); *Pinal Co.*, 1 ♂, 1 ♀ (Superior) (February, July); *Santa Cruz Co.*, 2 ♂, 5 ♀ (Ruby, Sycamore Canyon; Patagonia; 17 mi. W. Nogales) (March-May, August, November); *Yavapai Co.*, 1 ♀ (4 mi. S. Jerome) (July); *Yuma Co.*, 5 ♂, 1 ♀ (Parker Creek; Sierra Ancha Exper. Sta.) (May, August). NEW MEXICO: *Catron Co.*, 1 ♀ (Mogollon Mts.) (August); *Dona Ana Co.*, 2 ♂, 28 ♀ (Las Cruces; Organ Mts.: La Cueva ca. 5300 ft., 5100 ft., Riley's Ranch, Filmore Canyon 5700 ft., Dripping Springs) (April, June, August-September); *Grant Co.*, 2 ♂, 1 ♀ (6 mi. N. Silver City; 14 mi. N. Silver City; Pinos Altos) (June-July); *Otero Co.*, 1 ♀ (Alamogordo) (May). TEXAS: *Brewster Co.*, 1 ♂, 6 ♀ (65 mi. S. Marathon; Basin 5000 ft., Big Bend Nat. Pk.; Chisos Mts.) (June-July); *Jeff Davis Co.*, 11 ♂, 7 ♀ (Davis Mts.; Ft. Davis; 23 mi. W. Ft. Davis) (April-July); *Val Verde Co.*, 1 ♂, 6 ♀ (Devil's River) (May).

CHIHUAHUA: 5 ♂, 4 ♀ (92 km. N. Chihuahua; 80 km. N. Chihuahua; Terrero 5500 ft.; Valle de Olivos 5500 ft.) (May-July). DURANGO: 1 ♂, 5 ♀ (12 mi. N. Alamillo; Nombre de Diós; El Tascate 6400 ft.; 69 mi. N. Durango, Hwy. 31; 12 mi. W. Durango) (February, June-July). GUERRERO: 7 ♀ (2 mi. S. Chilpancingo; 5.2 mi. E. Chilpancingo 5700 ft.; 5 mi. S., 2 mi. E. Chilpancingo 3800 ft.; Chilpancingo 4000 ft., 3700 ft.) (August). HIDALGO: 1 ♂, 21 ♀ (23 mi. NE. Jacala 5075 ft.; 38 mi. NE. Jacala 3100 ft.; Zimapan; 6 mi. E. Tulancingo; 4-5 mi. W. Pachuca) (June-September). JALISCO: 5 ♀ (22 mi. NW. La Piedad; 15.5 mi. NE. Lagos de Moreno 6200 ft.; 6 mi. SE. Lagos de Moreno 5900 ft.) (July). MEXICO: 3 ♀ (Teotihuacan Pyramid; Valle de Bravo 6500 ft.) (June, August). MICHOACÁN: 1 ♂, 3 ♀ (Quiroga 6300 ft.; Morelia) (February, July). MORELOS: 1 ♂, 5 ♀ (Cuernavaca 5500 ft.; 5 mi. S. Cuernavaca 4000 ft.; 3 mi. W. Cuernavaca 6500 ft.; Yautepec 4000 ft.) (March-May). NUEVO LEÓN: 1 ♂, 7 ♀ (4 mi. W. El Cercado 2100 ft.; 12 mi. S. Linares; China) (June, August, December). OAXACA: 3 ♂, 6 ♀ (7 mi. SE. El Camerón; Tehuantepec; 5 mi. E. Oaxaca; 10 mi. NE. Oaxaca; Oaxaca; 23 mi. NE. Nochixtlán 7000 ft.; 12 mi. SE. Nochixtlán 7100 ft.) (April, June, July, December). PUEBLA: 3 ♀ (2 mi. NW. Petlalcingo 4600 ft.; 8 mi. SE. Tehuitzingo 4100 ft.; 13 mi. E. Villa Juárez 1300 ft.) (June). QUERETARO: 3 ♀ (Queretaro) (June). SAN LUIS POTOSÍ: 2 ♂, 30 ♀ (El Salto 1500-1800 ft.; 5 mi. E. Ciudad Maiz 4700 ft.; 3.4 mi. NE. El Naranjo 800 ft.; 5 mi. W. Xilitla; 14 mi. W. Xilitla 4200 ft.; 8 mi. W. Xilitla 3500 ft.; 4.3 mi. NW. Nuevo Morelos; El Huizache; 10 mi. NE. San Luis Potosí 6200 ft.; 29 mi. SW. San Luis Potosí 6800 ft.) (June-September). TAMAULIPAS: 2 ♀ (Llera, Victoria) (March, June). TLAXCALA: 1 ♀ (8 mi. W. Apizaco 8500 ft.) (June). VERACRUZ: 3 ♀ (4 mi. NW. Rinconada Antigua 1350 ft.) (June). ZACATECAS: 1 ♂, 4 ♀ (15 km. E. Sombrerete; 2 mi. S. Fresnillo; 9 mi. S. Fresnillo; Fresnillo 7000 ft.) (July-August).

GUATEMALA. Alta Verapaz, 1 ♀ (Trece Aguas).

PANAMA. Canal Zone, 1 ♂ (Fort Clayton) (May).

This species is widespread in the central plateau area of Mexico. The range extends northward through the Chihuahua desert to New Mexico and Arizona. It also extends southward at least as far as Panama. *Augochlorella n. neglectula* is not known from along the coasts of Mexico, although it approaches them in Oaxaca and Veracruz. It has been taken at elevations from 800 to 8500 feet in Mexico and from 1050 to 8100 feet in Arizona and New Mexico. (See also discussion under *pomoniella*.)

Titus (1901) reported two female specimens of *neglectula* from Ft. Collins and Greeley, Colorado. One specimen from each locality (8) with dates matching those given by Titus has been examined but both specimens were normal Colorado *striata* D. All other specimens examined from Colorado have also been *A. striata* and therefore it is assumed that Titus was mistaken in his identification and that *neglectula* extends only as far north as Catron Co., New Mexico, and Yavapai Co., Arizona.

Dreisbach (1945) reports *neglectula* from Michigan, but this is clearly a case of confusion in synonymy. (See distribution of *persimilis*.)

Seasonal Activity. Females have been collected from mid-February to the end of November in Arizona and to the end of December in Mexico. Males have been taken from March through November in the United States

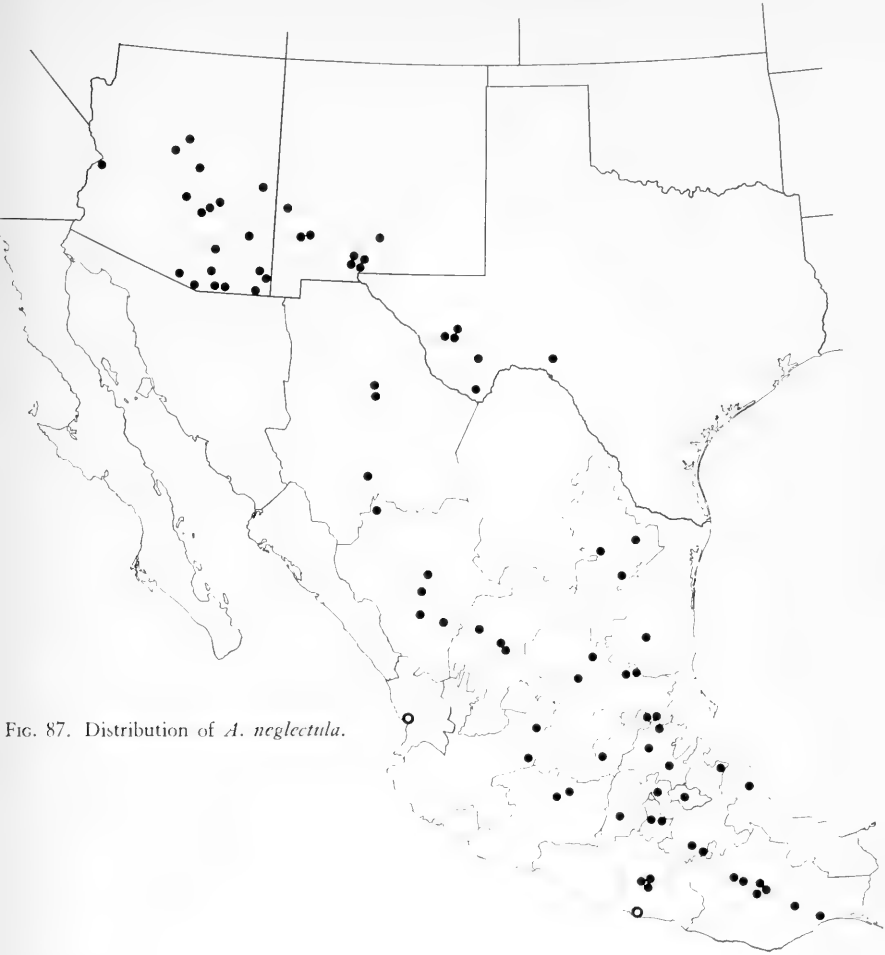

FIG. 87. Distribution of *A. neglectula.*

and all through the year in Mexico. Females with pollen in their scopas were collected from April through August in the United States and from February through December in Mexico.

It seems probable that there is little or no activity during December and January in the United States and that nesting takes place from the middle of April into September or October, depending on the elevation. In Mexico, the bees are apparently active and nesting throughout the year, at least at the lower elevations.

Flower Records. Acacia, Aesculus, Baccharis, Ceanothus, Chilopsis, Chrysanthemum, Chrysopsis, Dalea, Descurainia, Echinocactus, Erigeron, Eschscholtzia, Fendlera, Gaillardia, Gossypium, Gutierrezia, Helenium, Heterotheca, Lepidium, Manzanita, Melilotus, Opuntia, Penstemon, Prunus, Pyrus, Rosa, Senecio, Sida, Sisymbrium, Sphaeralcea, Ungnadia.

Augochlorella neglectula maritima new subspecies

Types. 22 males, 30 females (holotype male, allotype female and paratypes), 20 mi. E. Acapulco, Guerrero, Mexico, August 12, 1962 (Univ. Kansas Mexican Exped.). Additional paratypes as follows: MEXICO. Guerrero: 3 females, 5 males, 20 mi. E. Acapulco, 11 August 1962 (Univ. Kansas Mexican Exped.); 1 female, 20 mi. E. Acapulco, 11 August 1962 on *Microspermum nummulariaefolium* (E. Ordway); 6 females, Acapulco, 6 August 1954 (Univ. Kansas Mexican Exped.); Nayarit: 1 male, San Blas, 13 September 1957 (R. & K. Dreisbach).

Holotype, allotype and 31 female and 19 male paratypes are in the Snow Entomological Museum, The University of Kansas. Two female and two male paratypes are in each of the following collections: Michigan State University, American Museum of Natural History, U.S. National Museum and the California Academy of Sciences.

Description. This subspecies, known only from the Pacific Coast of Mexico, differs from the true *neglectula* only as follows:

Female: (1) Length of head greater than width (width 1.66 to 1.96 mm, averaging 1.81 mm). (2) Frons without bluish reflections. (3) Mandible with basal half brown. (4) Clypeus as long as broad with apical third brown. (8) Scutum finely and very closely punctured, punctures becoming indistinct on extreme anterolateral angles. (9) Tegula oblong, twice as long as wide; surface coarsely punctate and dull on dark brown area. (12) Edge of propodeal disc more angulate than in typical *neglectula*. (13) Legs dark brown with weak greenish reflections usually on fore and hind coxae, fore trochanter, fore and middle femora and fore tibia.

Male: (1) Length of head greater than width (width 1.52 to 1.84 mm, averaging 1.70 mm). (2) Color bright green, metasoma suffused with black; frons without bluish reflections. (7) Antenna with first flagellar segment entirely dark brown. (9) Tegula oblong, more than twice as long as wide, with distinct, close punctures on dark brown area; surface dull. (11) Pleuron coarsely punctured, becoming rugose laterally. (16) Genital capsule with inner lobe of gonostylus heavily sclerotized with straight outer edge and thick, coarse, long bristles to apex, without gap or finer bristles separating outer and apical series of setae (Fig. 39).

Comparisons. A. n. maritima looks similar to *neglectula* but can be readily distinguished by the size, shape, punctations and dullness of the tegulae. In addition, it lacks the blue areas on the frons and is less rugose on the face, thorax and posterior surface of the propodeum. The general appearance of the propodeum is smoother than in *n. neglectula* but otherwise little different. The first flagellar segment of the male is entirely dark in *maritima* and the inner lobe of the gonostylus of the male genitalia is more heavily sclerotized and bears stronger setae than most *n. neglectula*, although intergradations exist. The oculo-ocellar ratios show that the top of the head is slightly narrower than that of *neglectula* and the head is longer in relation to the width. The overall impression is of a longer head with the eyes narrower and less emarginate, and the clypeus longer than in *n. neglectula*. The habitat of *maritima* appears to be distinct from that of *n. neglectula*; the former has so far only been found on the sand dune areas along beaches of the west coast of Mexico (circles, Fig. 87).

Augochlorella edentata Michener

Augochlorella edentata Michener, 1954, Bull. Amer. Mus. Nat. Hist. 104:58-59 (descr.).

Types. Holotype female, from Panamá, Coclé Province, El Valle de Antón, April 1, 1945 (Michener), is in the American Museum of Natural History. One female paratype each: type locality, January, 1947 (Krauss), at The University of Kansas; Canal Zone, Summit, November, 1946 (Krauss); Balboa, May 25, 1914, in shady jungle (Hallinan).

Description. Female: (1) Length 6 to 7 mm; head width 1.55 to 1.87 mm, averaging 1.66 mm, width greater than length. (2) Color yellow-green to dark green with silky sheen or luster; frons without blue reflections; metasoma usually similar in color to head and thorax. (3) Mandible dark brown, becoming yellow-brown just before rufous tip, without greenish reflections at base. (4) Clypeus about as long as wide, almost flat; basal half green with distinct but shallow punctures, widely but uniformly spaced, usually finely and closely punctured or roughened along basal suture; apical half brown, very slightly beveled, with elongate, shallow, groove-like punctures separated by about their own diameters; surface between punctures shiny and smooth. (5) Face broadly convex from apex of clypeus to vertex; supraclypeal area flat to weakly rounded, smooth and shiny to minutely roughened with or without punctures. (6) Paraocular area finely and uniformly roughened throughout by widely scattered minute granules. (7) Antenna dark brown, becoming yellow-brown at tip; last flagellar segment entirely yellow-brown; flagellum lighter below than above; pedicel width subequal to length, first flagellar segment almost twice as wide as long; pedicel longer than and about as wide as first flagellar segment. (8) Scutum without distinct punctures, surface finely and irregularly roughened throughout (Fig. 79); anterior margin smooth medially to anterolateral angles, except for minute reticulations on surface. (9) Tegula about 1.33 times as long as wide. (10) Scutellum finely and irregularly roughened, without punctures. (11) Pleuron finely rugose, weakly areolate anteriorly. (12) Propodeum with disc almost twice as long as metanotum; outline of disc semicircular to broadly

U-shaped, profile type 4; posterior edge of disc smoothly and gradually rounded medially and laterally; striae fine and close, irregular and branching medially, straight and distinct laterally, occupying basal half to two-thirds of disc medially, sometimes attaining edge laterally; area beyond striae minutely reticulated; horizontal area of propodeum only partially occupied by disc laterally and at posterolateral corners; posterior vertical surface exceedingly finely and evenly granular in larger specimens, smooth and shiny with widely spaced minute punctures in smaller specimens; posterolateral corners finely roughened to nearly smooth; lateral vertical surface weakly roughened. (13) Legs brown with slight metallic reflections on hind coxa only. (14) Metasomal terga dark green to golden-green, suffused with brownish in some specimens; first tergum with anterior surface polished with widely scattered punctures laterally; dorsal surface with minute punctures evenly spaced; second tergum with minute punctures, more crowded than on first; first sternum without metallic reflections. (15) Pubescence white to golden-white dorsally on head and thorax, dorsally and ventrally on metasoma; white ventrally on head, thorax and basal parts of legs; golden on tibiae and tarsi.

Male: (1) Length 6 mm; head width 1.48 to 1.63 mm, averaging 1.56 mm, width slightly greater than length. (2) Color olive-green with yellow-green sheen, varying to yellow-green with golden sheen in some specimens; frons without bluish reflections; metasoma dark brown. (3) Mandible yellow-brown, only slightly rufous at tip, basal condyles usually dark brown; basal metallic reflections absent. (4) Clypeus with punctures shallow and widely spaced, sometimes closer basally; surface between punctures brightly polished. (5) Face broadly convex from apex of clypeus to vertex; supraclypeal area scarcely protuberant, impunctate but variably roughened. (6) Paraocular area smooth and polished below level of antenna with a few, widely spaced, minute punctures, becoming rougher toward frons; frons with dense mat of short white pubescence extending from antennal sockets to vertex. (7) Flagellum slightly darker above than below; scape and pedicel dark brown; last one and a half to two flagellar segments uniformly dark brown; pedicel and first segment each less than twice as wide as long. (8) Scutum shiny with satiny luster; punctures very weak, sparse and widely spaced (wider than own diameters), minute centrally, larger and closer laterally, becoming slightly deeper and contiguous to weakly and finely punctorugose anterolaterally; anterior margin smoothest medially, becoming rougher laterally; sculpturing exceedingly fine, shallow and indistinct (Fig. 79). (9) Tegula twice as long as wide. (10) Scutellum shiny, slightly roughened and punctate, punctures weak and widely spaced. (11) Pleuron shallowly and irregularly punctorugose, shallowly areolate anteriorly; surface between impression minutely roughened, dull. (12) Propodeum with disc about 1.75 times as long as metanotum; outline of disc U-shaped, posterior edge indistinct, smoothly and gradually rounded and shiny; striae distinct, fine, close, irregular, often branched, extending about three-fourths length of disc medially, reaching edge laterally; surface of disc beyond striae smooth, minutely reticulated, irregularly and minutely wrinkled; posterior vertical surface of propodeum and posterolateral corners shiny and smooth with widely spaced, minute punctures; lateral vertical surface of propodeum finely but regularly roughened becoming distinctly but shallowly punctate dorsally. (13) Legs dark brown; fore and hind coxae and femora with slight greenish reflections; tibiae and tarsi lighter brown at bases; hind basitarsus with erect hairs short, uniform in length, dense, slightly longer than width of segment; basal tuft indistinct. (14) Metasomal terga dark brown with slight bluish highlights and broad, reddish brown apical margins; first tergum polished anteriorly, with slight olive-green metallic reflections, smooth but less shiny dorsally, sparsely and minutely punctate; second and following terga smooth, dull, essentially impunctate but with widely scattered minute punctures; all sterna brown, finely and uniformly pubescent, without metallic reflections, with apical margins straight; surfaces smooth without reticulations or punctures. (15) Pubescence golden dorsally, white ventrally; face with mat of short, dense, white hair from antennae to vertex and longer, fine, golden hair dispersed over entire face; pubescence golden dorsally on thorax, entire metasoma and legs, white ventrally on head and thorax. (16) Genital capsule, seventh and eighth sterna and eighth tergum type 3 (Figs. 36, 42, 47).

Comparisons. This species has certain affinities with both the species of the north and those of the *Pereirapis* group. It is small, has the convex face and the similar fine, smooth sculpturing and discal shape, and has the straight margin of the fourth sternum in the male, all as in *Pereirapis.* But the genital capsule and the white apex of the clypeus of the male are more similar to those of the North American species than to *Pereirapis. A. edentata* is characterized by its round, convex face (Fig. 55), comparatively smooth, fine and very shallow body sculpturing, and usually by the yellow tipped antennae in the female. The clypeus is also flatter than in other North American species but comparative material is necessary to recognize this character.

Variation. The body color in both males and females varies from dark green to yellow-green. Although the bee is shiny, the color is dull, with olive-green tones. In females, the metasoma is green or only slightly suffused with brown in some of the darker specimens, or yellower green in lighter colored individuals. The metasoma is consistently brown in males.

There is greater variation of the head width to length ratio in females than in males. (However, the available males are nearly all from the same population.) Both the length and width are variable in females.

The clypeal punctures are generally rather uniform in males but variable in size, number and spacing in females. The basal punctures range from absent to crowded in both sexes.

The tips of the antennae of females are brownish yellow in all specimens examined from Mexico and Costa Rica, the intensity of the yellow varying only slightly. However, in the holotype the antennal tips are brown, only inconspicuously paler than the rest of the flagellum. The one paratype seen, also from the type locality, has the antennal tips yellower than the holotype but darker than those from Mexico and Costa Rica. More specimens should be examined to see if this is individual or geographical variation.

There is slight variation in the quality of the roughening of the scutum among females. On about half the specimens the smoothness of the anteromedial edge extends down each side of the median suture, creating a transverse gradient in degree of roughness from the center line to the parapsidal lines. However, the anterolateral angles are no more roughened than other parts of the scutum in either sex.

The punctures on the scutellum are variable in size, number, spacing and depth among males.

There is little variation in the propodeal area of males, but in females the length of the striae is variable, extending more than two-thirds the length of the disc in only one specimen [“Rin Antonio” (9*)]. In this specimen, only a small area is unstriated medially, and the lateral striae are strong, ending abruptly at the edge. Although lateral striae usually reach the edge, they my be shorter in the larger specimens. The sloping horizontal area of the propodeum is usually only partially occupied by the disc laterally, the rest of the horizontal area being characterized by sculpturing similar to that of the vertical surface (Fig. 67). The posterior vertical surface in females varies from very smooth, broken only by widely scattered minute punctures, to weakly uneven or slightly roughened. There is also some variation in amount of roughening of posterolateral angles. There is little variation in the lateral vertical surface.

The metasomal punctures are similar in all specimens; however, in females they may vary somewhat in depth and are barely detectable in some individuals.

The color of the pubescence is difficult to determine in most specimens of both sexes, usually because of wear or dirt. Some appear lighter than others so that the dorsal pubescence appears to range from all white to golden. The short, dense facial pubescence is matted and gummy in most specimens, giv-

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* See Table 1.

ing the face a yellowish cast. This facial hair is worn away on some specimens.

Distribution. This species has been taken only as far north as southern San Luis Potosí in Mexico. It ranges at least as far south as Panama and has been taken at elevations from 200 to 4500 feet (Map: Fig. 88).

The following specimens have been seen: MEXICO. MORELOS: 1 ♂, 2 ♀ (3 mi. N. Alpuyeca 3400 ft.; S. end Cuernavaca 4500 ft.) (March-April); OAXACA: 1 ♀ (Rin Antonio); SAN LUIS POTOSÍ: 12 ♂, 4 ♀ (Huichihuayan; Xilitla 1450 ft.; 5 mi. E. Xilitla) (July, September); VERACRUZ: 1 ♂, 6 ♀ (17 mi. NW. San Andrés Tuxtla 900 ft.; 6 mi. N. Jesús Carranza, Isthmus of Tehuantepec 200 ft.; 1.4 mi. N. Santiago Tuxtla 1150 ft.; Córdoba) (January, June).

GUATEMALA. ALTA VERAPAZ, 2 ♀ (Trece Aguas) (June).

Fig. 88. Distribution of *A. aurata* (solid dots) and *edentata* (rings).

EL SALVADOR. LA LIBERTAD, 6 ♀ (5 mi. W. Quezaltepeque) (June-August).

COSTA RICA. CARTAGO: 3 ♂, 1 ♀ (Turrialba) (August); LIMÓN: 2 ♂, 12 ♀ (Pandora) (August); PUNTARENAS: 1 ♂, 14 ♀ (6 mi. NE. Esparta; Gromaco 34 km. SE. Potrero Grande, Río Coto Brus 1000 ft.; Playón, 8 mi. N. Parrita 30 m) (June-July, December); SAN JOSÉ: 2 ♂, 5 ♀ (Pozo Azul, junc. Ríos Parrita and Candelaria 85 m) (August).

PANAMÁ. See localities for type material above.

Seasonal Activity. Females of *edentata* are apparently active throughout the year; males have been collected from March through August but are probably active in other months as well. Pollen collectors have been found during June and July in Mexico and in August and December (1 specimen) in Costa Rica.

Augochlorella bracteata new species

Augochlorella aurata: Sandhouse, 1937, Jour. Washington Acad. Sci. 27:70 (in part) (taxon.).

Types. Holotype female, Southmost, Cameron Co., Texas, March 27, 1951 (R. H. Beamer) taken on *Prosopis*; allotype male, same locality, April 13, 1950 (Beamer, Stephen, Michener, Rozen); 45 female paratypes, same locality, March 27, 1951 (Beamer); 26 female paratypes, same locality and date (Michener); 4 male paratypes, Brownsville, Texas, June; 2 male paratypes, Cameron Co., Texas, August 3, 1928 (J. G. Shaw); 1 male paratype, Brownsville, Texas, April 17, 1952 (Michener, Beamer, Wille, LaBerge).

Holotype, allotype, 55 female and 3 male paratypes are in the Snow Entomological Museum of The University of Kansas; one male and four female paratypes are in each of the following: the American Museum of Natural History, the U.S. National Museum, the University of Nebraska and the California Academy of Sciences. I have seen 14 males and 137 females from other localities in Texas and Mexico, not included in the type series. The holotype and female paratypes represent a series of large and uniformly similar bees, probably spring queens. Not included in this series are smaller and more morphologically diverse specimens, including probable worker-like individuals.

Description. Female: (1) Length 5 to 6 mm; head with 1.47 to 1.79 mm (holotype=1.79 mm), averaging 1.63 m, width equal to, or slightly greater than length. (2) Color yellow-green to dark green (bright green in holotype); frons without bluish reflection; metasoma often slightly browner than rest of body. (3) Mandible with basal third dark brown, yellowish brown centrally, rufous at tip, without green basal reflections. (4) Clypeal width equal to or subequal to length (length slightly greater than width in holotype), basal two-thirds green, punctures variable, irregularly spaced, smaller basally than apically; apical third brown and slightly beveled with large, deep punctures; surface between punctures shiny and smooth. (5) Supraclypeal area sparsely punctured medially, becoming densely punctured peripherally; surface smooth to minutely reticulated. (6) Paraocular area with large contiguous punctures below antenna, finely rugose above antenna. (7) Antenna dark brown; flagellum usually lighter below than above; pedicel longer than wide; first flagellar segment slightly wider than long; pedicel longer and narrower than first segment. (8) Scutum smooth, finely and uniformly punctured throughout, punctures small, close, distinct, extending almost to anterior edge; anterior edge with surface slightly roughened medially as on vertex becoming slightly rougher laterally to very finely rugose at anterolateral angles. (9) Tegula 1.5 to 2.0 times as long as wide. (10) Scutellum rough with fine, shallow, irregular to indistinct punctures. (11) Pleuron punctorugose to shallowly and finely rugose (finely punctorugose in holotype), areolate anteriorly. (12) Propodeum with disc equal to or slightly longer or shorter than metanotum (slightly longer in holotype); outline of disc semicircular, profile type 2, posterior edge of disc abruptly rounded, indistinct, more gradually rounded laterally; striae irregular, vermiform or straight (rather straight in holotype), fine and close together, usually ending almost at edge of disc medially, straight and reaching edge but not crossing it laterally; surface at ends of striae minutely roughened, narrowly shiny; posterior vertical surface and posterolateral corners shiny but surface uneven, without punctures or coarse roughening, often weakly granular posteriorly and finely granular at posterolateral corners; lateral surface moderately roughened to weakly rugose (weakly rugose in holotype), without basal subhorizontal rugae. (13) Legs brown, fore and hind coxae with strong green reflections, femora and hind trochanter with weak metallic reflections. (14) Metasomal terga green, suffused with brownish; apical margins narrowly pale brown; first tergum shiny, polished, with numerous, fine, distinct punctures anteriorly, almost impunctate along narrow median longitudinal area, smooth and shiny dorsally with numerous, small, close, distinct, regularly spaced punctures; second tergum with punctures more numerous and smaller; first sternum without metallic reflections. (15) Pubescence golden-white dorsally, white ventrally on head, thorax and basal parts of legs, golden on leg extremities and ventral part of metasoma.

Male: (1) Length 5 to 6 mm; head width 1.53 to 1.76 mm, averaging 1.63 mm, width less than, equal to, or greater than length (width equal to length in allotype). (2) Color yellowish green to dark green; frons without bluish reflections; metasoma variably suffused with brownish. (3) Mandible without metallic reflections basally. (4) Clypeus with punctures large medially, small and close basally and laterally; surface between punctures usually smooth and shiny. (5) Supraclypeal area finely punctate laterally; surface shiny basally, usually minutely roughened above. (6) Paraocular area finely and weakly rugosopunctate. (7) Antenna dark brown above, dark yellow below; scape usually narrowly yellow below; last flagellar segment entirely pale brown to dark brown, pedicel and first flagellar segment each less than 1.5 times as wide as long. (8) Scutum shiny and smooth with punctures small, distinct, usually separated by at least the width of a puncture medially, closer laterally and anteromedially; anterior margin weakly roughened as on vertex, becoming weakly rugose at extreme anterolateral angles. (9) Tegula slightly more than 1.5 times as long as wide. (10) Scutellum shiny and punctate; punctures distinct, closer posteriorly than elsewhere. (11) Pleuron rugosely punctate, areolate anteriorly. (12) Propodeum with disc slightly longer than metanotum; outline of disc obtusely V- or U-shaped to semicircular (semicircular in allotype), posterior edge sharply angulate to gradually rounded (abruptly rounded in allotype); striae fine to coarse, regular to irregular (fine and irregular in allotype), reaching edge medially, crossing edge laterally; marginal surface narrowly shiny and slightly roughened posteriorly, shiny posterolaterally; posterior vertical surface either with widely separated shallow punctures and surface between punctures shiny, or weakly roughened and impunctate; posterolateral corners evenly punctate; lateral vertical surface more closely punctate with punctures usually distinct, regular, separated by about the width of a puncture; surface between punctures finely roughened or entire surface weakly rugosopunctate (punctate in type). (13) Legs light brown; fore and hind coxae, trochanters and femora with metallic reflections; tibiae light brown, yellow-brown at apices; tarsi uniformly pale yellow-brown; hind basitarsus with erect hairs of uniform length, about as long as width of basitarsus, basal tuft slightly shorter. (14) Metasomal terga dark green, usually suffused with brownish, yellowish or reddish with apical margins brownish, scarcely contrasting in color with rest of tergum; first tergum polished anteriorly with small, widely spaced punctures throughout; smooth but less shiny dorsally, with punctures variable, usually large, distinct and irregularly spaced; second tergum with punctures of same size but very closely spaced; sterna dark brown, smooth, with short inconspicuous white pubescence; first sternum with weak metallic reflections; fourth sternum broadly and shallowly emarginate. (15) Pubescence short and white over entire body. (16) Genital capsule, seventh and eighth sterna and eighth tergum of type 1 (Figs. 31, 40, 43).

Comparisons. The females of this species look most like *persimilis* or the *striata-persimilis* integrades. The size is small, at most the size of *persimilis.* The female can be distinguished from the other species found in the United States by its small size, the small but distinctly separated punctures on the scutum, and the lack of coarse roughening or rugosity anteriorly on the scutum (Fig. 78). It is further separated from *gratiosa* and *neglectula* by the very smooth posterior surface of the propodeum. Although this is also consistently smoother than *aurata*, *persimilis* or *striata*, the differences among these species in the posterior surface of propodeum are usually too slight to be recognized without comparative material.

The male is about the size and color of the male of *persimilis* but has the characteristics of a small *striata* with an emarginate fourth sternum, short basitarsal hair, and with the last segment of the antenna dark. The male genitalia are not perceptibly different from those of other members of the eastern species group, although there is a tendency for the process of the inner lobe of the gonostylus to be shorter and blunter than in other species (Fig. 31). Like the female, the male can be distinguished from all forms of *striata* by both its small size and its smooth but distinctly punctured scutum.

Variation. The greatest variation in *bracteata* is found in the characters of the propodeum. Males are in general more variable than females, the females varying chiefly in connection with differences in size. There is little geographical variation, probably due to the limited range and to the few specimens available outside of Texas.

As with most of the eastern species of *Augochlorella*, there is considerably more size variation in females than in males. This may be due to caste differences. In females the width of the head is usually greater than the length, but sometimes the width and length are equal. No such general pattern can be established for the males since the length-width ratio is highly variable, even though the overall variation in size is not great.

Color varies from dark green to yellow-green in both males and females, with no apparent correlation between size, date or location. There seems to be an unusual amount of discoloration, fading or bleaching in many of the specimens, especially on the metasoma. Among males, many of the specimens are coppery or reddish (see section on Specific Characters). In spite of the large proportion of specimens thus discolored, freshly caught specimens are probably normally green.

The number and size of punctures on the clypeus of the female is variable. When the punctures are sparse, the clypeus looks smooth, shiny and gently rounded, with the apex also smooth. This condition is apparent especially in the smaller (worker?) individuals. There is little variation in the size and density of punctures in males.

The supraclypeal area in both males and females is usually punctate, with the surface between punctures variably roughened. A female with a sparsely punctate clypeus will usually have a sparsely punctate supraclypeal area, with the central portion smooth and shiny. In the male the supraclypeal area may be shiny with few punctures (14% of the specimens) or with the upper half rough and lower half shiny (67%) or entirely rough (19%).

There is little variation in the punctation of the thorax except as related to the size of the individual bee. On particularly small females the punctures are exceeding small and close and may give the scutum the appearance of being granular rather than punctate.

The rugosity of the mesepisternum also becomes very fine on small females so that the surface may look similar to that of the metepisternum.

The disc is the most variable structure in this species. Although the edge is rounded in both males and females, it may be smooth and shiny, minutely or weakly roughened, or smooth with minute reticulations. In males the punctures of the posterior vertical surface of the propodeum may reach the dorsal part of the edge on some shiny specimens, and the edge may be more or less sharply defined (but never carinate) with shininess often associated with a rounded edge and dullness with a more distinct edge. A V-shaped depression is rarely apparent but may be indicated on those specimens with a relatively defined edge.

The shape of the disc shows little variation in females. In all cases it is semicircular, like that found in *persimilis* or in the *persimilis-striata* intermediates. There is somewhat more variation in males, with the outline varying from semicircular to roundly V-shaped, but not bracket-shaped as in *striata* form A. The striae may be of any thickness from very fine to coarse, especially in males, and may vary from straight to vermiform or, as in some small females, may be so irregular as to be unrecognizable as striae. Striae usually reach the edge of the disc, at least medially, where they are usually branched or irregular. In both sexes they are frequently slightly shorter on each side of the median line, where the edge then becomes thicker (see Fig. 66). The striae are straighter and more regular in the larger females than in smaller ones. There is as much variation in the characters of the disc as in *persimilis* and its intermediates, with some specimens resembling the small *striata* form C and others resembling *persimilis*.

The posterior surface of the propodeum is smoother in some females than others but never equals the smoothness of the anterior part of the first tergum. The roughening takes the form of fine granulations or irregularities on an otherwise smooth surface.

The lateral vertical surface of the propodeum ranges from rugose to finely roughened in the females and distinctly and evenly punctured to weakly roughened, largely punctorugose or finely reticulate, in the males.

The metasomal punctures are variable in both sexes, although the type series of 72 females, all collected at the same time and place, are similar in this feature. The punctures on the first tergum in females may be absent in some small specimens or small and irregularly spaced to large, distinct, and closely spaced. There is little indication of regional variation, although most specimens with large, close punctures are from southern Texas. The four specimens from Mexico have small to minute punctures. In males the punctures of the first tergum vary from very small to large, close to widely spaced, with no regional pattern evident. The second tergum of females usually has very small punctures regardless of the size of those of the first tergum. In males both the size and the spacing of punctures on the second tergum are variable, but usually the punctures are smaller than on the first. The third tergum in males sometimes has small but distinct punctures.

There are a few females with all white pubescence over the body. These are usually discolored individuals with brown metasoma (Victoria, Kingsville, etc.).

Distribution. From northeastern to southern Texas, southward through eastern Mexico to Hidalgo (Map: Fig. 85).

In addition to the type series, 14 males and 137 females were seen: TEXAS: *Bexar Co.*, 5 ♀ (March, July-August); *Blanco Co.*, 2 ♀; *Cameron Co.*, 6 ♂, 33 ♀ (January-August, September); *Comal Co.*, 1 ♀ (May); *Dallas Co.*, 8 ♀ (March-May); *Hidalgo Co.*, 1 ♂, 4 ♀ (April-June); *Jackson Co.*, 2 ♀ (March); *Karnes Co.*, 6 ♀ (March, September); *Kleberg Co.*, 1 ♀ (June); *Lee Co.*, 2 ♂, 20 ♀ (February-June, September); *Mavarick Co.*, 3 ♀ (April); *Nacogdoches Co.*, 1 ♀ (June); ?*Nueces Co.*, 1 ♀ (April); *Refugio Co.*, 1 ♀ (April); *Robertson Co.*, 15 ♀ (April); *San Patricio Co.*, 3 ♀ (June-July); *Travis Co.*, 1 ♀; *Val Verde Co.*, 1 ♂, 1 ♀ (May-June); *Victoria Co.*, 1 ♂, 20 ♀ (March-April, September, November); *Webb Co.*, 6 ♀ (December); *Wilson Co.*, 1 ♀ (October).

HIDALGO: 1 ♂, 3 ♀ (18 mi. NE. Jacala 4750 ft.) (June). NUEVO LEÓN: 1 ♀ (General Terán) (July).

Seasonal Activity. The females are apparently active throughout the year, and the males are present at least from March through November. None of the 30 females taken between October and February was collecting pollen, and most of these specimens were clean and unworn, although both larger and smaller individuals were represented. Of the 90 specimens taken in March, the only 5 collecting pollen were captured on or after the 24th of the month. From April through September many specimens have pollen in the scopa; one was taken with a pollen load as late at September 29.

From these data it would seem that although the bees are active throughout the year, nesting takes place only from early spring into September. From variations in size of females it also seems that this species probably does have a worker caste, as do *striata* and *persimilis* (see Ordway, 1965a).

Flower Records. Agastache, Callirhoe, Chamaesaracha, Coreopsis, Dalea, Englemannia, Haplopappus, Helenium, Helianthus, Monarda, Oenothera, Opuntia, Phacelia, Prosopis, Pyrrhopappus, Ratibida, Rubus.

Augochlorella gratiosa (Smith)

Augochlora gratiosa Smith, 1853, Catalogue of the Hymenoptera in the British Museum 1:80 (descr.); Dalla Torre, 1896, Catalogus Hymenoptorum 10:95 (list); Bingham, 1897, Trans. Amer. Ent. Soc. 24:162 (list); Cockerell, 1905, Trans. Amer. Ent. Soc. 31:363 (list).

Augochlora (Augochlorella) gratiosa: Michener, 1951, *in* Muesebeck *et al.* U.S. Dept. Agr., Agr. Monogr. 2:1125 (list); Montgomery, 1957, Proc. Indiana Acad. Sci. 66:132 (list, fl.).

Augochlora festiva: Graenicher (not Smith, 1853), 1930, Ann. Ent. Soc. Amer. 32:157 (list, fl.).

Augochlorella gratiosa: Sandhouse, 1937, Jour. Washington Acad. Sci. 27:69 (tax.); Lovell, 1942, Kentucky Acad. Sci. Trans. 10:20, 21, 23 (key, descr.), Michener, 1954, Amer. Mus. Nat. Hist. Bull. 104:55 (descr.); Mitchell, 1960, Bees of the Eastern United States 1:460 (tax.).

Types. Augochlora gratiosa, holotype female, from Georgia, is in the British Museum (Natural History). Although labels on the holotype agree with those indicated by Smith's published description of *gratiosa*, the description agrees better with the holotype of *aurata*. Conversely, his description of *aurata* fits best the type of *gratiosa*. All recent descriptions and most determinations of *gratiosa* agree with the *gratiosa* type and not with Smith's description. Since Smith himself probably mixed labels and descriptions, since his descriptions are scarcely decisive, and since utmost confusion would result from reversing the application of the names in a group already so difficult taxonomically, it seems best to follow usage and the labeled types, which bear the proper locality data, and ignore the inconsistencies in the descriptions. I have not seen the types, but Dr. C. D. Michener took detailed notes on them and compared them with submitted specimens.

Description. Female: (1) Length 6 to 7 mm; head width 1.68 to 2.13 mm, averaging 1.92 mm; head length to width ratio variable. (2) Color yellowish green to blue; frons often with slight bluish reflections; metasoma usually more yellow or brownish than head and thorax. (3) Mandible without metallic coloration basally. (4) Clypeal width about equal to length, basal two-thirds shiny green with punctures irregular in size and shape, smaller and closer at margins of clypeus than centrally; apical third brown and slightly beveled with punctures large, elongate; surface between punctures smooth and shiny. (5) Supraclypeal area usually impunctate medially, lateral punctures variable in size, surface between punctures minutely roughened laterally. (6) Paraocular area punctorugose below level of antennae, coarsely rugose above. (7) Antenna dark brown; flagellum slightly lighter below than above; first segment of flagellum less than 1.5 times as wide as long, pedicel slightly longer and narrower than first flagellar segment with ratio of length to width variable. (8) Scutum roughly punctate to rugosopunctate; punctures small and contiguous; anterior margin rugose, becoming areolate at anterolateral corners. (9) Tegula almost 1.5 times as long as wide. (10) Scutellum coarsely roughened and granular, punctures indistinct or absent. (11) Pleuron coarsely rugose, areolate anteriorly. (12) Propodeum with disc equal to or shorter than metanotum; outline of disc bracket-shaped, profile type 1; posterior edge of disc sharply angulate posteriorly, rounded laterally; striae fine, straight, close together, extending full length of disc; posterior vertical surface finely, unevenly roughened or granular, usually dull, occasionally with very fine, indistinct, irregular, subhorizontal rugae; posterolateral corners coarsely and often linearly roughened; lateral vertical surface weakly rugose, rugae usually lineate along anterior and ventral edge, reticulate centrally. (13) Legs brown; fore and hind coxae and outer surface of fore femur with metallic reflections. (14) First metasomal tergum with anterior surface minutely and sparsely punctured, polished and finely pubescent; surface less shiny dorsally with close, minute punctures; second tergum with surface minutely reticulated, similar to following terga; sternum without metallic reflections. (15) Pubescence white ventrally on head and thorax, golden elsewhere; short and dense on genal area.

Male: (1) Length 6 to 8 mm; head with 1.72 to 2.00 mm, averaging 1.86 mm, greater than, equal to or less than length. (2) Color yellow-green to royal blue, usually bright, shiny green; frons without blue reflections on green specimens; metasoma usually slightly redder than rest of body or color uniform over entire body. (3) Mandible usually with metallic reflections basally. (4) Clypeus with large, irregularly shaped punctures separated by less than their diameters; surface between punctures smooth and shiny. (5) Supraclypeal area with punctures large, shallow and close; surface between punctures minutely roughened. (6) Paraocular area with punctures small, deep and crowded. (7) Flagellum brown above, yellow-brown below; scape dark brown except for narrow light area below; pedicel usually all yellow; last flagellar segment entirely dark; pedicel and first flagellar segment each less than 1.5 times as wide as long. (8) Scutum rough, with punctures deep and distinct medially, deep and contiguous at parapsidal lines, becoming rugose anteriorly; anterior margin variably roughened medially, rugose to areolate laterally. (9) Tegula 1.5 times as long as wide. (10) Scutellum shiny, coarsely punctate, punctures irregular in size and spacing. (11) Pleuron rugose, more coarsely so anteriorly. (12) Propodeum with disc equal or subequal in length to metanotum; outline of disc weakly bracket-shaped, dorsal surface slightly concave, posterior edge sharply to weakly angulate, well defined, rounded laterally; striae usually straight, regular, fine, widely to narrowly spaced, reaching edge posteriorly and laterally; posterior vertical surface coarsely rugose, usually without punctures; posterolateral corners rounded with posterior rugosity extending onto lateral surface; lateral vertical surface less coarsely rugose than posterior surface, rugae lineate, perpendicular to anterior and ventral edges. (13) Legs brown, fore and hind coxae brightly metallic anteriorly; trochanters and femora with at least slight metallic reflections; tibiae dark yellow, usually brownish centrally; basitarsi pale yellow with following segments slightly darker; posterior basitarsus with erect hairs very long on basal third of segment, four times as long as width of basitarsus, curved at tips, becoming shorter on apical two-thirds of segment; basal tuft reduced, often inconspicuous. (14) Metasomal terga green, sometimes lighter or browner than thorax; first tergum polished anteriorly with punctures separated by slightly more than their diameters medially, closer laterally, surface smooth but less shiny dorsally, with punctures slightly larger, more distinct and denser; second tergum with punctures similar to first; first sternum strongly metallic, fifth and sometimes fourth sterna with feeble metallic reflections; fourth sternum deeply and broadly emarginate apically. (15) Pubescence white to golden-white over entire body, yellowish on tarsi. (16) Genital capsule, seventh and eighth sterna and eighth tergum of type 1 (Figs. 34, 40, 44).

Comparisons. A. gratiosa is not a very common species. It has been collected during all months of the year and most frequently from Georgia and Florida. It comes in contact with *persimilis*, *aurata*, *striata* and *bracteata*, the females intergrading morphologically with both *aurata* and *striata*. Although the males of *gratiosa* are distinct and can usually be identified by the key characters (see exception below), females are more difficult to distinguish and the subtle differences can be difficult to recognize unless samples of each are available.

A. gratiosa is characterized chiefly by the propodeal characters in the females. The disc is as short as or shorter than the metanotum (Fig. 58). Its posterior border is usually well delineated, sometimes by a weak carina but more usually by its abruptly declivitous edge which has a weak, medial, V-shaped depression (Figs. 12, 20). The striae are fine, straight, and distinct, extending the full length of the disc; the posterior vertical surface is dull and granular, usually with short subhorizontal lineate irregularities (Fig. 76). The second metasomal tergum is granulose and similar to the following terga rather than minutely punctulate as is the first tergum.

Females of *gratiosa* differ from *aurata* by the distinct, clear-cut features of the propodeal disc, by the complete, straight striae and the nature of the posterior face and second metasomal tergum. Although *aurata* may also have striae as fine and close together as those of *gratiosa*, they are rarely as straight or regular, nor do they extend onto the posterior margin of the disc (Fig. 57). Also, in *aurata*, the edge of the disc is less sharply posteriorly, usually without the medial V-shaped depression, and the posterior surface is smoother, shinier and lacks the lineate irregularities. In Texas, the two species are easily distinguished by the above characters and in addition, the first metasomal tergum is strongly punctate in *aurata* (Fig. 82) but finely punctate as usual in *gratiosa* (Fig. 83). In *striata* the striae usually extend the full length of the disc, the disc in form A is frequently as well delineated posteriorly as in *gratiosa*, possesses the V-shaped depression and may approximate the bracket-shaped outline of *gratiosa*. However, if the striae are as straight and regular as those of *gratiosa* they usually are considerably coarser (fewer in number with greater space between them). If they are as fine as those of *gratiosa* they rarely are as straight, regular or well defined. In addition, the posterior vertical surface of the propodeum in *striata* is smoother, shinier, with minute punctures and without the lineate granular irregularities found in *gratiosa*, and the second tergum is similar to the first rather than the third or fourth terga.

A. gratiosa is apparenly more closely related to *striata* A or *aurata* than to any other group. There is comparatively little variation and variation attributed to it in the past is seemingly partly due to misidentification based chiefly, if not exclusively, on the nature of the propodeal disc. When other characters are also used, identification becomes easier. The strict definition of *gratiosa* is based chiefly on the distinct and unvarying characters in the male, as opposed to the high degree of variability found in males as well as females of *striata*.

Variation. The few variations that exist are associated chiefly with size and color. There is a wide variation in head size (Fig. 86) with the largest individuals being found in Louisiana and Alabama. A sample of 22 female specimens was measured from Florida, and all females from other states were measured. There is some indication that there may be caste differences in size although there is no correlation between width of head and season (i.e., large, small or average individuals may be found at any time of the year). Males show similar variations in size. The width of the head, with only a few exceptions is regularly greater than the length.

Body color is rather uniformly yellowish green except in Florida where it varies from dark green to deep violet-blue. Most males (14 out of 18) and about 40% of the females are blue in Florida. In these specimens there are weak metallic reflections at the bases of the mandibles in females and on the hind tibiae of males, variations rarely found in green specimens. Only 1 out of 20 females from Georgia [Tifton, Ga., 6-13-96, Lot 209 (38*)] showed such reflections on the mandibles and two green Floridian males had slight reflections on the hind tibiae [Jacksonville 9-3-11 (9); Levy Co., Fla., 9-10-55 (10)].

The extent of brown on the clypeus of females is variable from specimen to specimen with no apparent regional trend, but it does not exceed one-third of the total length.

The degree of roughness and amount of punctation on the supraclypeal area is also variable throughout the range. The frons shows very weak bluish reflections in most green specimens when the light is properly reflected from the surface but usually there are no readily visible spots of blue such as are found in *neglectula*. All blue-green specimens from Florida showed differential coloring on the various parts of the body with the head usually darker (bluer) than the thorax, and the metasoma lightest (greenest) in color.

In females from Louisiana the antennae are lighter below than above as usual, but the apical third of the flagellum is lighter above than the preceding segments.

The scutum in females is roughly and closely punctured throughout the range but is less so than that of *striata*. Punctures are usually distinct but are very close or become indeterminate or rugose anteriorly and laterally. This rugosity is not correlated with size, color or distribution, although in Florida rugosity occurs with higher frequency in blue specimens than in green ones (in 45% of the blue and 9% of the green).

The characters of the propodeum are remarkably stable in *gratiosa*, compared with the variability in the other eastern species. The sharply delineated disc is usually bracket-shaped and narrow in females, somewhat less distinctly so in males. Three of the seven females from Louisiana [2 from 8.5 a-l.ms. New Roads, 6-22-60 (20); Olivier, 5-04 (9)]; 2 of the 146 from Florida [Homestead 4-18-23 (32); Homestead 8-31-27 (9)] and one from Summerville, S.C. [5-10- (20)] out of seven seen, were found with a more rounded outline although it is difficult to draw the line between one type and the other. When the posterior margin is subbracket-shaped, the medial V-shaped depression is not evident and the sharply angulate edge becomes abruptly rounded. The size of the striae varies little and only in the males do the spaces between striae vary. On the lateral sides of the propodeum of females there may or may not be very fine lineate rugae perpendicular to the anterior and ventral margins. They are present in all males seen with the exceptions noted below in Texas. Again, this seems to be a variation within populations and not correlated with season or distribution.

The first sternum of the metasoma is variously metallic in females, strongly blue or blue-green in many darker specimens to brown with faint metallic reflections in others, especially the paler specimens.

The amount of metallic coloration on the legs of females is relatively constant although any or all trochanters and femora may be slightly colored in addition to the always colored fore and hind coxae.

All Floridian females have deep golden pubescence over all the body including the ventral parts of head and thorax, whereas in Texas, pubescence

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* See Table 1.

is paler with hairs whitish on the upper parts of the head and basal parts of the legs, in addition to the venter. The males do not vary in this character.

Male genitalia have the inner lobe of the gonostylus as shown in Figure 34. The fingerlike projection averages slightly longer than in the other eastern species but enough variation occurs in each of the eastern species that distinctions cannot usually be made. The outer lobe has long, unbranched hair as in other eastern species.

The two males from Texas [Nacogdoches, X-3-60 (42) and Victoria, VI-10-07 (9)] are divergent individuals falling between *gratiosa* and *persimilis*, not fitting either group well but appearing to be most like *gratiosa*. On the basis of characters 1, 3 and 7, the specimen from Nacogdoches is most like *gratiosa* (the specimen from Victoria is without a head). The thoracic and metasomal characters of both specimens resemble those of either *persimilis* or *gratiosa*, and the hind basitarsus of each specimen is intermediate between the two species although more similar to *gratiosa* than to *persimilis*.

Distribution. From New Jersey and Washington, D.C., southward to the keys of Florida, along the Gulf Coast states into southeastern Texas, extending inland as far as northern Georgia and eastern Tennessee (Map: Fig. 87).

A total of 29 males and 199 females have been seen: ALABAMA: *Mobile Co.*, 1 ♀; *Washington Co.*, 1 ♀ (June). FLORIDA: *Alachua Co.*, 1 ♂, 8 ♀ (February-May, August, October, December); *Bradford Co.*, 1 ♂, 1 ♀ (April); *Brevard Co.*, 1 ♂, 1 ♀ (April, November); *Broward Co.*, 2 ♀ (February, October); *Collier Co.*, 1 ♂, 5 ♀ (April); *Dade Co.*, 13 ♂, 49 ♀ (January-April, June-December); *Duval Co.*, 1 ♂, 2 ♀ (April, August, November); *Gadsden Co.*, 1 ♀ (April); *Hendry Co.*, 2 ♀ (July, October); *Hernando Co.*, 1 ♀ (December); *Highlands Co.*, 6 ♀ (April-June, August); *Hillsborough Co.*, 3 ♀ (April, August); *Lake Co.*, 8 ♀ (January-February, April); *Lee Co.*, 1 ♀ (March); *Levy Co.*, 1 ♂, 19 ♀ (February, April, June, September); *Manatee Co.*, 2 ♀ (February, April); *Marion Co.*, 4 ♀ (February, April); *Martin Co.*, 1 ♀ (March); *Monroe Co.*, 4 ♀ (January, May); *Nassau Co.*, 4 ♀ (July-August); *Orange Co.*, 4 ♀ (February-April, December); *Palm Beach Co.*, 2 ♀ (March, September); *Pasco Co.*, 3 ♀ (January, August); *Polk Co.*, 2 ♀ (May, September); *Putnam Co.*, 6 ♀ (May); *Seminole Co.*, 1 ♀; *St. Lucie Co.*, 1 ♀ (April); *Volusia Co.*, 1 ♀. DISTRICT OF COLUMBIA: 1 ♂ (May). GEORGIA: *Haralson Co.*, 1 ♀ (June); *Lowndes Co.*, 2 ♀ (July); *Thomas Co.*, 2 ♀ (April); *Tift Co.*, 5 ♂, 14 ♀ (June); *Townes Co.*, 1 ♂ (August); *Walker Co.*, 1 ♀ (June); *Ware Co.*, 1 ♂, 2 ♀ (July). LOUISIANA: *East Baton Rouge Parish*, 2 ♀ (July); *Iberia Parish*, 1 ♀ (May); *Pointe Coupée Parish*, 3 ♀ (June); *Tangipahoa Parish*, 1 ♀ (June). MISSISSIPPI: *Forrest Co.*, 3 ♀ (August-September). NEW JERSEY: 1 ♀. NORTH CAROLINA: *Columbus Co.*, 1 ♀ (August); *Moore Co.*, 1 ♀ (November); *Tyrrell Co.*, 1 ♀ (July); *Wake Co.*, 3 ♀ (April-May). SOUTH CAROLINA: *Dillon Co.*, 3 ♀ (April); *Dorchester Co.*, 1 ♀ (May). TENNESSEE: 1 ♀. TEXAS: *Colorado Co.*, 1 ♀ (March); *Jackson Co.*, 3 ♀ (March); *Nacogdoches Co.*, 1 ♂ (October); *Victoria Co.*, 1 ♂ (June).

A single male (9) from Washington, D.C., and one female labeled "N. J. 1786" (9) were examined, although no specimens of this species have otherwise been taken north of North Carolina. One female [Chickamauga, Ga. VI-24-98 (38)] taken in the northwest corner of Georgia in Walker County and one female labeled "E. Tenn." (38) represent the most inland records. Although specimens are scarce and widely scattered in this region, they do not differ from others except that the individual from Walker County is somewhat paler with more brown on the metasoma than usual.

Lovell (1942) records this species from Jefferson County, Kentucky, in the north central part of the state. I have not seen any of his specimens but it seems unlikely that *gratiosa* ranges that far inland.

Seasonal Activity. Females of *gratiosa* are active throughout the year in Florida and have been taken from April through September in other states.

Fig. 89. Distribution of *A. gratiosa.*

Males have been collected from March through December in Florida and June through October elsewhere. Pollen collectors are found from mid-April at least through July and probably well into the fall throughout the range and from the end of February to September in Florida.

Flower Records. Aster, Ampelopsis, Asclepias, Berteroa, Bidens, Callicarpa, Cassia, Chrysobalanus, Chrysopsis, Cirsium, Citrus, Clethra, Crataegus, Crotonopsis, Cunila, Erigeron, Eryngium, Galactia, Gerardia, Gossypium, Helianthus, Hypericum, Ilex, Ixora, Jacquemontia, Lepidium, Malva, Melilotus, Aenothera, Opuntia, Piriqueta, Polygala, Polygonum, Pterocaulon, Pycnothymus, Rhus, Rubus, Sabal, Senecio, Solidago, Taraxacum, Teucrium, Vaccinium, Verbena, Warea.

Augochlorella aurata (Smith)

Augochlora aurata Smith, 1853, Catalogue of the Hymenoptera in the British Museum 1:82 (descr.); Cresson, 1887, Trans. Amer. Ent. Soc., Suppl. 14s:293 (list); Dalla Torre, 1896, Catalogus Hymenoptorum 10:94 (list); Bingham, 1897, Trans. Amer. Ent. Soc. 24:162 (list); Brimley, 1938, Insects of North Carolina p. 454 (list, fl.).

Augochlora austrina Robertson, 1893, Trans. Amer. Ent. Soc. 20:147 (descr.); Dalla Torre, 1896, Catalogus Hymenoptorum 10:94 (list); Cockerell, 1922, Proc. U.S. Nat. Mus. 60:16 (descr.).

Augochlora (Augochlorella) aurata: Michener, 1951, *in* Muesebeck *et al.,* U.S. Dept. Agr., Agr. Monogr. 2:1125 (in part) (list).

Augochlorella aurata: Sandhouse, 1937, Jour. Washington Acad. Sci. 27:71 (in part) (tax.); Mitchell, 1960, Bees of the Eastern United States 1:459 (in part).

Types. Augochlora aurata, holotype female, from St. John's Bluff [? St. Johns Co.], Eastern Florida, is in the British Museum (Natural History). Although labels on the holotype agree with those in Smith's published description of *aurata*, the description agrees best with the holotype of *gratiosa*. Conversely, his description of *gratiosa* better fits the type of *aurata*. For further discussion of this problem, see *Augochlorella gratiosa*. I have not seen the type but Dr. C. D. Michener took detailed notes on it and compared it with submitted specimens. *Augochlora austrina*, holotype female, No. 12859 [Robertson's number], from Inverness [Citrus Co.], Florida, 1892, is in the Robertson Collection at the Illinois Natural History Survey. For the most part, the *aurata* of Sandhouse (1937) and Mitchell (1960) is *persimilis*.

Description. Female: (1) Body length 7 mm; head width 1.58 to 1.98 mm, averaging 1.84 mm, width to length ratio variable. (2) Color yellow-green to blue-green; frons without bluish reflections on green specimens, metasoma similar in color to other body regions. (3) Mandible with basal third dark brown, yellow-brown centrally, rufous at tip, rarely with metallic reflection at base. (4) Clypeal width subequal to length; basal part green with large, irregularly spaced punctures; apical fifth or less, brown, brown area not exceeding one-third, slightly beveled; punctures in brown area round, or slightly elongate when brown area exceeds diameter of puncture; surface between punctures usually shiny and smooth. (5) Supraclypeal area variably punctate, surface between punctures shiny and smooth or finely roughened. (6) Paraocular area punctorugose to rugose below antenna, more coarsely rugose above. (7) Antenna dark brown, often slightly lighter below than above; pedicel with length subequal to width, first flagellar segment wider than long. (8) Scutum coarsely punctate; punctures close to contiguous over entire dorsum, similar to frons; anterior margin and anterolateral corners finely rugose to finely areolate. (9) Tegula almost twice as long as wide. (10) Scutellum roughened or shallowly and irregularly punctate. (11) Pleuron finely rugose, becoming areolate anteriorly. (12) Propodeum with disc equal to or slightly longer than metanotum; outline of disc bracket-shaped to semicircular, usually weakly bracket-shaped, forming blunt point medially, profile type 2; posterior edge of disc distinct, abruptly rounded to sharp, gradually rounded laterally; striae fine, close, wavy, usually irregular, ending just before edge or at edge medially, often leaving edge slightly raised, roughened and dull, reaching or crossing edge laterally; posterior vertical surface evenly and finely granular, not rough; posterolateral corners not prominent, usually slightly more roughened than posterior surface; lateral vertical surface weakly rugose. (13) Legs brown, fore and hind coxae, mid and hind trochanters and femora with metallic reflections. (14) First metasomal tergum with anterior surface shiny but not polished, with numerous widely spaced punctures; dorsal punctures minute and close, or large, close and distinct (Texas); first sternum without metallic reflections. (15) Pubescence golden-white on dorsum and legs and ventrally on metasoma; white ventrally on head and thorax; pubescence short and thick but not dense on genal area.

Male: (1) Length 7 mm; head width 1.81 to 1.91 mm, averaging 1.86 mm, width to length ratio variable. (2) Color bright green; often with bluish reflections on frons; metasoma often slightly redder or browner above than on other parts of body. (3) Mandible with dark metallic reflections basally. (4) Clypeus with punctures variable in size and spacing; surface between punctures shiny and smooth. (5) Supraclypeal area variably punctured with surface smooth and shiny or irregularly roughened. (6) Paraocular area finely punctorugose. (7) Flagellum dark brown above, yellowish brown below; scape dark brown; pedicel partially light brown above, dark brown below; last flagellar segment entirely dark brown; pedicel and first flagellar segment each about 1.5 times wider than long. (8) Scutum with punctures distinct but crowded medially, separated by less than their diameters, becoming contiguous at parapsidal lines; anterior margin rugose, becoming areolate laterally. (9) Tegula twice as long as wide. (10) Scutellum shiny, punctate to punctorugose. (11) Pleuron rugose, becoming areolate anteriorly. (12) Propodeum with disc equal to or slightly longer than metanotum; outline of disc weakly bracket-shaped to obtusely V-shaped, posterior edge abruptly rounded; striae fine, wavy and irregular, reaching edge posteriorly, crossing edge laterally; posterior vertical surface and posterolateral corners finely rugose or roughened; lateral vertical surface rugose. (13) Legs brown, with fore and hind coxae, trochanters and femora reflecting green; tibiae reflecting green medially, testaceous at extremities; tarsi testaceous; hind basitarsus with erect hairs uniform in length, up to 1.5 times as long as width of segment, variable among individuals, pale yellow in color; basal tuft distinct. (14) Metasomal terga green; first tergum polished, with widely scattered fine punctures anteriorly, smooth but less shiny dorsally, punctures small and close; sterna brown, pubescence short, fine over entire sterna; first sternum with weak metallic reflections, fourth sternum shallowly emarginate. (15) Pubescence white on head, white to golden dorsally on thorax, golden on metasoma and legs. (16) Genital capsule, seventh and eighth sterna and eighth tergum all of type 1 (similar to Figs. 32, 40, 43).

Comparisons. Very few specimens of *aurata* have been collected outside of Florida and Texas although nine specimens are available from Alabama, Georgia and North Carolina. The females are most similar in appearance to those of *gratiosa* and the males to those of *striata*, the range of variation in Florida overlapping those of both *striata* A and *gratiosa*.

The females can usually be distinguished from *gratiosa* by the slightly longer propodeal disc, the flatter bracket-shape (Figs. 57, 58) and less acutely angulate posterior edge of the disc and the smoother posterior vertical surface of the propodeum. In Texas they can be additionally distinguished by the deep, crowded, distinct punctures on the first and second metasomal terga (Figs. 82, 83). They can be distinguished from *striata* A in North Carolina and Georgia by the flatter bracket-shaped disc with a less acutely angulate posterior edge and the finer, more irregular striae, and in Florida usually by finer more irregular striae and the less rugose sculpturing on the thorax. There are no *striata* females in the south with which this species could be confused.

The males are similar to *striata* with short basitarsal hairs of more or less uniform length, shallowly emarginate fourth metasomal sternum and dark tipped antennal flagellum. The range of variation is not known since only five males from Georgia have been positively identified and these were similar to one another. Ten males from Florida are also tentatively included. These look very similar to variants of *striata*. The males from Georgia differ from all *striata* males in the flatter, more finely striate, propodeal disc. The difference in scutal punctures will also separate what are believed to be Floridian *aurata* from Floridian *striata*.

I believe that *aurata* is more closely related to *striata* than to *gratiosa* although it is more difficult to distinguish the females from those of *gratiosa*. The paucity of males may reflect limited collecting at the proper time of year or their occurrence in locations other than where the females were taken or it may be that they have not been distinguished from *striata* males since the nature of the variation in *striata* has not been fully evaluated.

Variation. There is comparatively little variation in size although particularly large or small individuals may occasionally be found in Florida. The color, usually a yellow-green to bright green, is often blue-green in Floridian specimens although yellow-green individuals may also be found.

The clypeus is apically brown, usually for one-sixth to one-fourth its length in females, but is one-third brown in some specimens from Florida and one-half brown in some specimens from Georgia. The face looks long (Fig. 52) in all Texan and some Floridian specimens but round in the rest (Fig. 53).

The propodeal disc of the female is usually slightly longer than the metanotum, or it may be equal to the metanotum but is not shorter. The disc is nearly always at least weakly bracket-shaped and bluntly pointed medially (Fig. 57). The edge is usually abruptly rounded and distinct although it may be either sharply angulate or rounded and indistinct in some specimens from Texas and Florida. There is more variability among Floridian specimens in this character than elsewhere in the range; the four specimens from Georgia are all similar to Figure 57. The striae are rarely as straight and well defined as in *gratiosa* (except for a few from Florida) but are very fine, irregular or vermiform, with no definite spaces between them. The posterior edge is usually minutely roughened when rounded and the striae end gradually in this roughened area. The most striking variation occurs in the metasomal punctures of specimens from Texas. Throughout the rest of the range the punctures are small, close, shallow, and almost inconspicuous as in *gratiosa* (Fig. 83). In Texas, the punctures, although also close, are slightly larger, much deeper, and more conspicuous (Fig. 82), giving the tergum a coarse or roughened appearance.

Males have been seen only from Georgia and Florida. Those from Georgia have the disc resembling that of the females, widely bracket-shaped, with fine irregular striae ending in a minutely roughened area at the edge. None of the presumed *aurata* males from Florida have discs similar to this or to that of the females. The shape of the disc in Florida varies from weakly bracket-shaped and narrow to long and roundly V-shaped. The striae are usually rather thin and close, and the posterior edge is usually abruptly rounded; the posterior surface may be weakly roughened as in the Georgian specimens or rugose as in many male *striata*. These specimens are all different from one another, resembling males of *striata* s but are unlike the *striata* A from Florida. There is considerable variation in the characters of the disc of females in Florida; perhaps the variability is as great in males. Due to the uncertainty in identification of the Floridian males, the above description of the male is based solely on the specimens of *aurata* from Georgia.

Throughout Florida, occasional female specimens are found that are brilliantly shiny, very finely punctured, with a body surface finely roughened or at most, weakly rugose on the thorax. These individuals are always dark blue-green in color but in all other respects are similar to other Floridian *aurata*. Eleven such specimens have been seen. They do not form an isolated population nor have corresponding males been found and therefore it seems improbable that these few specimens represent a different species. [Such specimens are from: W. Palm Beach, IX-3-27 (Graenicher) (32*); Highlands Co., VI-6-60 (Weems) (10); Pasco Co., III-2-57 (Weems) (10); Port Sewell, II-24-29-44 (Sanford) (32); Jacksonville Beach, VIII-5-36 (Mitchell) (33); Archibald Res. Sta., Lake Placid, IV-6-61 (Dietrich) (32)].

Distribution. This species is found from Florida along the Gulf coast into Texas and northward along the east coast as far as North Carolina (Map: Fig. 88).

A total of 15 males and 163 females have been seen: ALABAMA: *Houston Co.*, 1 ♀ (July). FLORIDA: *Alachua Co.*, 1 ♂, 8 ♀ (March-May, October, December); *Brevard Co.*, 1 ♂, 10 ♀ (March-April, July, November); *Broward Co.*, 2 ♀ (February); *Collier Co.*, 1 ♀ (April); *Dixie Co.*, 1 ♂ (August); *Duval Co.*, 1 ♂, 16 ♀ (May, August-September); *Flagler Co.*, 2 ♀ (February, December); *Glades Co.*, 1 ♀ (March); *Hendry Co.*, 1 ♂ (July); *Highlands Co.*, 5 ♀ (April, June); *Hillsborough Co.*, 3 ♀ (April); *Indian River Co.*, 1 ♀ (March); *Jackson Co.*, 1 ♀ (August); *Levy Co.*, 1 ♀ (September); *Marion Co.*, 1 ♀ (March); *Martin Co.*, 1 ♀ (February); *Nassau Co.*, 2 ♀ (July); *Okeechobee Co.*, 1 ♀ (April); *Orange Co.*, 1 ♂, 9 ♀ (March-June); *Palm Beach Co.*, 2 ♂, 5 ♀ (September); *Pasco Co.*, 1 ♀ (March); *Pinellas Co.*, 1 ♀ (April); *Polk Co.*, 3 ♀ (March-April); *St. Lucie Co.*, 1 ♀ (April); *St. Johns Co.*, 2 ♀ (April); *Seminole Co.*, 4 ♀ (May, July); *Volusia Co.*, 2 ♂, 6 ♀ (June-September). GEORGIA: *Brooks Co.*, 1 ♀ (March); *Dougherty Co.*, 1 ♂ (June); *Lowndes Co.*, 4 ♂ (July); *Pike Co.*, 1 ♀ (April); *Thomas Co.*, 1 ♀ (April). NORTH CAROLINA: "N.C." 1 ♀. TEXAS: *Aransas Co.*, 4 ♀ (July-August); *Bastrop Co.*, 2 ♀ (May); *Bee Co.*, 1 ♀ (May); *Cal-*

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* See Table 1.

houn Co., 2 ♀ (April); *Cameron Co.*, 4 ♀ (June); *Colorado Co.*, 1 ♀ (April); *Fayette Co.*, 3 ♀ (March); *Goliad Co.*, 5 ♀ (May); *Jackson Co.*, 4 ♀ (March, July); *Kenedy Co.*, 2 ♀ (April); *Lee Co.*, 20 ♀ (March-June); *Nacogdoches Co.*, 3 ♀ (April, September); *Refugio Co.*, 1 ♀ (April); *Victoria Co.*, 16 ♀ (February-May, August, October); *Waller Co.*, 1 ♀ (April).

Seasonal Activity. Females of *aurata* are apparently active throughout the year and have been collected from early February through December. Males are active from early June through November. Pollen collectors have been found from early February to the beginning of September although nesting activities may continue later into the fall.

Flower Records. Aster, Cirsium, Citrus, Crataegus, Lythrum, Opuntia, Polygonum, Rubus, Viburnum.

Augochlorella persimilis (Viereck) (n. comb.)

Halictus (Oxystoglossa) persimilis Viereck, 1910, *in* Smith. Ann. Rept. New Jersey State Mus. for 1909, p. 688 (list) (new name for *Augochlora similis* Robertson, preoccupied in *Halictus;* Viereck's identification was in error but his new name stands for *similis* Robertson).

Augochlora persimilis: Rau, 1922, Trans. Acad. Sci. St. Louis 24:33 (list, fl.); Graenicher, 1935, Ann. Ent. Soc. Amer. 28:302 (list).

Augochlorella persimilis: Ordway, 1964, Jour. Kansas Ent. Soc. 37:139-152 (biol.); Ordway, 1965, Insectes Sociaux 12:291-308 (biol.); Ordway, in press, Jour. Kansas Ent. Soc. (biol.).

Augochlora similis Robertson, 1893, Trans. Amer. Ent. Soc. 20:146 (descr.); Robertson, 1894, Trans. Acad. Sci. St. Louis 7:436-472 (fl.); Robertson, 1896, Trans. Acad. Sci. St. Louis 7:175 (fl.); Dalla Torre, 1896, Catalogus Hymenoptorum 10:96 (list); Bridwell, 1899, Trans. Kansas Acad. Sci. 16:210 (list); Cockerell, 1899, Ent. News 10:3 (list); Graenicher, 1911, Bull. Pub. Mus. Milwaukee 1:234 (list); Banks, 1912, Ent. News 23:107 (fl.); Brimley, 1938, Insects of North Carolina, p. 455 (list, fl.).

Augochlora (Oxystoglossa) similis: Robertson, 1902, Canad. Ent. 34:247 (key).

Oxystoglossa similis: Robertson, 1928, Flowers and Insects, pp. 1-221 (fl.); Pearson, 1933, Ecol. Monogr. 3:386, 396 (biol.).

Halictus (Oxystoglossa) xystris Vachal, 1911, Misc. Ent. 19:50 (key, descr.); Mitchell, 1960, Bees of the Eastern United States 1:460 (tax.).

Augochlorella aurata: Sandhouse, 1937, Jour. Washington Acad. Sci. 27:71 (in part) (tax.); Lovell, 1942, Kentucky Acad. Sci. Trans. 10:20, 21, 23 (key, descr.); Mitchell, 1960, Bees of the Eastern United States 1:459 (in part) (tax.); Sakagami and Michener, 1962, Nest Architecture of Sweat Bees, pp. 1-135 (biol.); Eickwort and Fischer, 1963, Ann. Ent. Soc. Amer. 56:350 (list) (misidentifications).

Augochlora (Augochlorella) aurata: Michener, 1951, *in* Muesebeck *et al.,* U.S.

Dept. Agr., Agr. Monogr. 2:1125 (in part) (list); Montgomery, 1957, Proc. Indiana Acad. Sci. 66:132 (distr., fl.) (misidentifications).

Augochlorella neglectula: Dreisbach, 1945, Michigan Acad. Sci. Arts and Letters. Papers 30, p. 225 (misidentification).

Types. Augochlora similis, lectotype female here designated, No. 1104, from Carlinville, Macoupin Co., Illinois, 1891, is in the Robertson Collection at the Illinois Natural History Survey. This specimen has been selected from among 19 syntype females. It agrees with the original description and may be considered "typical" of the species. There are eight male syntypes in the Robertson Collection, one (No. 474, Robertson's number) being a large *striata* and 18 syntype females all from Carlinville, Macoupin Co., Illinois, with dates from 1885-1887 and 1890-1892. *Halictus xystris* Vachal, lectotype female and two syntypes each labeled "xystis [sic] ♀ Vach." are located in the Vachal collection at the Museum National d'Histoire Naturelle, Paris. I have designated as lectotype one of the three syntypes that best fits the description and the only one with a locality label. The handwritten label reads "*Augochlora pura*, from *Potentilla*, S. Ill. June. . ." The label has been cropped closely, obliterating the rest of the date. It is probable that Vachal mistook the handwritten "S. Ill." for "S.W." and published the locality as "southwestern United States". Two of the three specimens including the lectotype resemble *persimilis* from southern Illinois. The third is a *persimilis-striata* intermediate that might be a small *striata* form c. It does not agree as well with the original diagnosis as the propodeal striae are regular and almost reach the edge of the rounded disc so that there is scarcely any smooth shiny area beyond the striations. I was able to see these specimens thanks to the generosity and cooperation of Mademoiselle S. Kélner-Pillault of the Museum National d'Histoire Naturelle, who lent them to me.

Although Sandhouse (1937) synonymized this species with *aurata* Smith 1853, the type of *aurata* is different from Robertson's *similis.*

Description. Female: (1) Length 5 to 6 mm; head width 1.44 to 1.91 mm, averaging 1.69 mm; head width greater than length. (2) Color bright green to yellow- or coppery-green; frons without bluish reflections; metasoma usually more golden, coppery or brownish than head and thorax. (3) Mandible with basal third dark brown, yellow-brown centrally, rufous at tip, without green basal reflections. (4) Clypeal length equal to width or slightly longer; basal part green with punctures variable in size, smallest and closest near basal angles, becoming larger apically and separated by about twice their diameters or more; apical third to two-thirds of clypeus brown and slightly beveled, with elongate punctures becoming shallow and indistinct at apex, giving apex roughened appearance; surface between punctures smooth and shiny. (5) Supraclypeal area with surface weakly roughened, punctures small just below antennae and along subantennal sutures, sometimes with few scattered punctures centrally. (6) Paraocular area usually closely punctate below antenna, finely rugose above antenna. (7) Antenna brown, flagellum lighter below than above; first flagellar segment wider than long; pedicel slightly longer and narrower than first flagellar segment, ratio of length to width variable. (8) Scutum coarsely and irregularly punctured, punctures close, usually with little or no space between them, rarely separated by as much as a puncture width centrally, becoming closer and coarser laterally; surface between punctures, when present, smooth and shiny centrally; anterior margin roughened with surface finely lineolate and dull medially, becoming rugose laterally and at anterolateral angles. (9) Tegula twice as long as wide. (10) Scutellum shiny and roughened, irregularly punctate or rugose. (11) Pleuron irregularly rugose, becoming coarsely areolate anteriorly. (12) Propodeum with disc slightly longer than to a little more than 1.5 times as long as metanotum; outline of disc roundly semicircular, profile type 2, posterior edge indistinct and gradually rounded; striae variable, usually irregular, branched, vermiform, occupying 60 to 80 percent the length of disc medially, reaching edge laterally; surface beyond striae smooth but minutely lineate or finely roughened; posterior vertical surface shiny and smooth with sparsely scattered minute punctures, or surface finely granular with granular texture extending across upper part of posterolateral corner to lateral surface; lateral vertical surface weakly rugose or coarsely roughened with widely separated or reticulated rugae. (13) Legs brown; fore and hind coxae strongly metallic; trochanters and femora with feeble metallic reflections. (14) First metasomal tergum with anterior surface brilliantly polished with a few widely spaced fine punctures; punctures more numerous and surface less brilliant dorsally; second tergum with numerous fine punctures separated by about twice their diameters; surface usually dull; first sternum sometimes darker than others, often greenish but not metallic. (15) Pubescence golden-white dorsally on head, thorax, apical segments of legs, and on dorsal and last two ventral metasomal segments; white ventrally on head and thorax; white or golden on basal segments of legs and ventral part of metasoma.

Male: (1) Length 7 mm; head width 1.45 to 1.80 mm, averaging 1.66 mm; head width equal to, greater than or less than length with no regional or seasonal pattern. (2) Color yellow-green to coppery-green; frons without blue reflections; metasoma usually more golden or reddish than rest of body. (3) Mandible with or without metallic reflections basally. (4) Clypeal surface shiny between rather large punctures; punctures irregular in size, shape and spacing, smallest along basal edge. (5) Supraclypeal area with small scattered punctures; surface between punctures minutely roughened, dull; rougher immediately below antennae than just above clypeus, or shiny and smooth. (6) Paraocular area finely and closely punctate to rugosopunctate. (7) Flagellum dark brown above, yellow below; scape entirely dark brown except for small apical yellow area on underside; pedicel dark brown and yellow; last flagellar segment rarely darker below than preceding segments, but if so, then only partially dark apically; pedicel and first flagellar segment about 1.5 times as wide as long. (8) Scutum shiny with punctures distinct, separated by less than their own diameters medially, slightly closer laterally, smaller and closer posteriorly; anterior margin roughened to finely rugose medially to rugose laterally. (9) Tegula more than 1.5 times as long as wide. (10) Scutellum shiny, coarsely punctate, punctures distinct but irregular in size and spacing. (11) Pleuron rugose to rugosopunctate, coarsely areolate anteriorly. (12) Disc of propodeum longer than metanotum; outline of disc semicircular, posterior edge prominent, abruptly rounded medially, gradually rounded laterally; striae variable, usually moderately coarse, irregular or wavy, not quite reaching edge medially, attaining edge laterally; surface of disc beyond median striae coarsely roughened to smooth and shiny with minute reticulations; posterior vertical surface usually smooth and brilliant, or only weakly and irregularly roughened, upper part of posterolateral corners minutely punctate to weakly roughened; lateral vertical surfaces roughened to rugose or finely areolate with weak horizontal rugae along anterior and ventral margins. (13) Legs with fore and hind coxae, trochanters and femora bright green, tibiae yellow-brown, usually darker centrally, hind tibia sometimes weakly reflecting green on inner surface; tarsi pale yellow; hind basitarsus with erect hairs along apical two-thirds of segment only, longer basally than apically; longest hairs about twice as long as width of segment, usually slightly curved at tips; basal third of segment without erect hairs; basal tuft short and sparse. (14) Metasomal terga green with apical margins usually narrowly brown; first tergum polished anteriorly with few, widely scattered fine punctures, smooth but less shiny dorsally, punctures denser, minute, separated by 1.5 times their diameters or less; sterna brown, first sternum with green reflections; fourth sternum emarginate apically. (15) Pubescence short, thick and white between antennae and on paraocular areas, white on cheeks, venter of thorax and basal segments of legs; white to golden-white on clypeus, frons and vertex, dorsum of thorax, on tibiae and tarsi and metasoma. (16) Genital capsule, seventh and eighth sterna and eighth tergum of type 1 (Figs. 33, 40, 43).

Comparisons. Although the range of *persimilis* overlaps that of four other species of *Augochlorella*, females intergrade only with form c of *striata*. There is no sure way of separating females of the two species where intermediates occur although the key will distinguish a majority. Males of the two species remain distinct and are readily distinguishable by the key characters.

Both males and females of *persimilis* may superficially resemble *bracteata* in size, coloration and often in characters of the propodeal disc. There is however, only slight overlap in ranges and the consistantly rougher thorax of *persimilis* effectively serves to distinguish the two species.

Apart from *bracteata* and *striata* c, *persimilis* can be distinguished from the eastern species by its generally smaller size, smoother body and propodeal disc with rounded posterior edge and short medial striae. The males are distinguishable by the long hind basitarsal hairs (Fig. 50) although in Texas two male specimens of *gratiosa* were found that looked very similar to those of *persimilis* (see variation under *gratiosa*). The fourth metasomal sternum of the males is about as emarginate as that of *gratiosa*, so that any distinction is difficult to make, especially when the segments are telescoped.

Variation. Body color varies in *persimilis* from blue-green to golden or coppery-yellow. The metasoma is usually lighter in color than the head and thorax (it may be browner or yellower). The males are predominantly yellowish green throughout the range except in Arkansas, Virginia and Georgia where all individuals seen are coppery in color. In Kansas, where a large sample was available, 85% of the females are bright green, 14% yellow-green or coppery and 1% blue-green. More than half the specimens are yellow-green or coppery-green in Tennessee, North Carolina, Maryland, Texas, Arkansas, Indiana, Missouri, Minnesota and Virginia, but populations are predominantly bright green in Illinois, Kansas, Nebraska and Wisconsin. About half the specimens are bright green in Louisiana and Oklahoma.

In both males and females, the width of the head varies widely within any one area. When measurements were pooled for each sex, however, normal distributions were obtained with only a slightly skewed distribution in the case of males. The head width may be greater than, equal to or less than the length in the case of the males with only slight differences between width and length. In females the width is consistently greater than the length. Little difference in size was found between populations from different areas. In females, the average head width of field caught bees is greater during the spring (March, April, May) (Fig. 89) than during other months; at least throughout much of the range only queens are present in spring. During the rest of the season, both queens and workers are present. (See Ordway, 1965a, for discussion of size and caste data.)

The length of the clypeus in females is about equal to the width giving the face a round appearance, especially in smaller individuals. The spacing and number of punctures on the clypeus are variable among individuals. Also, the extent of the brown color on the apical portion varies from about one-third to one-half the length. No regional trends were observed for either character.

The supraclypeal area is always roughened in females and at least partially so in males. The amount of punctation in this area is variable as is the degree of roughness. The paraocular areas are usually punctate near the lower ends of the eyes and finely rugose elsewhere. However, in about one percent of the females from throughout the range the roughness extends to the bases of the mandibles.

The antennae of some males have the last flagellar segment slightly darker below than the preceding segments but the segment is only partially dark and the darkening is slight.

The punctures of the scutum in females are rather constant in size but vary in respect to their spacing. The punctures are always distinct centrally but are closer toward the edges and the scutum may become rugose laterally and anteriorly. The amount of space between the central punctures varies; usually the punctures are close together with little space between, giving the surface a rather rough appearance. The surface looks smoother when the punctures are more widely spaced as in many of the specimens from Arkansas and a few from Virginia. The anteromedial surface is finely lineolate or roughened. This roughening extends for varying distances along the median suture but is always evident at least at the anterior end of the suture. There is little variability in scuta of males.

The scutellum in males and many females has punctures of various sizes and unequal spacing. In the females the scutellum may have distinct punctures or the punctures may run together or the surface may be entirely rugose, with all conditions occurring in populations throughout the range. When the punctures are distinct in females, they are closer and smaller at the edges, becoming rugose along the posterior margin and along the medial line, usually being shallower and smaller than those on the scutum. In males the punctures may vary from widely spaced to crowded.

There is little variation in the pleural region. Although the sculpturing of the mesepisternum and metepisternum is about equally coarse, the rugose patterns of the two areas are different.

As in other eastern species the propodeal area is highly variable, yet in females, it remains the most diagnostic character available. The disc is longer than the metanotum in both sexes. Only 1 male out of about 50 measured was found with disc and metanotum equal in length [Illinois, 566, Hart Coll. (14*)]. In males the metanotum showed greater variation in length than the propodeum; in females, both structures varied in length.

The shape of the margin of the disc and the lack of a V-shaped midapical depression is unvarying in all males. In 2 males out of about 300 examined, the usually thick posterior margin was thin, abruptly angulate and almost

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* See Table 1.

carinate [Indiana, Warren Co., VII-25-50 (16); Missouri, Tecumseh, VI-9-60 (25)]. In females the shape of the margin varies little and there is no V-shaped depression. Although the smooth, lineate, posterior part of the disc does extend onto the posterior surface in the shape of a V, there is no median depression as is found in *gratiosa* or some *striata*. The posterior edge in females usually is thickened as in males, but may be very narrow, flat or in certain cases completely rounded so that there is no clear demarkation of the margin [Illinois, 16966 (14); Nebraska, Nebraska City, VIII-23-01 (28)]. The striae are extremely variable in both sexes although more so in females. Variation in males is limited chiefly to the thickness of the striae and to the amount of their separation. The striae in both males and females may be regular and straight or, more usually, at least partially wavy, branched or irregular. All grades of irregularity occur in the striae of females, but rarely are the striae straight and distinct in the central area, and in no case was a specimen found in which the striae were both thick and straight, *and* widely spaced as in the large *striata* C or Floridian *striata* A. Although the striae rarely exceed 80% of the length of the disc centrally, specimens may be found where they reach into the lineate region medially [Texas (38); Kansas, Douglas Co. (20) etc.]. The lateral striae are nearly always rather straight and distinct in both males and females. Various types of "extreme" conditions appear periodically in females of various populations. It is not feasible to cite them all, but they include forms without striae and with only fine roughening along the basal half of the disc [Kansas, Lawrence, VIII-3-58 (20); Wisconsin, Oshkosh, VIII-7-16 (47)], or with fine rugae running transversely and joining with lateral striae [Kansas, Douglas Co., IX-5-53 (28); Missouri, Buffalo, VI-8-52 (20)] or with striae so irregular that there is no linear quality at all [Illinois, Algonquin, VI-4-09 (14); Missouri, Big Spring St. Pk. (20) etc.]. The posterior surface of the propodeum of females may be shiny and smooth or slightly less brilliant and granular in nature. No specimen was seen with rugae on this area. Specimens from the east (Maryland, Georgia, North Carolina, Virginia) are predominantly shiny and smooth; in other areas both conditions occur in about equal proportions. Three specimens were found in which the propodeal area was somewhat misshapen with the result that the posterior surface was "wrinkled looking," shiny and without the usual minute punctures [Arkansas, Jonesboro, VI-29-52 (20); Wisconsin, Oshkosh, VIII-7-16 (47); Nebraska, Nebraska City, VIII-23-01 (28)]. In males the posterior surface is usually very shiny and only slightly but variously roughened. This roughening may be in the form of shallow punctures which may or may not be distinct or may be merely unevenness of the surface. Two specimens, however, were found with very rough and somewhat duller posterior surfaces [Illinois, 32408 (14); Illinois, Willow Spr., VIII-12-05 (14)].

There is little variation in coloration of the legs in either males or females except for the intensity of green. This coloration seems to be correlated with the darkness of body coloration, the paler (yellower) individuals having less strongly green legs. Such variation occurs throughout the range. The length of the hairs on the hind basitarsus of the male is rather constant. Only one male was found where the long hairs were as short as one-half the width of the basitarsal segment and in this case they originated close to the basal tuft with somewhat less space separating the tuft and the hairs than is normal [Arkansas, Malvern, VI-15-58 (25)].

The metasoma shows the usual color variation of other body regions. The first sternum of the male is variously tinted with green. Some specimens have the metallic nature barely visible [Louisiana, 2392 (9); several Minnesota specimens, etc.] whereas others are bright green or intermediate. In females the first sternum is not green although it may vary from light brown to dark brown and may be shiny and greenish but never metallic.

One male was found in which the second tergum is granulose and similar to the third rather than punctate as is the first [Missouri, Buffalo, VI-8-52 (20)]. The third tergum is frequently punctate like the first in females. In females the second tergum may be similar either to the first or third or even occasionally intermediate [Indiana, Tippecanoe Co., VI-16-53 (16)]. Again, this variation appears to be individual rather than regional in nature.

The color of pubescence in females varies regionally to a slight extent. In the eastern states (Georgia, Maryland, North Carolina, Virginia, Tennessee, Louisiana) the ventral part of the metasoma and basal segments of the legs have golden rather than white hair. In the midwest (Oklahoma, Wisconsin, Minnesota, Nebraska, Kansas, Missouri, Texas, Arkansas) most specimens are paler below with the hairs on the basal leg segments white and on the venter white or golden-white, although, in Iowa, Indiana, Oklahoma and Arkansas, individuals are variable so that all combinations can be found. One male was found that had all white pubescence [Illinois, "Airport Region" Peoria, VII-20-41 (14)].

On the male genital capsule, the inner lobe is variable and usually similar to that of *striata*. There is a tendency for the rounded portion to slope off sooner at each side of the apex, whereas in *striata* it is more broadly rounded. The finger-like process is variable in length although it is rarely as long as in *gratiosa* or *striata*.

Distribution. From the eastern Appalachian Mountains, Maryland to Georgia, westward to about the 97th parallel, from southeastern Minnesota and Wisconsin southward to northeastern Texas and Arkansas (Map: Fig. 90). Detailed data are omitted for areas where there are numerous localities (see Methods), but Figure 90 shows all localities.

More than 300 males and 2,300 females were seen: ALABAMA: *Cull-*

man Co., 1 ♂ (July); *Jefferson Co.*, 1 ♂ (August). ARKANSAS: (Fig. 90). GEORGIA: *Clark Co.*, 1 ♂, 1 ♀ (June); *Cobb Co.*, 1 ♀ (July); *Fulton Co.*, 3 ♂ (June); *McDuffie Co.*, 1 ♀; *Meriwether Co.*, 1 ♀ (July); *Polk Co.*, 1 ♀ (May); *Rabun Co.*, 1 ♂, 1 ♀ (June-July); "Head River" 1 ♀ (July). ILLINOIS: (Fig. 90). INDIANA: *Harrison Co.*, 1 ♀ (July); *Lake Co.*, 1 ♀ (August); *Spencer Co.*, 1 ♀ (September); *Tippecanoe Co.*, 6 ♂, 102 ♀ (April-September); *Warren Co.*, 1 ♂, 2 ♀ (July-August). IOWA: *Fremont Co.*, 1 ♀ (July); *Louisa Co.*, 1 ♀ (June); *Story Co.*, 5 ♀ (May). KANSAS (see Fig. 90). KENTUCKY: *Graves Co.*, 1 ♂ (June). LOUISIANA: *St. Landry Parish*, 1 ♂, 5 ♀. MARYLAND: *Montgomery Co.*, 6 ♀ (July). MICHIGAN: *Lenawee Co.*, 1 ♂ (September). MINNESOTA: *Fillmore Co.*, 2 ♀ (May); *Houston Co.*, 25 ♀ (May); *Le Sueur Co.*, 1 ♀ (August); *Olmsted Co.*, 1 ♂ (July); *Ramsey Co.*, 1 ♀ (May). MISSOURI (see Fig. 90). NEBRASKA: *Cass Co.*, 13 ♀ (May-July); *Douglas Co.*, 1 ♀ (August); *Lancaster Co.*, 1 ♀ (July); *Otoe Co.*, 4 ♀ (May, August); *Richardson Co.*, 1 ♀ (July); *Saunders Co.*, 5 ♀ (May); "Child's Point", 2 ♀ (July). NORTH CAROLINA: *Haywood Co.*, 1 ♂, 5 ♀ (May, July-August); *Rutherford Co.*, 1 ♀ (June); *Swain Co.*, 4 ♀ (April, June). OHIO: *Lawrence Co.*, 1 ♂, 1 ♀ (August); *Washington Co.*, 1 ♀ (June). OKLAHOMA (see Fig. 90). PENNSYLVANIA: *Delaware Co.*, 1 ♀ (June). SOUTH CAROLINA: *Greenville Co.*, 1 ♀ (August). TENNESSEE: *Knox Co.*, 1 ♂, 2 ♀ (May, August); *Lincoln Co.*, 1 ♀ (April); *Montgomery Co.*, 1 ♀ (July); *Sevier Co.*, 7 ♀ (July); *Shelby Co.*, 2 ♂, 7 ♀ (June). TEXAS: *Bowie Co.*, 3 ♀ (March); *Fannin Co.*, 2 ♀ (May); *Hunt Co.*, 7 ♀ (March-June); *Lamar Co.*, 1 ♂, 1 ♀ (June); *Nacogdoches Co.*, 2 ♂ (October); *Red River Co.*, 1 ♀ (April); *Tarrant Co.*, 1 ♂ (June). VIRGINIA: *Botetourt Co.*, 4 ♂, 3 ♀ (June); *Fairfax Co.*, 1 ♂, 14 ♀ (March, May-August); *Fauquier Co.*, 1 ♂, 2 ♀ (July); *Fredrick Co.*, 2 ♀ (May); *Prince William Co.*, 1 ♀ (July); "Barcroft", 11 ♀ (May-July, September). WISCONSIN: *Dane Co.*, 1 ♂, 12 ♀ (May-August); *Grant Co.*, 2 ♂ (July); *La Crosse Co.*, 1 ♀ (August); *Pierce Co.*, 1 ♂, 4 ♀ (July-August); *Vernon Co.*, 5 ♂, 3 ♀ (July-August); *Winnebago Co.*, 1 ♀ (August).

This species seems to be most common in eastern Oklahoma and Kansas, and throughout Arkansas, Missouri and Illinois. Although it does range east of the Mississippi River as far as the eastern slopes of the Appalachian chain, the populations apparently decrease in numbers. This is not entirely due to lack of collecting since ample specimens of *striata* have been obtained from many of these areas, but rather seems to reflect an actual thinning out of the species. One male was taken on the southern border of Michigan but specimens have not been taken further north in this state in spite of intensive collecting. South of Michigan the apparent gap could be due to inadequate collecting in northeastern Indiana and northwestern Ohio. In the West, the abrupt line at about the 97th parallel reflects the decrease in rainfall and therefore corresponding changes in edaphic and vegetational conditions in this region.

Sandhouse (1937) limited the range of the species (using the name *aurata*) to south of 42 degrees north latitude even though she saw specimens from Minnesota, north of this line. Specimens recorded by her and others from Colorado and New Mexico are now recognized to be *striata* and *neglectula*. The Floridian specimens recorded by Sandhouse as *aurata* are the true *aurata* of Smith, 1853.

The distribution given by Mitchell (1960) was largely taken from the literature and reflects the complex errors in identification and synonymy. For example, J. B. Smith (1910) and Viereck (1916) record "*aurata*" and "*persimilis* (=*similis* Robt.)" from New York, New Jersey and Connecticut. It is uncertain what they were regarding as *aurata*, but their *persimilis* was undoubtedly the small *striata* form c that is occasionally found in these states or small individuals of other forms of *striata*.

The report by Rau (1922) concerning the nests of *A. similis* in a log refers to *Augochlora pura*. But perhaps the most complex error was made by Dreisbach (1945) who refers to "*Augochlorella neglectula* (=*A. aurata* Sm.)" as occurring in Michigan and gives as his reference Titus 1901, who referred to this species under the name *A. similis*. These specimens are not *aurata*, *neglectula* or *similis* (= *persimilis*) but are undoubtedly *striata*, essentially the only *Augochlorella* found in Michigan.

Seasonal Activity. A. persimilis is active from early April to about mid-October although nesting takes place only from the end of April to about the middle of August. Males start appearing with the emergence of the first brood at the end of May and can be found on flowers until the first frost in the fall. Although there is division of labor in colonies of this species, morphological castes cannot be distinguished. For details of the biology of *persimilis*, see Ordway (in press, a, b).

Flower Records. Achillea, Agastache, Ailanthus, Alisma, Althaea, Ammannia, Amorpha, Antennaria, Anthemis, Aphanes, Apocynum, Arabis, Asclepias, Asparagus, Aster, Barbarea, Bidens, Blephilia, Borago, Brassica, Callirhoe, Camassia, Campanula, Capsella, Cardamine, Cassia, Ceanothus, Celastrus, Cerastium, Chrysanthemum, Chrysopsis, Cichorium, Cirsium, Citrullus, Claytonia, Convovulus, Coreopsis, Cornus, Cotoneaster, Crataegus, Cucurbita, Daucus, Descurainia, Diospyros, Echinacea, Erigeron, Erysimum, Eupatorium, Euphorbia, Fragaria, Geranium, Geum, Gnaphalium, Gutierrezia, Hedeoma, Helenium, Helianthus, Heliopsis, Heterotheca, Heuchera, Houstonia, Hypoxis, Ipomoea, Justicia, Kolkwitzia, Krigia, Lepidum, Lespedeza, Lippia, Lobelia, Lotus, Ludwigia, Lycopus, Malva, Medicago, Meli-

lotus, Monarda, Nepeta, Nothoscordum, Oenothera, Oxalis, Paeonia, Parosela, Parthenium, Passiflora, Pastinaca, Petalostemum, Phacelia, Plantago, Polemonium, Polygonum, Polytaenia, Potentilla, Prunus, Psoralea, Pycnanthemum, Ranunculus, Raphanus, Rhus, Rorippa, Rosa, Rubus, Rudbeckia, Sabatia, Sagittaria, Salix, Salvia, Senecio, Sida, Silphium, Sisyrinchium, Smilacina, Smilax, Solidago, Specularia, Stellaria, Symphoricarpos, Taenidia, Taraxacum, Thaspium, Tradescantia, Trifolium, Valerianella, Verbena, Verbesina, Vernonia, Veronica, Virburnum, Zigadenus, Zizia.

FIG. 90. Distribution of *A. persimilis.*

Augochlorella striata (Provancher)

Augochlora striata Provancher, 1888, Additions et Corrections au Volume II de la Faune Entomologique du Canada, traitant des Hyménoptères 2:317-318 (descr.); Dalla Torre, 1896, Catalogus Hymenoptorum 10:96 (list); Procter, 1938, Biological Survey of the Mount Desert Region, part VI, p. 443 (list); Procter, 1946, Biological Survey of the Mount Desert Region, part VII, p. 506 (list); Evans & Lin, 1959, Wasmann Jour. Biol. 17:120, 123, 127, 131 (biol.).

Augochlorella striata: Sandhouse, 1937, Jour. Washington Acad. Sci. 27:70 (tax.); Procter, 1938, Biological Survey of the Mount Desert Region, part VI, p. 443 (list); Lovell, 1942, Kentucky Acad. Sci. Trans. 10:20-22 (key, descr.); Dreisbach, 1945, Michigan Acad. Sci. Arts and Letters, paper 30, p. 225 (distr.); Procter, 1946, Biological Survey of the Mount Desert Region, part VII, p. 506 (list); Moure, 1950, Dusenia 1:310 (key); Stephens, 1951, North Dakota Agr. Exper. Sta. Bull. 14:63 (list); Mitchell, 1960, Bees of the Eastern United States 1:461 (tax.); Michener & Wille, 1961, Univ. Kansas Sci. Bull. 42:1130 (biol.); Knerer & Atwood, 1962, Proc. Ent. Soc. Ontario 92:174 (dist., fl., biol.); Sakagami & Michener, 1962, Nest Architecture of Sweat Bees 1-135 pp. (biol.); Eickwort & Fisher, 1963, Ann. Ent. Soc. Amer. 56:350 (descr.); Ordway, 1964, Jour. Kansas Ent. Soc. 37:139-152 (biol.); Judd, 1964, Canad. Ent. 96:1475 (fl.); Evans, 1964, Psyche 71:142, 147 (biol.); Michener, 1964, Am. Zool. 4:233 (biol.); Ordway, 1965, Insectes Sociaux 12:291-308 (biol.); Ordway, in press, Jour. Kansas Ent. Soc. (biol.).

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Augochlora matilda Robertson, 1893, Trans. Amer. Ent. Soc. 20:147 (descr.); Dalla Torre, 1896, Catalogus Hymenoptorum 10:95 (list); Cockerell, 1922, Proc. U.S. Nat. Mus. 60:16 (list).

Augochlora confusa Robertson, 1897, Trans. Acad. Sci. St. Louis 7:324 (descr.); Bridwell, 1899, Trans. Kansas. Acad. Sci. 16:210 (list); Cockerell, 1899, Ent. News 10:3 (list); Titus, 1901, Canad. Ent. 33:134 (descr.); Cockerell, 1902, Amer. Nat. 36:811, 816 (descr., biol.); Cockerell, 1906, Trans. Amer. Ent. Soc. 32:295 (list); Lovell, 1908, Psyche 15:40 (list); Cockerell, 1911, Canad. Ent. 43:391 (list); Graenicher, 1911, Bull. Public Mus. Milwaukee 1:234 (list); Crawford, 1913, Canad. Ent. 45:271 (list); Cockerell, 1915, Pomona Jour. Ent. Zool. 7:232 (descr.); Stephens, 1921, Canad. Ent. 53:68 (list); Rau, 1922, Trans. Acad. Sci. St. Louis 24:32 (biol.); Hendrickson, 1930, Iowa State Coll. Jour. Sci. 4:162 (list); Phillips, 1933, Jour. Agr. Res. 46:860 (list); Michener, 1937, Ann. Mag. Nat. Hist. (10)19:314 (descr.); Brimley, 1938, Insects of North Carolina p. 455 (list).

Augochlora (Oxystoglossa) confusa: Robertson, 1902, Canad. Ent. 34:247 (key).

Oxystoglossa confusa: Hart & Gleason, 1907, Bull. Illinois State Lab. Nat. Hist. 7:256 (list); Robertson, 1928, Flowers and Insects pp. 1-221 (fl., list); Pearson, 1933, Ecol. Monogr. 3:386, 396, 416, 417 (biol.); Procter, 1938, Biological Survey of the Mount Desert Region, part VI, p. 443 (list).

Halictus (Oxystoglossa) confusus: Viereck, 1916, Connecticut Geol. Nat. Hist. Survey Bull. 22:701, 703, 705 (key, list); Britton, 1920, Connecticut Geol. Nat. Hist. Survey Bull. 31:342 (list); Leonard, 1926, Cornell Univ. Agr. Sta. Mem. 101:1025 (list).

Augochlora coloradensis Titus, 1901, Canad. Ent. 33:133 (descr.); Cockerell, 1911, Canad. Ent. 43:390 (list); Hicks, 1931, Canad. Ent. 63:176 (biol.); Cockerell, 1934, Amer. Mus. Novitates 697:1 (list).

Augochlora confusa coloradensis: Cockerell, 1906, Trans. Amer. Ent. Soc. 32:295 (list); Cockerell, 1907, Univ. Colorado Studies 4:243 (list); Cockerell, 1915, Ann. Mag. Nat. Hist. (8)15:269 (descr.); Cockerell, 1928, Univ. Colorado Studies 16:101 (list).

Augochlora pseudopurella Strand, 1914, Archiv. Naturg. 80:163 (list).

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Augochlora pura: Robertson, 1893, Trans. Amer. Ent. Soc. 20:146; Robertson, 1894, Trans. Acad. Sci. St. Louis 7:436-480 (in part) (fl.) (misidentifications).

Augochlora neglectula: Titus, 1901, Canad. Ent. 33:134; Cockerell, 1928, Univ. Colorado Studies 16:101; Dreisbach, 1945, Michigan Acad. Sci. Arts & Letters, paper 30, p. 225 (misidentifications).

Augochlora similis: Titus, 1901, Canad. Ent. 33:134 (misidentification).

Oxystoglossa similis: Britton & Viereck, 1906, *in* 29th Ann. Rept. Connecticut Agr. Exper. Sta., New Haven, 1905, part 4, p. 212 (misidentification).

Halictus (Oxystoglossa) persimilis: Viereck, 1910, *in* Smith, Ann. Rept. New Jersey State Mus. 1909:688; Viereck, 1916, Connecticut Geol. Nat. Hist. Surv. Bull. No. 22, 5:701, 703, 705; Britton, 1920, Connecticut Geol. Nat. Hist. Surv. Bull. No. 31, p. 342 (misidentifications).

Halictus (Augochlora) auratus: Viereck, 1910, *in* Smith, Ann. Rept. New Jersey State Mus. 1909, p. 688 (misidentification).

Halictus (Oxystoglossa) purus: Vachal, 1911, Misc. Ent. 19:50, 53, 111 (misidentification).

Types. Augochlora striata, female lectotype, male lectoallotype, from Quebec, Canada, are in the collection of Laval University, Department of Biology, Ste. Foy, Quebec, Canada. These specimens have been carefully compared by Dr. René Beiqué, Curator of Entomology at Laval University, with specimens I submitted. Dr. Beiqué's careful examination and illustration clearly show that these specimens are typical of *striata* of eastern Canada and typify form A of the discussion below. According to Dr. Beiqué (personal communication), these types are the only two specimens of this species in the Provancher collection, although the original series contained two females and four males. The lectotypes were labeled (but not published) by Mr. Noel Comeau, the former curator of the Provancher collection, in 1941, and are labeled as follows: female specimen No. 119: with a small yellow label marked 1475 (Provancher number), a white label with red border bearing the identification in Provancher's handwriting, a red label marked lectotype with the identification, Comeau's signature, dated 1941 and No. 119; male specimen No. 120: with a small white label with ♂ sign, a yellow label with Provancher's number 1475 A, and a purple label marked Allotype, No. 120, with Comeau's signature and dated 1941. The lectotype designation is here published for the first time. The location of the rest of the syntype series is not known.

Augochlora confusa, lectotype female No. 927 (Robertson's number) is from Carlinville, Macoupin Co., Illinois, 1886, and is in the Robertson Collection at the Illinois Natural History Survey. This specimen was selected from among 33 females of *Augochlorella striata* in the syntype series. Eighteen other females in the series are *Augochlora pura*. I have also seen seven male syntypes, all *striata*, and similar in appearance. I have not seen one female and four males of the original species. It seems certain that Robertson's description was based upon the *Augochlorella striata* and not the *Augochlora pura*. This lectotype designation is also published here for the first time.

Augochlora coloradensis, lectotype female, Ft. Collins [Larimer Co.], Colorado, June 13, 1899, is at the U.S. National Museum. It has a red U.S. National Museum cotype label No. 19459, and an identification label by Titus. I have selected this specimen as the lectotype because it agrees as well as any with the description, is in good condition, and will be located at the same museum as other Titus types. Other known female syntypes are located at the Museum of Comparative Zoology (1 specimen), U.S. National Museum (1 other specimen), Purdue University (2 specimens), University of Kansas (1 specimen), and Colorado State University (6 specimens). This species was originally described from numerous females and two males. I have not seen the males or other females, if any.

Augochlora matilda, lectotype female, No. 12247 (Robertson's number), from Inverness, Citrus Co., Florida, 1892, is in the Robertson Collection at the Illinois Natural History Survey. I have seen only one of the two syntypes and here designate it as the lectotype.

Augochlora pseudopurella Strand was proposed for *Halictus purus* Vachal (not Say). It does not seem likely that Strand designated a holotype from among the "numerous" specimens which Vachal misidentified as *H. purus* Say. I have not seen these specimens which are in the Museum National d'Histoire Naturelle de Paris, but Pe. J. S. Moure (personal communication) has verified that they are *Augochlorella* and not *Augochlora*. The specimens from Canada, the northeastern United States and possibly Louisiana would be *striata*; those from Orizaba and Oaxaca, Mexico, are probably *neglectula*.

This species consists of highly variable, intergrading groups of individuals. In order to describe and discuss the variation, four forms (A-D) have been recognized. The variability is such over most of the range that no definite line can be drawn between the four groups and therefore it is not always possible to assign certain specimens to any of the groups. These unplaced individuals are called "s". Although detailed studies were made of variations among the males, it seemed impractical to characterize the forms, so that many of the males are therefore assigned to group s. The following discussions of the forms concern only females unless specific reference is made to males. Biological information from Kansas (see Biosystematics) indicates that there may be at least two populations or species, but until further ecological and behavioral data are obtained, there is little justification for recognizing more than one species. However, when possible, I have kept the information concerning the four groups separated in the following discussion and records, in the event that further biological work substantiates the hints that there may be sibling species involved.

In discussing regional variation among the different forms, the specimens are compared with a standard." This is a specimen of each form chosen from an area where the form is usually distinct, where there are few, if any, intergrades, and where the majority of specimens look alike. The term "standard" refers *only* to these specimens in the following discussions. The standard of form A is from Philadelphia, Pennsylvania, IX-24-14 (38); that of form B is from Alleghany Co., North Carolina, along Little River, nr. Eunice, VIII-26-28-57 (R. Baileys & C. F. Walker) (25); that of form C is from Lee Co., Iowa, VI-28-29- (Parks) (6); and that of form D is from Colorado Springs, Colorado, VI-6-52 (W. E. LaBerge) (20).

The type of *striata* is form A. Robertson's *matilda* is also form A but is too coarsely sculptured to be typical except in Florida. The type of Robertson's *confusa* is typical of form C. Form B is morphologically between A and C. In some areas it intergrades with form A, in other areas with form C. Occasionally there is a continuum from A to C but usually B is entirely separable from both A and C. The type of *coloradensis* Titus is a representative of form D. In some areas this form appears to be a variable intergrade between A, B and C but in other areas it is quite distinct.

The following descriptions apply to all forms of *striata* except as noted.

Description. Female: (1) Length 5 to 8 mm; head width 1.55 to 2.82 mm, averaging 1.96 mm, width greater than length. (2) Color varying regionally from blue-green to yellow-green; frons without bluish reflections in green specimens; metasoma similar in color to head and thorax. (3) Mandible with basal third dark brown, reddish brown centrally, rufous at tip; without green reflections basally. (4) Clypeal length equal to, or slightly greater than width; basal part green with large, irregularly spaced punctures, smaller and closer basally; apical one-fourth to one-half brown, slightly beveled, with elongate punctures or irregularities; surface between punctures smooth and shiny. (5) Supraclypeal area variously punctate with surface between punctures smooth or roughened. (6) Paraocular area punctorugose to rugose below antennae, coarsely rugose above antennae. (7) Antenna dark brown, flagellum slightly lighter below than above, pedicel as long as broad, first flagellar segment slightly wider than long; pedicel longer than but equal in width to first flagellar segment. (8) Scutum coarsely punctate to rugose (some form A only) medially, becoming more coarsely rugose between parapsidal lines; anterior margin smoothly roughened at midline, becoming coarsely areolate laterally. (9) Tegula about 1.5 times as long as wide. (10) Scutellum finely and irregularly roughened, without distinct punctures. (11) Pleuron rugose, becoming areolate anteriorly. (12) Propodeum with disc variable in size, shape and sculpturing; length equal to metanotum (some form A) or more usually, longer than metanotum, rarely more than twice metanotal length; outline of disc sharply to roundly bracket-shaped (forms A, D) to deeply roundly or obtusely V-shaped (forms A, B) to broadly U-shaped or semicircular (form C), profile types 1-4; posterior edge sharp or weakly carinate (form A), abruptly rounded and thickened (forms B, D) to smoothly and gradually rounded and indistinct (form C); striae usually distinct, slightly irregular or straight, usually reaching edge posteriorly; posterior vertical surface coarsely and deeply roughened (some form A only) to smooth, shiny and granular; posterolateral corners finely granular to finely roughened (forms B, C, D), to strongly roughened (forms A, B) or rugose (form A); lateral vertical surface finely to coarsely (some form A only) rugose or reticulated. (13) Legs brown; coxae bright green, trochanters and femora usually with weak metallic reflections. (14) Metasomal terga with apical margins narrowly, often inconspicuously margined with brown; first tergum with anterior portion polished, sparsely and finely punctate, dorsal surface variously punctate with punctures minute and inconspicuous to large, and widely to closely, regularly to irregularly spaced; second tergum with punctures similar to first but with punctures closer; first metasomal sternum with or without weak metallic reflections. (15) Pubescence golden on dorsum and legs and ventrally on metasoma; golden to white ventrally on thorax and head.

Male: (1) Length 6 to 8 mm; head width 1.63 to 2.13 mm, averaging 1.85 mm, usually equal to or less than length, rarely wider than long. (2) Color yellow-green to dark blue-green, usually bright shiny green, frons without blue reflections on green specimens, usually uniformly colored over entire body. (3) Mandible with or without metallic reflections basally. (4) Clypeus with punctures variables in size and number, separated by about their own diameters, surface between punctures usually smooth and shiny. (5) Supraclypeal area protuberant, variably punctate, with surface between punctures roughened or somtimes smooth and shiny at least basally. (6) Paraocular area with small close punctures below level of antennae, minutely but deeply punctorugose above level of antennae. (7) Flagellum dark brown above, yellow-brown below; scape and pedicel dark brown with yellow apical area below; width of pedicel and first flagellar segments variable, each averaging 1.5 times as wide as long. (8) Scutum shiny with punctures variable in size and spacing; anterior margin and anterolateral angles areolate, smoother anteromedially. (9) Tegula about two times longer than wide. (10) Scutellum with surface irregular, punctate to rugose; punctures, when present, distinct to indistinct, irregular in size and spacing. (11) Pleuron punctate to rugose, becoming areolate anteriorly. (12) Propodeum with disc equal to or slightly longer than metanotum; outline of disc varying from distinctly bracket-shaped to obtusely U-shaped or semicircular, posterior edge varying from sharply angulate and prominent to gradually rounded; striae fine to coarse, regular to irregular or branched, straight to wavy, widely separated to close together, usually reaching edge posteriorly, or slightly before when edge of disc gradually rounded, reaching edge laterally; posterior vertical surface minutely to finely rough; posterolateral corners with or without subhorizontal rugae extending from lateral to posterior faces; lateral vertical surface irregular, rugose with weak lineate rugae perpendicular to anterior and ventral edges. (13) Legs brown, fore and hind coxae, trochanters and femora green, tibiae dark brown, with greenish reflections at least on anterior side of hind leg, usually yellow-brown apically and basally; tarsi brown; hind basitarsus with erect hairs of uniform length, equal to or longer than basal hairs, length variable, not exceeding 1.5 times width of segment; basal tuft present. (14) Metasomal terga green with brown apical margins; first tergum polished with widely scattered, fine punctures anteriorly, smooth but less shiny dorsally, punctures variable in size and spacing; second tergum with punctures variable in size, denser than those of first, indistinct on third and following terga, surface minutely reticulated in appearance, pubescence fine, short to long depending on wear; first sternum usually with metallic reflections variable in intensity; fourth sternum distinctly but weakly emarginate. (15) Pubescence white to golden, usually golden dorsally, white ventrally with long golden hairs and short white hairs on head and ventral part of abdomen; golden on tibiae and tarsi, white on coxae, trochanters and femora. (16) Genital capsule, sterna 7 and 8 and tergum 8 of type 1 (Figs. 32, 40, 43).

FORMS

The following accounts describe the "standard" individual of each form and a series from the same locality. They do not include total variation of the form or attempt to describe intergrades among the forms. The males were described only from specimens that could be definitely placed as to form and were usually from the same areas as the females.

A. striata form A

Female: Disc sharply bracket-shaped to obtusely V-shaped (Figs. 59, 60), shorter to slightly longer than metanotum, these sclerites usually about equal in length; length of disc at posterolateral corners as long as length posteromedially; edge of disc weakly carinate to sharply defined posteriorly (Fig. 21), becoming rounded laterally; disc pointed or sharply V-shaped medially and depressed onto posterior vertical surface. Striae variable, straight, thick and well defined to irregular, branched and close, or thin, fine and very close; always reaching well defined edge. Posterior vertical surface of propodeum smoothly granular to coarsely roughened or rugose.

Male: Disc usually as long as metanotum or only slightly longer, with distinct, usually sharp edge, often bracket-shaped; striae well defined, regular but wavy, reaching edge; posterior surface of propodeum variable, usually uneven, may be rather smooth to rough. Hind basitarsus with hairs appearing short and sparse, only slightly longer than width of basitarsus, contrasting only slightly in length with basal tuft.

All *striata* with sharp bracket-shaped discal areas belong in this group. As the bracket-shape and edge become rounded it is less easy to recognize this form. This form grades gradually into forms B, C and D as the disc becomes more rounded in shape and rounded along its edge. The outline of the disc is similar to that of *gratiosa* and females may look similar to *gratiosa* and *aurata* when the striae are fine.

A. striata form B

Female: Disc longer than metanotum, up to twice as long, obtusely V-shaped, longer medially than laterally, with medial portion of V rounded and sometimes extending onto posterior vertical surface (Fig. 63), edge distinct, often thickened, rough and abrupt but rounded (Fig. 23), not ridged or carinate. Striae large, irregular and branched, reaching edge at all points; posterior vertical surface of propodeum finely and regularly granular (Fig. 74), lateral vertical surface rugose.

Male: Disc long medially, obtusely V-shaped, up to twice as long as metanotum, with edge thickened but rounded and often roughened; striae wavy but regular, reaching edge; posterior surface of propodeum usually shiny but rough to smooth, punctured or finely rugose, variable throughout range; hind basitarsal hair dense, usually of more or less uniform length, about twice as long as basal tuft; hind basitarsus usually appearing large, with long, dense hair.

These bees are usually large and light green. They grade into forms A, C and D in certain areas but are predominant and most similar to the standard in the southeastern part of the range.

A. striata form C

Female: Disc large, up to twice length of metanotum, broadly U-shaped (Fig. 62); edge of disc indistinct, smoothly and gradually rounded from vertical to horizontal plane; striae large and distinct, straight or irregular, wavy and branched, sometimes widely separated; striae ending gradually at indistinct edge of disc; surface between striae shiny and smooth or minutely reticulated or minutely roughened; posterior vertical surface of propodeum evenly granular (Fig. 74), lateral vertical surface rugose.

Male: Disc broadly and deeply U-shaped, longer than metanotum; edge of disc smoothly rounded, shiny; striae straight, often widely separated with surface shiny between, usually reaching edge or ending gradually just before edge; posterior surface of the propodeum shiny but uneven or roughened and irregularly and minutely punctured, often rough; hind basitarsus with hairs long but sparse, distinctly longer than basal tuft.

There is wide variation in size in this form but the most distinctive or characteristic bees of this group are large. Small individuals look similar to *A. persimilis*, especially if the striae fade out before the edge of the disc leaving a shiny area between the striae and the edge. These bees are most prevalent in the northern part of the range and are most similar to the standard in Iowa and Illinois.

A. striata form D

Female: Propodeal disc equal to or usually slightly longer than metanotum, obtusely U-shaped to weakly bracket-shaped (Fig. 71), edge distinct, often slightly thickened and rough or uneven, sometimes extending medially onto posterior surface as indistinct or rounded V; striae large, irregular or vermiform, usually reaching edge posteriorly; posterior vertical surface of propodeum smooth and finely granular (Fig. 74); lateral vertical surface coarsely reticulate to rugose.

Male: Disc similar to those of female but with smoother, rounded posterior edge and often straighter striae; edge slightly extended medially but rounded rather than V-shaped; posterior vertical surface of propodeum shiny, shallowly punctured to weakly rugose, finely and linearly rugose or punctorugose over posterolateral corners and on lateral vertical surface;

hairs of hind basitarsus less than twice as long as width of segment but appearing long, rather dense and distinctly longer than basal tuft.

These bees are usually bright green to dark green. They intergrade with forms A, B and occasionally with C. They are predominant and most similar to the standard in the western part of the range from Texas to the Dakotas.

Comparisons. A. striata is the most widely distributed and morphologically diverse of all the North American species of *Augochlorella.* It overlaps the ranges of all the species north of Mexico except *pomoniella* and intergrades morphologically, at least in the females, with these species. It frequently is the largest and most coarsely sculptured of the eastern species but due to the wide variability in size, cannot always be distinguished by these features.

In the southeastern region most specimens of *striata* are distinctive although gradations toward *aurata* and *persimilis* do exist. Males of *striata* A, in particular, are easily confused with those of *aurata*, and although the key separates the two, without biological information I am uncertain whether the separation represents a valid difference between populations or merely an artificial or arbitrary dichotomy. Females of *striata* A may be separated from *aurata* and *gratiosa* where ranges overlap by their generally coarser striae, the rougher sculpturing and other key characters.

A few specimens in the south and southeast and many in the central region that are small individuals of *striata* C or possibly D, intergrade completely with *persimilis*, so that differentiation of females cannot always be certain. In these individuals the body size, the characters of the disc, and the body sculpturing all resemble those of *persimilis.*

In Texas, some *striata* D may resemble *bracteata* in the characters of the disc but in this region most *striata* are larger and more rugose than *bracteata*, and the two species should not be confused.

There seems to be little if any intergradation with *neglectula* where the ranges overlap in southeastern New Mexico. *A. striata* (mostly D) are usually less rough on the posterior vertical surface of the propodeum than *neglectula* and can be easily separated by the key characters.

Variation (all forms). Body size and head width in both males and females varies considerably throughout the range (Fig. 86), with the largest specimens (8 mm) occurring among Floridian specimens of form A and the smallest (6 mm) among New Mexican specimens of form D. Small workerlike individuals were found in all forms usually during summer months, the small individuals of form C usually intergrading with, or becoming indistinguishable from, *persimilis.*

Body color varies regionally in both sexes with dark blue-green individuals found chiefly in Florida and New Mexico. Elsewhere, throughout the range, most specimens are a bright green but may range from yellow-green to blue-green. The different regions of the body of any one specimen are similar in coloration, so that *striata* is more uniform in color than other eastern species. The mandibles of females are usually brown as described; however some Floridian specimens do have weak greenish reflections at the bases.

The supraclypeal area in both sexes is variously punctate. In females, the surface between punctures is usually shiny and smooth but may be minutely roughened or weakly rugose as in some Floridian specimens. In males, the supraclypeal area is roughened but may be smoother basally than just below the antennae.

The punctation patterns on the scutum of males can be divided into four groups, all groups occurring throughout the range but with one pattern often regionally predominant. This character appears to be more geographically variable than it is variable among forms and cannot be correlated with any of the other major characters. The following puncture patterns can be recognized: a) Punctures distinct and widely spaced centrally, separated by distances equal to or greater than one diameter; closer laterally, distinct to almost contiguous at the parapsidal lines. b) Evenly and widely spaced (separated by two times their diameters) over entire scutum. c) Evenly and closely spaced (separated by distances, equal to or less than their own diameters) over entire scutum. d) Distinct but unevenly spaced medially, becoming very close and rugose just medial of the parapsidal lines. No such variation is found in females.

Males are less easily separated into forms than females on the basis of propodeal characters and show a wider range of variation so that in certain areas each of a number of individuals has a different combination of characters (Florida, Kansas, Nebraska, etc.). Deviations from the descriptions of the four forms occur among the intergrades between different forms and among intergrades of *striata* and other species but it is not feasible to describe all the variations found in the continuum.

The legs show little color variation; paler specimens show less metallic coloration than darker ones. In males, the extent of metallic coloration on the outer surface of the hind tibia is individually variable. The hairs on the hind basitarsus of males, although similar in length for all forms, look longer and denser in form B with the hairs of the basal tuft appearing proportionally shorter than in forms A, C and D. Although differences do exist in these characters, they form a continuum and cannot be correlated with other characters.

The metasomal punctures are variable in size and spacing in both sexes, but like scutal punctures can be divided into groups. Any one group may be regionally predominant (Indiana, Illinois, Michigan, etc.) or the punctation may vary among individuals within any one region (Nebraska, Minnesota, Texas, Connecticut, etc.). In males the punctures are always distinct, although regularly or irregularly spaced and separated by more than to less than their own diameters. In the females the punctures are frequently very small or inconspicuous but may also become large. Spacing varies from very close to widely scattered and regularly or irregularly spaced. Not all specimens show the greenish reflections on the first sternum, and in those that do, the amount or intensity is variable. This coloration occurs more often in males than in females, and there seems to be no correlation between this character and the form or region.

Distribution. Southern Canada to southern Florida, westward to the Rocky Mountains. More than 6700 females and 1400 males were seen. Due to the abundance of this species throughout its range, locality data are indicated only by Figure 91 (see Methods).

Seasonal Activity. A. striata is active from early April to about the middle of October throughout most of its range. Pollen collectors are found from the end of April through middle or late August and males occur from late May to late October. In the North the season is slightly shorter, lasting from the end of April to the end of September, whereas in the South the bees are active throughout the year with pollen collectors being found from early April to early September.

Fig. 91. Distribution of *A. striata.*

There is considerable variation in size in this species (Fig. 86) within all forms. Usually the small individuals are similar in structure and appearance to the larger females of the same form although somewhat less coarsely sculptured. There is a queen and usually one or more workers (individuals that do not lay eggs) in each nest, but these cannot always be distinguished morphologically. Where both large and small individuals are present in one nest, one of the large females is always the queen and the remaining large and small females are workers. All gradations in size may occur within one colony, or all bees of a colony may be approximately the same size. Small individuals (probably of form c) do sometimes found nests in the spring, but then all offspring are as small as the queen or smaller. For further details on the biology of this species, see Ordway (1965a; in press).

Flower Records. Achillea, Aesculus, Agastache, Agoseris, Althaea, Amelanchier, Amorpha, Anemone, Anemonella, Antennaria, Apocynum, Aqui-

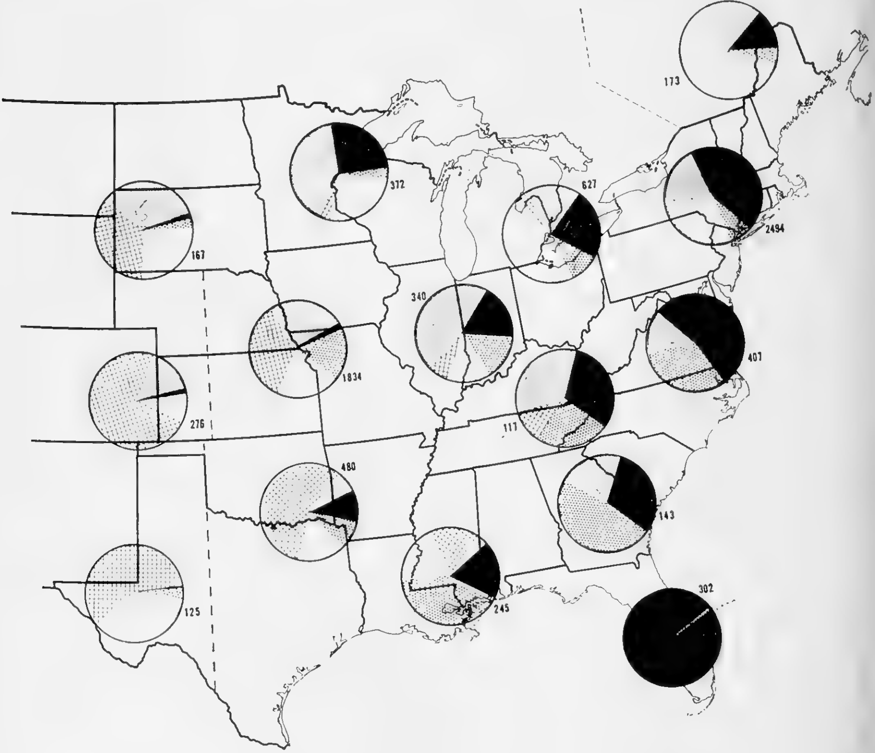

FIG. 92. Distributions of forms of *A. striata*. (Black—form a; dots—form b; gray shading—form c; cross-hatched—form d; white—group s.)

Each circle includes each state it overlaps except where the state is divided by broken line. Circle No. 117 includes West Virginia, Kentucky, Tennessee only. Circle No. 276 does not include New Mexico. The numbers beside each circle represent the total number of specimens examined from the area represented by the circle.

legia, Arabis, Aralia, Argemone, Aruncus, Asclepias, Aster, Astragalus, Barbarea, Berteroa, Bidens, Brassica, Callirhoe, Calopogon, Camassia, Camelina, Campanula, Capsella, Cardamine, Carduus, Cassia, Caulophyllum, Ceanothus, Celastrus, Centaurea, Cephalanthus, Cercis, Chaerophyllum, Chrysanthemum, Chrysopsis, Cichorium, Cicuta, Circaea, Cirsium, Citrullus, Claytonia, Clethra, Convovulus, Coreopsis, Cornus, Crataegus, Crypthantha, Cryptotaenia, Cubelium, Cucumis, Cucurbita, Cunila, Daucus, Dentaria, Diervilla, Dodecatheon, Echinacea, Echium, Ellisia, Erigenia, Erigeron, Erysimum, Euonymus, Eupatorium, Euphorbia, Fragaria, Gaillardia, Geranium, Gerardia, Glechoma, Gnaphalium, Gossypium, Grindelia, Gutierrezia, Haplopappus, Hedeoma, Heiracium, Helenium, Helianthus, Heliopsis, Heracleum, Heterotheca, Heuchera, Hieracium, Houstonia, Hybanthus, Hydrangea, Hydrocotyle, Hydrolea, Hydrophyllum, Hypericum, Impatiens, Inula, Ipomoea, Iris, Isopyrum, Kolkwitzia, Krigia, Lactuca, Lathyrus, Lepidium, Lespedeza, Lesquerella, Linum, Lippia, Lobelia, Lomatium, Lonicera, Lotus, Lycopersicum, Lycopus, Lythrum, Malus, Malva, Medicago, Melilotus, Mentha, Mertensia, Mikania, Monarda, Myosoton, Nigella, Nothoscordum, Oenothera, Onopordum, Opuntia, Osmorhiza, Oxalis, Paeonia, Parthenium, Parthenocissus, Paspalum, Pastinaca, Penstemon, Perideridia, Petalostemum, Phryma, Physalis, Polemonium, Polygonatum, Polygonum, Polymnia, Polytaenia, Pontederia, Potentilla, Prenanthes, Prunella, Prunus, Psoralea, Ptelea, Pteridium, Pycnanthemum, Pyrrhopappus, Pyrus, Ranunculus, Ratibida, Rhamnus, Rhus, Ribes, Rorippa, Rosa, Rubus, Rudbeckia, Sagittaria, Salix, Salvia, Sanicula, Sapindus, Satureja, Scrophularia, Scutellaria, Sedum, Senecio, Sericocarpus, Sida, Silphium, Sisymbrium, Sisyrinchium, Smilacina, Smilax, Solanum, Solidago, Sonchus, Specularia, Sphaeralcea, Spiraea, Stellaria, Stokesia, Strophostyles, Symphoricarpos, Syringa, Taenidia, Tanacetum, Taraxacum, Teucrium, Thaspium, Tradescantia, Tragopogon, Trifolium, Trillium, Triosteum, Vaccinium, Verbascum, Verbena, Vernonia, Viburnum, Vicia, Viola, Vitis, Waldsteinia, Xanthoxylum, Zizia.

BIOSYSTEMATICS OF *A. STRIATA* AND *PERSIMILIS*

The biology of *persimilis* and *striata* is discussed in detail by Ordway (1965a; in press). Some of the results obtained by excavating 133 nests near Lawrence, Kansas, are of systematic importance and are discussed here since populations from these nests shed some light on the complexities of the interspecific and intraspecific variation. Except as otherwise indicated, the following discussion relates only to females.

About 21% of the nests contained unquestionable *persimilis*; 54% were clearly *striata* (*s.l.*) and 25% contained apparent mixtures of *persimilis* and *striata* or individuals of uncertain identity intermediate between the two species.

The 72 nests of *striata* contained pure colonies of forms B, C, or D individuals, or mixed colonies of both B and D individuals, mixed colonies of B-C or B-D intermediates or more usually, mixtures of B and B-C, B and B-D or C and C-D individuals. One nest was found to contain A-D intermediates. There were six nests containing recognizable *striata* of forms B, C, D, or their intermediates, as well as small, *persimilis*-like individuals, but in all cases the small individuals looked more like small *striata* C than like *persimilis*. In contrast, two nests were found with small but clearly *striata*-like females as well as males of *persimilis*.

Of the 25 nests containing *persimilis-striata* mixtures or intermediates, 20 contained individuals intermediate between *persimilis* and *striata* and five contained apparent mixtures of both *persimilis* and *striata*. None of these nests contained males.

Since males of *striata* and *persimilis* are easily distinguished, 30 females intermediate between the two species were brought into the laboratory and allowed to establish nests. Male progeny from these females were examined after they emerged from the nests or as they were leaving. Of the 116 males recovered throughout the summer, 94% were *persimilis*, indicating that most of the original females belonged to this species. Judging by the frequency and periodic appearance of the *striata* males, it appeared probable that they were produced by a single female.

Although these data are fragmentary, they do serve to crystallize some of the problems involved. Within the species *striata*, it seems that forms B and D are not different biologically since both can be regularly found within a single nest population. Form C may be biologically distinct since no nests were found in which both C and another form coexisted, although C-D intermediates occur in nests with form C.

The small specimens, intermediate between *striata* and *persimilis* that were found within the *striata* nests, were probably *striata*, and those in nests of *persimilis* were probably *persimilis* although the possibility that F_1 hybrids exist cannot be ignored. Male (presumably haploid) offspring of both *striata* and *persimilis* are produced by the intermediate females but it has not been established if any one female can produce both.

So far, biological, behavioral or ecological differences have not been found between the forms of *striata* as they occur in eastern Kansas and such differences between the two species are only slight if extant. If significant differences are discovered or if methods could be found to keep progeny of various females segregated in the laboratory, it would be worth the time and effort to examine in much greater detail the interspecific and intraspecific variation in an attempt to define or categorize those individuals now being

TABLE 2. Per Cent Occurrence of Species of *Augochlorella* from Each Area.

Area	% striata	% gratiosa	% persimilis	% bracteata	% aurata	% neglectula	% pomoniella	% edentata	Total Augochlorella
Northeast	99.9	0.1	0	0	0	0	0	0	2,889
Southeast*	81.2	6.1	11.4	0	1.3	0	0	0	701
Florida*	54.3	28.6	0	0	17.1	0	0	0	574
South	60.0	2.1	3.4	23.8	7.4	3.3	0	0	984
Central	58.7	0	41.3	0	0	0	0	0	6,202
West	12.8	0	0	0	0	21.0	66.2	0	909
Mexico	0.5	0	0	1.2	0	44.8	37.7	15.8	406

* For the purposes of this table this region has been divided into two parts.

TABLE 3. Per Cent Occurrence of Forms of *A. striata* from Each Area.

Area	% form A	% form B	% form C	% form D	% group S	Total specimens
Northeast	40.1	6.8	19.1	0	34.0	2,885
Southeast**	46.4	35.3	15.3	0.2	2.8	569
Florida**	96.2	0.3	0.3	0	3.2*	312
South Central	15.1	20.5	1.0	45.1	18.3	590
North Central	7.8	13.8	28.4	28.7	21.3	3,640
West-Mexico	0	3.4	0	61.0	35.6	118

* These are *aurata-striata* intergrades (probably *striata* form A).

** For this table the southeastern region has been divided into two parts.

classed as intermediates between the forms or species. We have here an excellent case of very similar, sympatric populations with no apparent ecological segregation.

REGIONAL ACCOUNT OF THE SPECIES

The area under consideration in this paper, including Canada, the United States and Mexico, has been divided into regions, as indicated for the Regional Keys, in order to discuss and compare variation within and among species.

The relative abundance of each species within each region is shown in Table 2, and the relative abundance of each of the forms of *striata* is given in Table 3 and Figure 92. The regions in the latter are subdivided to give a more accurate indication of the relative frequency of the different forms. Unless otherwise stated, the discussions of *striata* below concern only females.

NORTHEAST

Species represented: *A. striata* A, B, C.

A. striata is the only species known to occur widely in this region, although other species have been reported in the literature, presumably erroneously, and occasional specimens of *gratiosa* or *persimilis* may occur along the southern borders of this region. The three forms of *striata* are sometimes difficult to distinguish, especially in this region, and therefore the percentage of group S (unplaced specimens) is comparatively large (Fig. 92).

In the southern part of the region, as far north as New Hampshire and Vermont, form A is distinct and easily separated from B and C, though extremely variable. The disc is seldom bracket-shaped but is characterized by a sharp to carinate posterior edge, at least medially, with the median portion coming to a distinct point. Its length is usually equal throughout and its shape is a broad but well defined V (Fig. 60). The length of the disc and the size and regularity of the striae are variable as is the size of individual specimens. Nearly all specimens of form A are weakly rugose or finely roughened on the posterior vertical surface of the propodeum. Large, coarsely rugose specimens resembling form A from Florida (Fig. 59) are occasionally found as far north as Massachusetts, but they have the light green color of northern specimens. In Massachusetts [Revere, VII-28-92 (F. A. Eddy Coll'n) (22), 2 specimens; Needham, V-18-20 (F.X.W.) (22), 1 specimen] these large individuals contrast strikingly with other individuals of form A, but to the south they tend to intergrade with other form A variants and are less noticeable. In Maine and Canada nearly all specimens differ from the standard of form A in that the posterior edge of the disc is less sharply angulate, the shape of the disc is more variable, usually somewhat rounder, and the median V is often only weakly indicated.

In Canada and Maine, group S consists chiefly of individuals that have characteristics of all forms rather than resembling variants of any one form. In the rest of the northeastern region specimens of group S are mostly variations of form A that do not agree with the standard either because they lack the median V or the angulate edge of the disc or because the shape of the disc is unlike that of the standard or the usual variants of form A from this region. A few scattered unplaced specimens resemble form D and a few may be variations of B or C.

Form C is generally more common than B in the Northeast, especially to the north. Only in Pennsylvania is B more abundant. Specimens similar to the standards for forms B (Fig. 63) and C (Fig. 62) are present throughout the region, but because of modifications of the shape and distinctness of the posterior edge of the disc, complete intergradation occurs making the separation of the two forms difficult (Fig. 65). In Canada and Maine the two forms are more clearly separable, with fewer intergrades.

If form D is present in this region it is not common and cannot be recognized as distinct. An occasional specimen resembles form D, especially some small individuals of form B, but these are few even in New York State from which more than 900 specimens were examined.

The color of most specimens of all forms is a bright green, although yellow-green or dark green specimens are not uncommon and blue-green individuals are occasionally found. The scutal and metasomal punctation is variable in both sexes throughout the area. Many males can be segregated into the lettered forms, especially form A, but individual variation is great and numerous and complex combinations of characters can occur, adding to the confusion rather than clarifying the nature of the variation.

SOUTHEAST

Species present: *A. striata* A, B, C, *aurata, gratiosa, persimilis.*

In Florida three species occur throughout the state, *striata*, *gratiosa*, and *aurata.* In Georgia, *striata* A, B, and C occur throughout the state, form B being most common. *A. gratiosa* and *aurata* occur chiefly in the southern counties but are also found sporadically in the mountains of the north; *persimilis* is found in the northern part of the state. In the Carolinas, *persimilis* has been taken in the mountains to the west, *gratiosa* appears nearer the coast and the three forms of *striata* occur throughout. The one specimen of *aurata* seen from North Carolina lacked detailed locality data. In Virginia, *striata* A, B, and C occur throughout the state, and *persimilis* ranges along the western border as far as Maryland, apparently its northern limit in the east. *A. gratiosa* probably occurs in Virginia as it has been taken in nearby Maryland, but this appears to be its northern limit also. Except for the few *gratiosa* from Maryland, only *striata* has been found in that state.

A. striata. There is comparatively little variation within the three forms of *striata* in this region. Only form A is present in Florida (except for one female of form B from Gainesville and a male of form C simply labeled "Florida"). About 90% of the female specimens are large, dark green to blue-green and very coarsely sculptured, especially on the scutum and propodeum. The other 10% are less rugose and resemble *striata* A from other regions. The disc in both sexes is usually bracket-shaped with a sharply angulate or carinate posterior edge (Fig. 59), although the disc may become more V-shaped and develop a well defined but less sharply angulate posterior margin in some specimens. The posterior vertical propodeal surface varies from rugose to smooth in females (always rugose in males), and the punctures on the first metasomal tergum are variable but usually small and widely spaced. Small workerlike individuals are rare and always look similar to the larger, rough specimens. All but four of the males from Florida belong to the large, robust and coarsely sculptured form A. One of the four is form C, the other three, similar to males from outside Florida, cannot be classified as to form. Each differs from the others in the shape and size of the disc and in the type of scutal and metasomal punctures.

Throughout the rest of the southeastern region, form D as a distinct group is not found although B-D intermediates (Fig. 72) do occur. A few of the coarsely rugose Floridian representatives of form A range into Georgia but most specimens from Georgia and elsewhere in this region are similar to the standard of form A. Most such form A specimens are bright green in color although some are yellow-green. They differ from forms B and C throughout the region, without intergradation.

Form B is usually distinctive although intergrades with D and C are found in both sexes. Most specimens of form B have a long, roundly V-shaped disc (Fig. 63) with the edge of the disc well defined. In Georgia, the disc may be slightly shorter and rounder than normal, resembling that of form D (Fig. 72), or less V-shaped in appearance, thus resembling form C (Fig. 65).

Form C is considerably more variable than either A or B. The shape of the disc varies from semicircular to U-shaped and grades into the V-shape of form B. The edge is smoothly rounded and shiny, with little differentiation between the disc and the vertical surfaces. A few small females throughout the area resemble *persimilis* but have the striae reaching or almost reaching the posterior margin of the disc. Both B and C are usually yellow-green in the southern part of the region and a yellow-green to bright green in Virginia, Maryland and the District of Columbia. The metasomal punctures in all forms are usually small, close, distinct and regularly spaced in both males and females although other punctation patterns may also occur. Most of the males can be placed as to form even though the size, shape and sculpturing of the disc is variable within any one form.

A. persimilis. There is little variation in *persimilis* in this region. Specimens are generally a light green to yellowish or coppery-green color and the disc (Fig. 64) and posterior vertical surface of the propodeum (Fig. 74) are similar to those of other specimens throughout the range. The pubescence, however, may be more golden in color than it is to the west. The species is not numerous and occurs chiefly in the western edge of the region. Intermediates between *persimilis* and small *striata* C may occasionally be found among the females.

A. gratiosa. This species is particularly abundant throughout Florida and probably Georgia but becomes sparse to the north. Specimens are usually dark green to deep blue in Florida but are generally a yellow-green to bright green in the rest of the region. This species shows little morphological variation except in Florida where the propodeal disc is often exceedingly short (Fig. 58) with the posterior edge of the disc more sharply angulate than elsewhere in the range. The characters of females in this species intergrade with those of *aurata* in Florida although most specimens can be distinguished by the key characters.

A. aurata. In Florida, the range of variation of *aurata* overlaps that of both *striata* A and *gratiosa.* In Georgia, however, the species seems to be distinct. Most female specimens look similar to *gratiosa* with a rather short, weakly bracket-shaped disc (Fig. 57), fine striae and a similar body size. The males are most similar to *striata* with short hair on the hind basitarsus and a narrowly emarginate fourth metasomal sternum. The variation in specimens from Florida mainly involves body color, and the size and sharpness of the posterior edge of the disc in both sexes. The few specimens seen from Georgia were all alike in coloring and characters of the propodeum.

NORTH CENTRAL

Species present: *A. striata* A, B, C, D, *persimilis*.

In the northern part of this region (Michigan, northern Wisconsin and Minnesota) only *striata* is found, forms A, B, and C occurring to the east and B, C, and D to the west. In the east form A is the most abundant, in the west form D is most abundant, form C being more abundant than B throughout the region (Fig. 92). Further south, *persimilis* is also found, its greatest abundance in the western part of its range, particularly in Kansas, Iowa and Illinois. In the southern part of the region, *striata* C is more abundant than B, with form A decreasing in abundance and form D increasing from east to west. *A. persimilis*, though present, is less abundant than it is farther north.

Throughout this region where *persimilis* and *striata* C are common, intermediates between the females of the two species are found. In all areas, *striata* is more abundant than *persimilis*.

A. striata. In the North Central region there is a shift in the proportional abundance of forms from east to west. Form A is distinct from other forms in Ohio, Indiana, Illinois, Tennessee and Kentucky (Fig. 56). There seem to be several variants of this form present, so that the form could be easily divided into a number of subtypes based chiefly on shape of the disc and robustness of the bee. To the north, in Michigan, Minnesota and Wisconsin, the edge of the disc becomes less sharp than in the standard and eastern specimens, and the shape of the disc is variable so that none of the subtypes are well defined or distinctive. One specimen similar to those from Florida (Fig. 59) was found in Iowa [Ames, XI-1-59 (D. Easterman) (18)]. It contrasts strongly with the other specimens, the usual form A being smaller, yellower, less robust and less coarsely rugose. Form A becomes less abundant to the west and grades into form D, although a few rather distinct individuals of form A occur in Nebraska, Kansas and Colorado. They are apparently absent in Oklahoma, Arkansas and Missouri although the form may be represented as intergrade types in these areas exhibiting an abrupt, but not sharp, posterior discal edge, with or without a medial V.

Form B usually is distinct, most specimens agreeing well with the standard (Fig. 63). The proportional abundance, however, decreases sharply to the west and the form is entirely absent in Colorado. Variants from the standard grade into both C and D. Form B-C intergrades (Fig. 65) are found frequently to the north in Michigan and Minnesota, and Ohio to Illinois and possess an elongate disc grading from V- to U-shaped, usually with a distinct but rounded edge. Form B-D intergrades (Fig. 72) are found more frequently to the west in Illinois, Iowa and Kansas where the disc becomes shorter and more semicircular. Form C-D intergrades are found throughout the Central region. In Kansas, four nests were found containing both B and d individuals, but in no case did any of the specimens agree with the standards. Also, there were four nests containing b-c intergrades, two of the nests also containing at least one specimen distinctly of form b.

Form c is variable and poorly defined in the eastern part of the North Central region but numerous and distinctive to the north and west. There are a number of different subtypes represented, with specimens resembling the standard (Fig. 62) found chiefly in Illinois, although they also occur in varying proportions elsewhere throughout the region. In Ohio, Tennessee, and Indiana there are many individuals resembling b-c intermediates (Fig. 65), but in Indiana and lower Wisconsin the majority of the individuals of this form are small and intergrade with *persimilis* (Fig. 28). In Kansas, Missouri, Arkansas and Oklahoma about 50% of the form c group consists of these small *persimilis*-like intermediates. These small specimens also occur sparsely in Minnesota, Iowa and Nebraska. In Michigan, South Dakota and Colorado there are some individuals with *persimilis*-like discs but the specimens are large and would not be confused with *persimilis*, a smaller species. These larger subtypes also occur in Kansas, Nebraska and Missouri. Other variations from the standard also occur throughout the North Central region (Fig. 61); sometimes they represent intergrades with forms b or d.

Form d is not abundant nor distinct as a form in the eastern and northern states, although d-like specimens are occasionally found. It intergrades chiefly with form a in Michigan and Wisconsin, where the disc is weakly bracket-shaped and the edge of the disc may become sharper than normal, with a weakly developed medial V. This form intergrades with form b in South Dakota, where the disc becomes more V-shaped and longer than the standard. Form d individuals are proportionally more abundant than other forms in the Great Plains states and although variable, the majority are similar to the standard of form d (Fig. 71). Small workerlike individuals are present, some resembling the larger individuals, others being intermediate between the small form c and *persimilis*. Biological data are scarce but six nests of this form were found in Kansas, all containing large and rather standard individuals, without worker forms. Four other nests contained both distinct b and d individuals.

A. persimilis. There is little variation in size or structure in *persimilis* throughout this region, although specimens tend to be somewhat greener (less yellowish) and the pubescence generally whiter than in the east. Throughout the region the disc of the propodeum is as in Fig. 64.

A. gratiosa. *A. gratiosa* is not known in this region, although it may be found along the southeastern borders. It will look similar to *striata* a but with finer, closer striae (Fig. 58) and a rough or granular posterior vertical propodeal surface (Fig. 76). One specimen has been seen from eastern Tennessee.

SOUTH CENTRAL

Species represented: *A. striata* A, B, D, *persimilis*, *gratiosa*, *neglectula*, *aurata*, *bracteata*.

In the western part of this region, the southwestern portion of Texas along the Mexican border as far east as Val Verde Co. and north into the Davis Mountains, *neglectula* and occasionally *striata* have been found. In the southern part of Texas, east of the Edwards Plateau, both *bracteata* and *aurata* occur, *bracteata* occurring as far north as Dallas Co., and *aurata* into Nacogdoches Co. *A. bracteata* has also been taken along the Rio Grande west to Val Verde Co., where it meets but probably does not overlap the range of *neglectula*.

A. striata, gratiosa and *persimilis* also occur to the east of the Edwards Plateau, *gratiosa* coming from the east and occurring from south of Galveston to Nacogdoches, *persimilis* going only as far south as Nacogdoches, and *striata* ranging south to near Corpus Christi. *A. striata* is the only species on the Edwards Plateau, and although there seems to be a gap between the eastern populations and those of New Mexico and southwestern Texas, all the bees of this species look similar to one another. In Louisiana, Mississippi and Alabama, *gratiosa* and probably *aurata* occur to the south, *persimilis* is rare, and *striata* occurs commonly throughout.

A. striata. In the eastern part of this region, form A looks similar to its standard (Fig. 60) but becomes less distinct to the west and all but disappears as a distinct form, grading into form D. Thus, the posterior edge of the disc becomes less sharply defined than in the standard although abruptly rounded, and the disc becomes less angular and the bracket-shape less well defined.

In the eastern part of the region, most specimens of form B are large and agree well with the standard. Toward the west the characters of form B grade into those of form D. The posterior edge of the disc remains abruptly rounded but the length of the disc decreases and the outline gradually changes from the broad V typical of form B (Fig. 63) to the semicircular shape of D (Fig. 71). Form B also decreases in proportional frequency although a few specimens similar to the standard are found in eastern Texas.

In form D the length of the striae and angulation of the posterior margin of the disc as well as the shape of the disc are variable but in general resemble that in Figure 71. Form C is not distinct in this region, although occasional specimens may show some resemblances to it.

In Louisiana and Texas, a few small *persimilis*-like individuals are present that would belong to form C in other parts of the range, but are probably worker individuals of form D in this region. These are always distinct *striata*, however, and except for size do not intergrade with *persimilis*. To the west the percentage of form D increases.

Throughout the region both color and punctation of females are variable. Males are individually variable with only a few specimens distinctive enough to be placed in one form or another; none of the males in this region seem to intergrade with any other species.

A. persimilis. A. persimilis occurs very sparsely in this region and appears to differ little from those elsewhere in the range (Fig. 64). Most specimens are a yellow-green or coppery green in color. This species does not intergrade with *striata* C or D in this region, although there are small individuals of *striata* in Texas and Louisiana.

A. gratiosa. Only a few specimens of *gratiosa* have been seen from this area. All are similar, usually bright green or yellow-green in color. The propodeal disc is usually about equal in length to the metanotum, sharply defined but rarely carinate. Some females may be confused with females of *aurata* in this region.

A. aurata. Females of this species have been taken from throughout southeastern Texas and, although variable in disc characteristics, can be distinguished from other species by the key characters. The females are most similar to *gratiosa.* No males have been seen, and no specimens of either sex have been taken between southeastern Alabama and Texas, probably due to lack of collecting in this area.

A. neglectula. This species is a dark green, roughly sculptured species (Figs. 70, 75) with all specimens similar to one another in this region. Although *striata* and *bracteata* have also been taken in the same area, it is probable that the three species occur in different habitats.

A. bracteata. This species is similar to the small *striata* C-*persimilis* intermediate in size and in appearance of the propodeal disc (Fig. 66). Both of these characters show considerable variation, but the thoracic sculpturing (Fig. 78) is distinctive and unvarying and serves to separate this species from *persimilis*, *aurata* and *striata* in Texas.

WEST

Species represented: *pomoniella*, *neglectula*, *striata* B, D.

The only species occurring in California, Utah and Nevada is *pomoniella.* *A. pomoniella* enters Utah only in the extreme southwestern corner, in Washington Co. In Arizona, both *neglectula* and *pomoniella* are found, *pomoniella* to the west and *neglectula* to the east, with their ranges broadly overlapping in the center of the state. In New Mexico, *striata* comes in from the northeast and ranges southward to the Mexican border through the eastern half of the state. *A. neglectula* ranges across the southern half of the state.

A. striata. Most of the individuals of *striata* are small (6 mm), about the size of large *persimilis.* The scutum is rather finely punctured or finely rugose, and the shape of the disc is somewhat variable, but the striae in all cases fill the discal area and reach the distinct posterior edge. The posterior surface of the propodeum is finely granular or weakly roughened, shiny or dull, and the color of the body varies from dark green to blue-green. Most *striata* belong to form D in this region, although an occasional form B is found. Individuals weakly A-like and intergrades between B and D are also occasionally found.

A. neglectula. There is little overall variation in this species except that the propodeal area varies in the degree of roughness of the posterior and lateral vertical surfaces. The smoother individuals superficially resemble *pomoniella* in Arizona or *striata* in New Mexico, although there is usually little difficulty in distinguishing the species, and the number of specimens showing this similarity is few.

A. pomoniella. There is little variation in size, color or morphological characters in specimens from California, Nevada and Utah, but in Arizona, specimens are smaller and more variable in the propodeal characters and in color. *A. pomoniella* is, however, distinctive throughout the area and does not intergrade with *neglectula* which it overlaps in Arizona.

Mexico

Species present: *A. neglectula*, *pomoniella*, *bracteata*, *edentata.* Other species found only in the Neotropical region and belonging to *Pereirapis* are not included here.

Throughout the central part of Mexico from the northern border into Central America, *A. neglectula* is the most common of the species considered in this paper. It occurs throughout Mexico except along the coasts. Both *edentata* and *bracteata* are also found in the central area but occur only sparsely in the eastern part.

In Baja California and along the western coastal area, *pomoniella* is found, and along some beaches of the west coast, *maritima*, a subspecies of *neglectula* is found. Apparently both *pomoniella* and *neglectula* occur together south of Morelos although they have not been collected simultaneously from any one area. In Chiapas and Yucatan, only *pomoniella* has been collected.

A. neglectula. This species shows little variation in Mexico, except for Pacific Coast populations placed in the subspecies *maritima.* Occasional female specimens are dull rather than shiny, with the body surfaces minutely reticulated, especially on head and thorax. The blue patches on the frontal areas are rarely conspicuous on Mexican specimens, and occasional specimens with unusually smooth propodeal areas may look similar to *pomoniella.*

Many of the specimens of the subspecies *maritima* are from the same population and therefore show little morphological variation among themselves.

A. pomoniella. This species is rather variable in size, color and sculpturing, especially in southern Mexico. Specimens from Baja California and Sonora are large and much like those from California, but those from further south are small, often with paler brown and darker green coloration. The range of *pomoniella* overlaps that of *neglectula* in Guerrero and Oaxaca, and females from these areas may intergrade morphologically.

A. bracteata. Only a few specimens of this species have been taken in Mexico so that the nature of the variation has not been determined. The specimens seen are like those from Texas and are easily differentiated by the key characters from other species of this region discussed in this paper.

A. edentata. This species is somewhat variable in both color and sculpturing, but until more specimens can be seen, the extent of the variation cannot be described. It is distinguished from other Mexican species discussed here by its smaller size, smooth sculpturing (Fig. 79), convex face and other key characters.

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THE BIONOMICS OF *TENUIPALPOIDES DORYCHAETA* PRITCHARD AND BAKER (1955) (ACARINA, TROMBIDIFORMES, TETRANYCHIDAE)

By

George Singer

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The Bionomics Of *Tenuipalpoides dorychaeta* Pritchard and Baker (1955) (Acarina, Trombidiformes, Tetranychidae)[1, 2, 3]

By

GEORGE SINGER[4]

ABSTRACT

The species *T. dorychaeta* is discussed in detail with regard to its biology and morphology. Rearing techniques involved the use of a live honey locust tree and isolation cells of plastic and glass affixed to the trunk of this tree. At 72°F the egg has an incubation period averaging 12 days. A low percentage of emergence at this stage is attributed to unfavorable humidity. The hexapod larva requires 2 days each for a completion of the active and quiescent stages. The octopod protonymph stage has the same duration as the larva. The deutonymph may be identified to sex. Five days are required for completion of this stage. Adult males are active, feed intermittently, and have an average longevity of 10 days. Adult females feed almost continuously and deposit an average of 14 eggs during their 20-day life span. They are arrhenotokous. After oviposition the female lays down a network of fine silk strands over the egg. This was the only time that spinning was observed in this species. Adult females remain in a feeding position on the host throughout the winter in Kansas.

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[2] Portion of a thesis submitted in partial fulfillment of the requirements for the degree of Master of Arts in Entomology at the University of Kansas.

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[4] The author wishes to express his sincere appreciation to Dr. R. E. Beer for his assistance, interest, and encouragement during the course of this study. Present address: Zoology Department, University of Montana, Missoula, Montana.

INTRODUCTION

The genus *Tenuipalpoides* Rekk and Bagdasarian (1948) has characters similar to both the subfamilies Bryobiinae and Tetranychinae. The character and placement of the setae of tarsus I, the complex distal enlargement of the peritreme, the integumental structure, and the lateral position of the inner sacral setae are all characteristic of the Bryobiinae. It is, however, included in the Tetranychinae by the following characters: no tenant hairs on empodium; adult female, male, and all immature instars with two pairs of anal setae.

Tenuipalpoides dorychaeta is the only known North American representative of the genus and is the second species recorded for the genus. Little has been published on its life history, other than comments on repeated collection from the bark of honey locust (*Gleditsia triacanthos* L.) and black locust (*Robinia pseudo-acacia* L.) in Louisiana, North Carolina, and Utah. Both males and females are recorded from these hosts during the summer (Pritchard & Baker 1955).

Tenuipalpoides zizyphus Rekk & Bagdasarian (1948) is the other species, recorded from Erevan, Armenia, on *Zizyphus vulgaris* Lam. (Rhamnaceae). Descriptions of this species are from females; males are not recorded.

REARING METHODS

A survey for these mites was conducted in the spring of 1960. Good populations were found on two widely separated honey locust trees on the University of Kansas campus. Individuals collected from these trees were used for the life history studies and morphological descriptions. Collections were made during June and November, 1960, and February, 1961.

Branches ½ inch in diameter and smaller were cut from the trees. These were then cut into sections about one foot in length to facilitate handling. In the laboratory the leaves were removed from the branches, beaten with a pencil over white paper, and then checked under a dissecting microscope. No *T. dorychaeta* individuals were ever collected from the leaves. The branch sections were also beaten, but this method proved inferior to using the dissecting microscope for locating and dislodging the mites from the bark where they were normally found wedged into cracks with their mouthparts inserted. In such a position they were not readily dislodged by beating. Occasionally mites were observed moving over the surface of the bark.

Attempts were made to rear the mites on freshly cut bark chips floating on tap water or sucrose solutions. This proved inadequate because the chips became waterlogged and overgrown with mold within 12 hours. Sections of branches with one end sealed with paraffin and the other immersed in water also proved inadequate. There was no means for insuring a relatively constant food source, nor could the mites be prevented from falling into the water. Therefore, a method of rearing was developed that employed a minimum of handling because the mites were easily injured and time involved in manipulations would prohibit the study of the large numbers needed for observations.

The most satisfactory method for rearing the mites included the use of a live tree for a constant food source and cells of plastic and glass for isolating them. A three-year-old thornless variety of honey locust was obtained in July, 1960, and the branches and tree top were pruned so that the tree stood five feet tall. The roots were washed clean of soil and potted in a round plastic bucket 9x12 inches deep to facilitate handling. Cheesecloth was tied to the trunk and the rim of the bucket to prevent a loss of soil when the container was tilted. By this arrangement the tree could be laid horizontally on a table and rolled back and forth to expose areas of the trunk under the dissecting microscope. While the tree was in this position, cells were affixed and the mites were observed and handled. Between obsrvations of this sort the tree was returned to an upright position.

Isolation cells were construced from washers with a ½ inch outer and 5/16 inch inner diameter, drilled and cut from a sheet of 0.40 inch clear plastic. These washers were affixed to the bark with melted paraffin, using a hot needle. A No. 1, 12 mm round coverglass, secured by a small amount of paraffin on one edge of each washer, provided a lid for the cell which could be easily removed, quickly and securely replaced with a hot needle, and through which observations could be made easily. The bark under each cell was first scraped to remove excess wax and then washed with alcohol and distilled water to remove any acaricidal chemical residues. The cells were oriented in rows parallel to the axis of the tree. Mites from the field or those isolated after emergence were introduced into separate cells with the use of a fine sable brush.

A glass tube, inserted through the soil to the bottom of the bucket, provided a means for watering and fertilizing the plant. This device assured that water reached the roots at the bottom of the bucket and reduced fertilizer odors. Of the three commercial fertilizers tried, Ortho-gro, Vigoro, Ra-pid-gro, the first appeared to give the best results in fostering rapid growth.

From November, 1960, until the end of the study, in March, 1961, the photoperiod in the laboratory was kept above 13 hours so that some of the green foliage was retained by the tree. Normally, in greenhouses where the temperature never reaches freezing, the reduction of the photoperiod by early winter results in dormancy defoliation until March. It was hoped that a more constant host environment would be maintained by a retention of summer-type conditions.

The mites and their eggs were found to be very susceptible to handling injury; therefore, handling was kept at a minimum. Egg deposition times were recorded and their positions were plotted on a map diagram of each cell. By this means the incubation period for each egg could be determined without disturbing it.

Observations were conducted at approximately 12 hour intervals to reduce developmental-time error. The temperature and relative humidity during the study averaged 74°F and 30% respectively.

LIFE HISTORY

The life cycle of *T. dorychaeta* follows the generalized pattern found in the Tetranychidae: a normally developing egg, hexapod larva, eight-legged protonymph, deutonymph, and adult male or female. Each active stage, other than the larva, is preceded by a quiescent or "pupal" stage during which the succeeding stage develops. Prior to each pupation the mites engorge with plant protoplasm and then become quiescent with their chelicerae inserted and their claws hooked to the substrate. After a period of six hours their appendages become white from autolysis of the tissues, and the gut content is reduced in quantity and in coloring matter by digestion and assimilation. At emergence, the old exoskeleton splits transversally between the propodosoma and the hysterosoma and then posteriorly along the lateral margins. The emergent instar backs out of this slit and begins feeding after a short rest period.

In nature, the mites appear to feed on non-chlorophyll-bearing cells under the cork layer of the bark and remain a unicolorous orange-red throughout the life cycle. Under the conditions afforded during this study, however, the mites were exposed to chlorophyll-bearing trunk tissues and acquired dark greenish-black areas in the idiosoma. The red color was modified from a red to orange to yellow in the gnathosoma and legs. During feeding the mites flexed their legs close to the body and remained in this position for long periods of time, apparently until the food source had become depleted at that site. In this feeding position, only the dorsum of the legs and idiosoma were exposed. The tough nature of the dorsal idiosoma, coupled with the presence of large serrate setae, probably tends to repel or discourage predators. The mites were observed to move rapidly when disturbed. At no time did they attempt to feed on leaf tissues of the host, even when this was offered as the only food source. The preferred site for feeding was in cracks and crevices of the stem or branch bark, and it is in such locations that they are usually found in nature. When such cracks or bark irregularities were not available, the mites fed through the smooth bark but changed feeding sites more often. At no time did their presence seem to affect the vitality of the host.

The Egg: The spherical egg has a smooth chorion and a deep carmine-red color. The diameter varies from 125 to 143μ with a 25 egg average of 137μ. Immediately after oviposition the female lays down a fine network of silk strands over the egg that tends to flatten and cause it to become somewhat disc-shaped. During embryonic development, a dark brown area occupying about one quarter of the sphere is formed at about the fifth day, while the rest of the egg becomes straw-colored. As the embryo develops further, the egg returns to a unicolorous red and, in a dorsal view, a flat area appears on one side occupying about ¼ of the circumference. At this time the carmine eyes of the embryo can be seen. The egg then takes on a pearly sheen as the larva detaches itself from the chorion and prepares for emergence, which is accomplished through a circular slit in the dorsum of the egg shell and through the retaining silk strands. Total developmental time for 62 eggs (reared through to adults) was 9 to 14 days, with an average of 12. From a total of slightly over 600 eggs, only 73 completed embryonic development and emerged as larvae. In many cases the embryos appeared to complete development but apparently could not extricate themselves from the egg shell or became trapped by the silk strands. The remainder either failed to differentiate at different levels of development or embryonic development was not initiated. The reason for this low percentage emergence is believed to be due to unfavorable relative humidity in the cells, as such a factor has been observed to influence emergence rates while not affecting emergence time: Kremer (1956) found that in *Bryobia praetiosa* Koch the greatest percent hatch of winter eggs occurred at 10 to 30% relative humidity. Humidity in excess of 80% induced the lowest percent emergence. Anderson (1948) found the opposite for *Paratetranychus pilosus* Can. & Franz. (=*Panonychus ulmi*), where the lower humidity reduced the percentage of emergence. The effect of humidity on emergence rate, but not on emergence time, is not restricted to the tetranychids but is also known to occur in species in other suborders of the Acarina (Camin, 1953).

The Larva: The hexapod larva is orange-red on emergence and its sex is not identifiable. The larva does not begin to feed immediately on emergence but will wander about for an undetermined period of time. This may be of some selective advantage in aiding or increasing the dispersal of the species on a given host tree or, by air currents, to other trees. Once a feeding site is selected the larva will remain motionless, feeding constantly. Pupation usually takes place at the feeding site. The active larval instar has a duration of about two days while the quiescent period that follows requires somewhat less than two days before the emergence of the succeeding instar.

The Protonymph: The octopod protonymph emerges and begins feeding almost immediately. No clear distinction was found that would separate the sexes in this instar. The active feeding period of two days is followed by a two day quiescent period.

The Deutonymph: The sexes are distinguishable in this stage; males are smaller and have a relatively pointed abdomen as compared to females. This form begins feeding almost immediately after emergence. The completion of each of the active and quiescent stages required about 2.5 days.

The Adult Male: After emergence, the males feed for a short time and then begin to wander apparently at random. The front legs are tapped up and down ahead of the mite as it walks. The following is an account which summarizes several observations: When a male blunders upon a female deutonymph pupa, it becomes excited and circles the female stroking it with his palps. After a short period of time the male becomes quiet and stradles the quiescent female. Several hours later the male moves to the side of the female and feeds for a period of time, then it resumes its former position. As the adult female begins to emerge the male becomes highly excited, orienting himself behind the emerging female, stroking her with his palps, and pulling on her dorsal setae with his palps. The emergent female characteristically moves to the side of the exuvium and attempts to feed. The male's advances, including pulling on her dorsal setae and stroking her with his front legs and palps, appears to cause the female to raise her opisthosoma and remain motionless. At this point the male moves forward and under the female, at the same time arching the tip of his opisthosoma dorsally and anteriorly. The male continues moving forward under the female while probing the venter of the female with his palps until their genitalia contact and copulation takes place. During this interlude the female remains motionless with her stylets inserted into the bark. In several observed instances copulation required from five to seven minutes, after which the male relaxed his opisthosoma into its normal position and backed out from under the female. Following copulation, both mites moved off several steps and then began feeding. Quiescent stages of larvae, protonymphs, male deutonymphs, and all the active immature instars arouse the adult males only momentarily, with the males moving off after only a brief moment of probing. Adult virgin females mated readily, in the manner described above. Mated females did not allow a second mating, preventing copulation by not responding to the male's advances. Longevity of males was four to 21 days, with an average of 10 days for 31 individuals observed.

The Adult Female: Immediately after emergence the female selects a feeding site in a crevice or next to some irregularity in the bark and begins feeding. Feeding continues fairly constantly throughout the life span of the adult female, individuals moving only to new feeding sites or during oviposition. The oviposition period is preceded by a preoviposition period of three to four days, after which an egg is deposited every 12 to 24 hours. Cracks and rough surfaces of the bark are generally selected for oviposition sites. After oviposition, the female turns around and begins to spin a fine, loose network of silk over the egg. This is the only time that any of the mites were observed to spin silk. Grandjean (1948) states that the silk ducts open into the palpal thumb of the Tetranychidae. Blauvelt (1945) did not commit himself on this matter; however, his diagram indicates that the common silk duct extends into the gnathosomal rostrum in *Panonychus ulmi* (Koch) (=*Paratetranychus pilosus* Can. & Franz.). My observations of these mites during spinning were not conclusive, as it was not possible to see from what part of the gnathosoma the silk was emitted.

There was no difference between mated and virgin females with respect to longevity or egg-laying capacity. A maximum of 31 eggs was recorded from one female, with an average of 14 eggs for 30 females observed. Longevity averaged 20 days with a maximum of 39. Eggs deposited by virgin females developed only into males while eggs from mated females produced both males and females.

The fact that most species of tetranychids commonly exhibit the phenomenon of producing only males from unfertilized eggs and both males and females from eggs of mated females is an old and well documented fact (Ewing, 1914; Garman and Townsend, 1938; Cagle, 1943, 1946, 1949; English and Snetsinger, 1957). Ewing (1914) suggested that the mechanism of sex determination in tetranychids is linked with chromosome number, haploidy in males and diploidy in females. Cytological confirmation of this phenomenon has been demonstrated for *Tetranychus telarius* (Linn.) by Schrader (1923), where males were found to have three chromosomes and females six.

Overwintering of this species in Kansas is accomplished by the adult females. Only adult females were found on the trees after the first frost in November, 1960, even though prior to this frost all stages were in evidence. A second survey in February, 1961, following −5°F temperatures, disclosed numerous live, feeding, adult females. These females, when brought into the laboratory, began feeding immediately and continuously as evidenced by their acquiring a green-black coloring in the idiosoma. Four females collected in November had a preoviposition period averaging 17 days after which an average of four eggs was deposited per female. Their longevity was 20 to 31 days after introduction into the laboratory. Seventeen females collected near the end of February had an average preoviposition period of 10 days, an average of 11 eggs per female, and a longevity of 9 to 32 days, averaging 28. From these data it appears that metabolism is greatly reduced by exposure to a period of subfreezing temperatures. The longevities of both these groups, after being brought into the laboratory, were the same even though there was a lapse of three months between the two collections. It is believed that no eggs or immature instars were present during this interlude. Samples of soil and leaf litter from beneath the host trees failed to yield any *T. dorychaeta* individuals during the course of this study, although the University of Kansas acarological collection contains one specimen taken from leaf litter in November, 1960, by Dr. R. E. Beer. Eggs that were produced by overwintering females developed into males and females indicating that most, if not all, of the females had mated before the first frost in November. No males were collected after this frost.

MORPHOLOGY AND TAXONOMY

The dorsal body chaetotaxy is constant in number and position from the larva to the adult, the only variation being in the size of setae, increasing in length and width with each succeeding instar. These setae are broadly lanceolate and serrate, appearing opaque white in life. The three pairs of dorsal propodosomal setae are arranged in the usual tetranychid triangular pattern: 3 dorsocentral pairs, 3 pairs of dorsolaterals, and 1 pair each of humeral and clunals. The sacrals are 2-paired and their marginal position is considered to be a primitive condition according to Pritchard and Baker (1955). The ventral idiosomal setae increase in number from the larva to the adult, and the chaetotaxy of this area is therefore valuable in identifying the instars. The 2 pairs of post-anals are plumose and easily distinguishable from the other ventral setae. There are 2 pairs of simple anal setae. The palpal tarsus bears 3 simple and 3 rodlike setae, lacking pronounced setal bases. Distally the palpal tarsus bears a small papilla, except in the adult male. The pretarsus of each leg bears 1 simple empodial claw, flanked laterally by the reduced, padlike, true claws, each one giving rise to 2 tenent hairs distally. Dorsally the propodosoma is sculptured and the hysterosoma is wrinkled. The idiosoma is reticulated with short dashes in all stages except the adult male, where there are fingerprintlike striations of lines and dashes. Ventrally the medial portion of the idiosoma is patterned by line striations and the lateral margins are wrinkled.

Adult Female (Figs. 1, 2): Length of idiosoma 331 to 375μ, width of idiosoma 218 to 312μ, averaging 353μ x 250μ for 17 individuals.

Palpal femur with 1 dorsal, simple seta; genu with 1 dorsal, simple seta; tibia with 1 dorsal, one lateral, 1 medial simple seta, and a terminal claw of thumb-claw complex.

Coxa I with 2 setae ventrally, the medial one simple and twice the length of spiculate lateral one; trochanter with 1 simple seta; femur with 1 simple, 1 spiculate, and 1 broadly serrate seta; genu with 1 simple, 1 spiculate, and 3 broadly serrate setae; tibia with 2 serrate, 3 spiculate, 1 simple, and 1 short, peglike, solenidion; tarsus with 4 solenidia, 3 simple, 2 terminal, spatulate-plumose setae, and 2 distal sets of duplex setae. Distal members of duplex setae greatly exceeding proximal members in length, the lateral distal member longest of the 4.

Coxa II with two ventral setae, the medial one simple and twice the length of spiculate lateral one; trochanter with 1 simple seta; femur with 2 serrate setae and 1 simple; genu with 4 serrate setae and 1 simple; tibia with 3 serrate setae, 1 spiculate and 1 simple seta; tarsus with 3 solenidia, 2 simple, 2 terminal spatulate-plumose setae, and 1 distal set of duplex setae, the distal member short and peglike while the proximal member is simple.

Coxa III is bare; trochanter with 1 serrate seta; femur with 2 broadly serrate setae; genu with 1 serrate seta; tibia with 2 serrate setae, 1 spiculate and 1 simple seta; tarsus with 5 simple and 2 terminal spatulate-plumose setae.

Coxa IV with 1 spiculate seta ventrally; trochanter with 1 spiculate seta; femur with 1 spiculate seta; genu with 1 serrate seta; tibia with 1 serrate, 1 spiculate and 1 simple seta; tarsus with 5 simple and 2 terminal spatulate-plumose setae.

Ventrally with 1 pair of simple setae on palpal coxa; 4 pairs of simple setae on ventral podosoma, the anterior pair between coxae I and II, 2 pairs medial to coxa III, and 1 pair medial to coxa IV; opisthosoma with 3 pairs of simple setae anterior to anus, these being 2 pairs of genitals plus 1 pair lateral to the genital aperture.

Adult Male (Figs. 3, 4): Length of idiosoma 256 to 300μ, width of idiosoma 156 to 169μ, averaging 281 x 162μ for 10 individuals.

Palpal femur with 1 peglike tactile seta dorsally; genu with 1 simple seta dorsally; tibia with 1 dorsal, 1 lateral, and 1 medial simple seta, and a terminal claw of thumb-claw complex.

Coxa I with 2 ventral setae, the medial one simple and twice the length of spiculate lateral one; trochanter with 1 simple seta; femur with 2 simple setae and 1 broadly serrate seta; genu with 4 broadly serrate setae and 1 simple seta; tibia with 1 serrate seta, 1 solenidium, 3 spiculate, and 2 simple setae; tarsus with 6 solenidia, 2 simple, 1 spiculate, 2 terminal, spatulate-plumose setae, and 2 distal sets of duplex setae, distal members being considerably longer than proximal members and lateral distal member longer than other 3.

Coxa II with 2 ventral setae, the medial one simple and twice the length of spiculate lateral one; trochanter with 1 spiculate seta; femur with 1 spiculate, 1 serrate, and 1 simple seta; genu with 3 serrate, 1 spiculate, and 1 simple seta; tibia with 3 spiculate and 2 simple setae; tarsus with 5 solenidia, 3 simple, 2 terminal, spatulate-plumose setae, and 1 distal set of duplex setae, the distal member peglike and shorter than the simple proximal member.

Coxa III bare; trochanter with 1 spiculate seta; femur with 1 serrate and 1 simple seta; genu with 1 spiculate seta; tibia with 2 serrate, 1 simple, and 1 spiculate seta; tarsus with 5 simple and 2 terminal, spatulate-plumose setae.

Coxa IV with 1 simple seta ventrally; genu with 1 spiculate seta; tibia with 1 serrate seta, 1 spiculate seta and 1 simple seta; tarsus with 5 simple and 2 terminal, spatulate-plumose setae.

Ventrally with 1 pair of simple setae on palpal coxa; ventral podosoma with 4 pairs of simple setae, the anterior pair medial to coxae I and II, 2 pairs medial to coxa III and 1 pair medial to coxa IV; opisthosoma with 3 pairs of simple setae anterior to anus.

Deutonymph (Figs. 5, 6): Female; length of idiosoma 250 to 312μ, width 162 to 193μ, averaging 281 to 187μ for 15 individuals. Male; length of idiosoma 225 to 256μ, width 156 to 168μ, averaging 250 x 162μ for 14 individuals.

Males may be distinguished from females by their smaller body size, and male deutonymphs have relatively pointed abdomens in contrast to those of the females.

Palpal femur with 1 simple dorsal seta; genu with 1 simple seta; tibia with 1 dorsal, 1 lateral, and 1 medial simple seta, and a terminal claw of thumb-claw complex.

Coxa I with 2 simple ventral setae; trochanter with 1 simple seta; femur with 2 simple setae and a broadly serrate one; genu with 4 broadly serrate setae and a simple one; tibia with 3 serrate and 2 spiculate, 1 simple seta and 1 short, peglike, solenidium; tarsus with 4 solenidia, 3 simple, 2 terminal, spatulate-plumose setae, and 2 distal sets of duplex setae, the distal members greately exceeding proximal members in length, and distal lateral member exceeding the other 3 in length.

Coxa II with 2 ventral setae, medial member simple and twice length of lateral spiculate member; trochanter with 1 simple seta; femur with 1 broadly serrate and 1 spiculate seta; genu with 3 serrate setae, 1 spiculate and 1 simple seta; tibia with 3 serrate and 2 simple setae; tarsus with 3 solenidia, 3 simple 2 terminal spatulate-plumose setae, and 1 distal set of duplex seta, the distal member short and rodlike and proximal member long and simple.

Coxa III bare; trochanter with one serrate seta; femur with 2 serrate setae; genu with 1 serrate seta; tibia with 2 serrate and 2 simple setae; tarsus with 5 simple and 2 terminal, spatulate-plumose setae.

Coxa IV with 1 simple seta; trochanter bare; femur with 1 simple seta; genu with 1 serrate seta; tibia with 1 serrate and 2 simple setae; tarsus with 5 simple and 2 terminal, spatulate-plumose setae.

Ventrally with 1 pair of simple setae on palpal coxa; podosoma with 4 pairs of simple setae, the anterior pair medial to coxa II, 2 pairs medial to coxa III, and 1 pair medial to coxa IV; opisthosoma with 2 pairs of simple setae anterior to anus.

Protonymph (Figs. 7, 8): Males and females are not distinguishable from each other. Length of idiosoma 187 to 224μ, width 125 to 156μ, averaging 218 x 143μ for 20 individuals.

Palpal femur with 1 dorsal, simple seta; genu with 1 dorsal simple seta; tibia with 1 lateral, 1 medial and 1 dorsal, simple setae, and a terminal claw of thumb-claw complex.

Coxa I with 2 simple setae ventrally; trochanter bare; femur with 1 broadly serrate and 2 simple setae; genu with 3 broadly serrate setae and a simple one; tibia with 2 serrate and 4 simple setae and 1 short, peglike, sensory seta; tarsus with 3 solenidia, 2 simple, 2 terminal, spatulate-plumose setae, and 2 distal sets of duplex setae, the distal members greatly exceeding proximal members in length and the lateral distal member exceeding other 3 in length.

Coxa II with 1 spiculate seta; trochanter bare; femur with 1 simple, 1 spiculate, and 1 broadly serrate seta; genu with 2 serrate and 2 simple setae; tibia with 3 serrate and 2 simple setae; tarsus with 3 solenidia, 3 simple, 2 terminal, spatulate-plumose setae, and 1 distal set of duplex setae, distal member rodlike and shorter than simple proximal member.

Coxa III bare; trochanter bare; femur with 1 serrate and 1 simple seta; genu with 1 simple seta; tibia with 1 serrate, 1 spiculate, and 1 simple seta; tarsus with 5 simple and 2 terminal, spatulate-plumose setae.

Coxa IV bare; trochanter bare; femur with 1 simple seta; genu with 1 simple seta; tibia with 1 serrate and 2 simple setae; tarsus with 3 simple and 2 terminal, spatulate-plumose setae.

Ventrally with 3 pairs of simple podosomal setae, the anterior pair medial to coxae I and II, mesal pair between propodosoma and metapodosoma, and posterior pair medial to coxa III; opisthosoma with 1 pair of simple setae anterior to anus.

Larva (Fig. 9, 10): Males and females are not distinguishable from each other. Length of idiosoma 143 to 185μ, width 106 to 131μ, averaging 168 x 118μ for 10 individuals.

Palpal femur with 1 dorsal simple seta; genu with 1 dorsal simple seta; tibia with 2 simple setae, and a terminal claw of thumb-claw complex.

Coxa I with 1 simple ventral seta; trochanter bare; femur with 1 broadly serrate and 2 simple setae; genu with 2 serrate and 2 simple setae; tibia with 5 simple setae and a short, peglike, solenidium; tarsus with 4 simple, 2 terminal solenidia, and 1 distal set of simple duplex setae, the distal member of set considerably longer than proximal member.

Coxa II bare; trochanter bare; femur with 1 broadly serrate and 2 simple setae; genu with 2 serrate and 2 simple setae; tibia with 5 simple setae; tarsus with 2 solenidia, 3 simple, and 1 distal set of duplex setae, the distal member of set rodlike and shorter than proximal simple member.

Coxa III bare; trochanter bare; femur with 1 serrate and 1 simple seta; genu with 1 simple seta; tibia with 1 serrate and 3 simple setae; tarsus with 3 simple and 2 terminal, spatulate-plumose setae.

Ventrally podosoma with 2 pairs of simple setae, anterior pair medial to coxae I and II, and posterior pair medial to coxa III.

The above descriptions were made from specimens collected in Lawrence, Kansas on *Gleditsia triacanthos* L. or progeny from these specimens reared in the laboratory.

Type specimens are females and males, collected in Natchez, Louisiana, from black locust (*Robinia pseudo-acacia* L.). Holotype female, type No. 2175, in the U.S. National Museum, Washington, D.C. The known distribution of this species includes Louisiana, North Carolina, Utah and Kansas.

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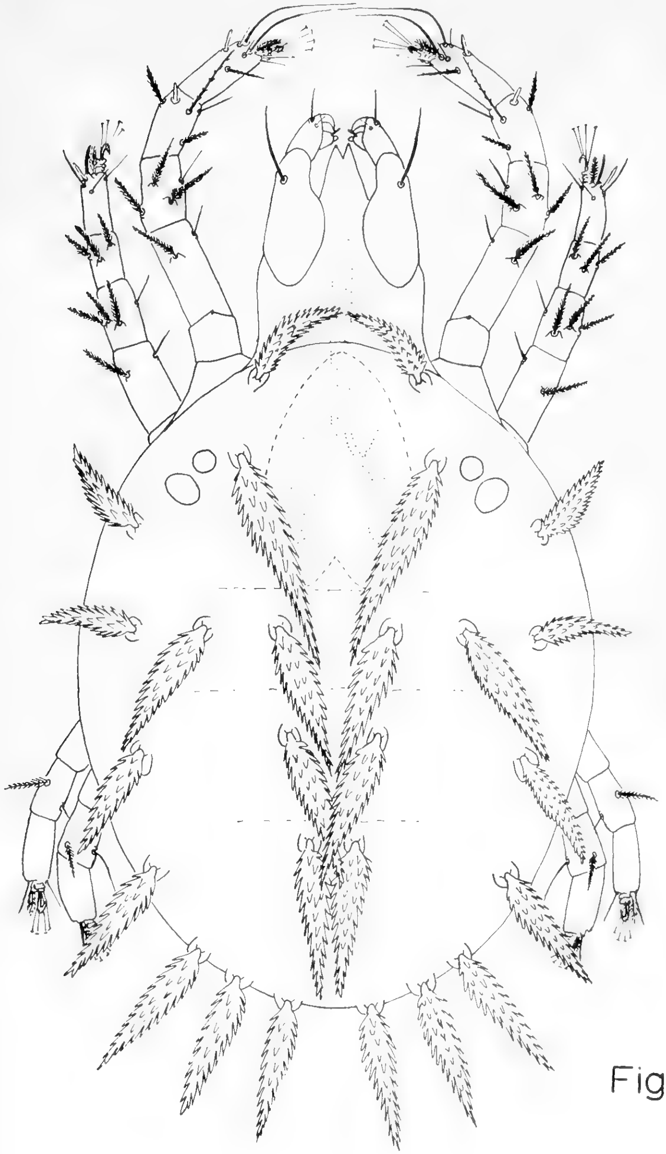

FIG. 1. *Tenuipalpoides dorychaeta.* Dorsal aspect of adult female.

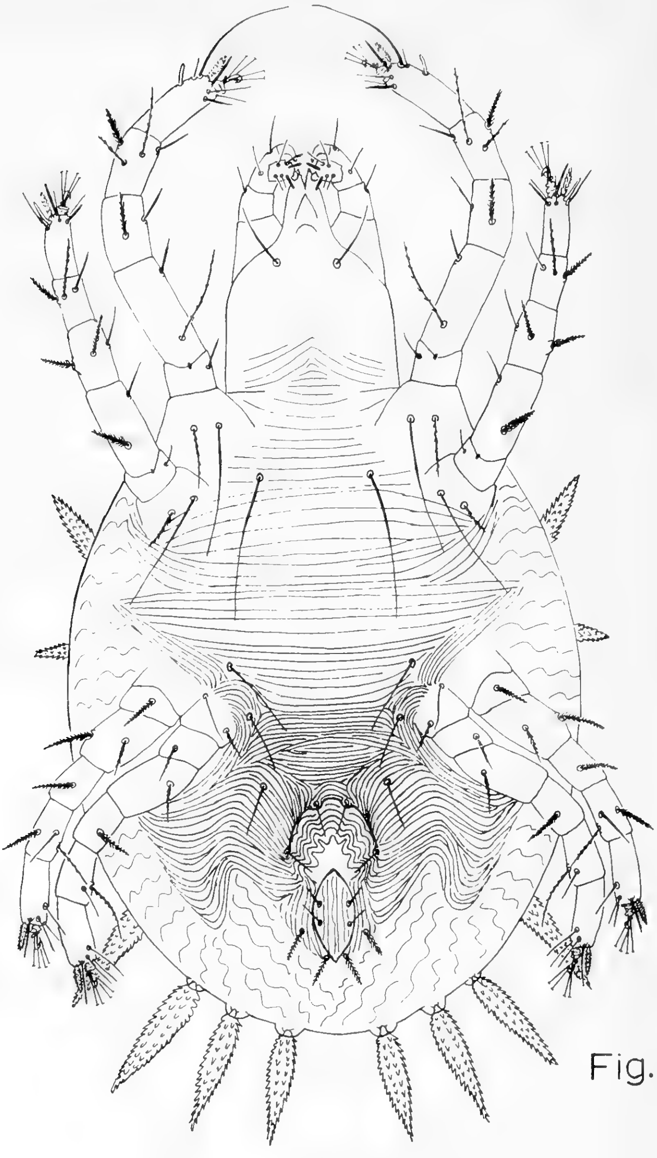

Fig. 2

Fig. 2. *Tenuipalpoides dorychaeta.* Ventral aspect of adult female.

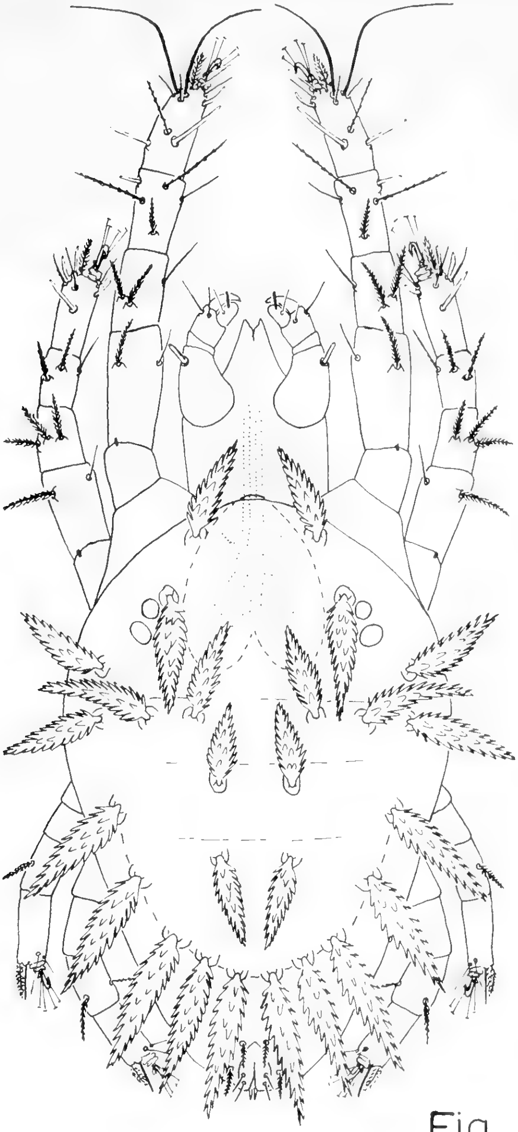

Fig. 3

FIG. 3. *Tenuipalpoides dorychaeta.* Dorsal aspect of adult male.

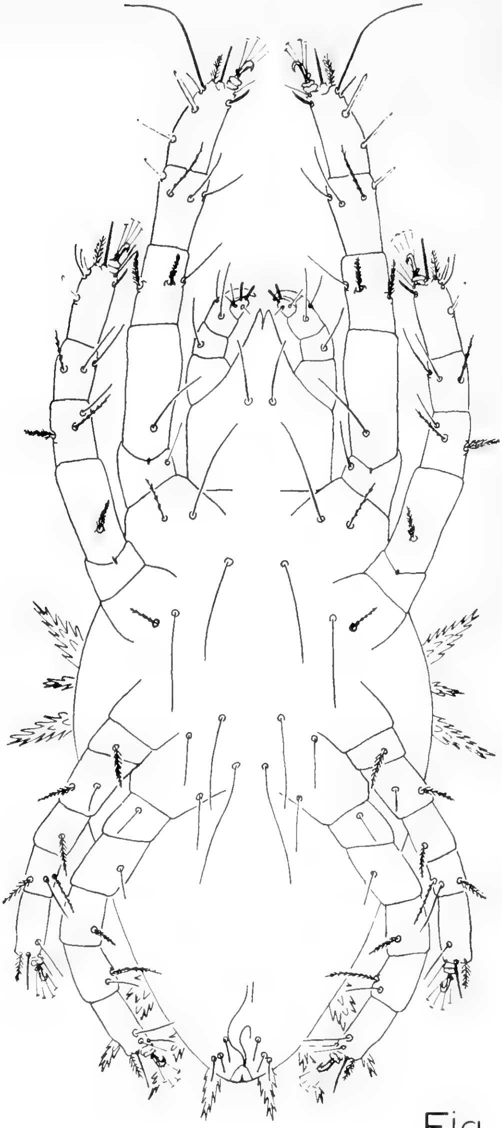

Fig. 4

FIG. 4. *Tenuipalpoides dorychaeta.* Ventral aspect of adult male.

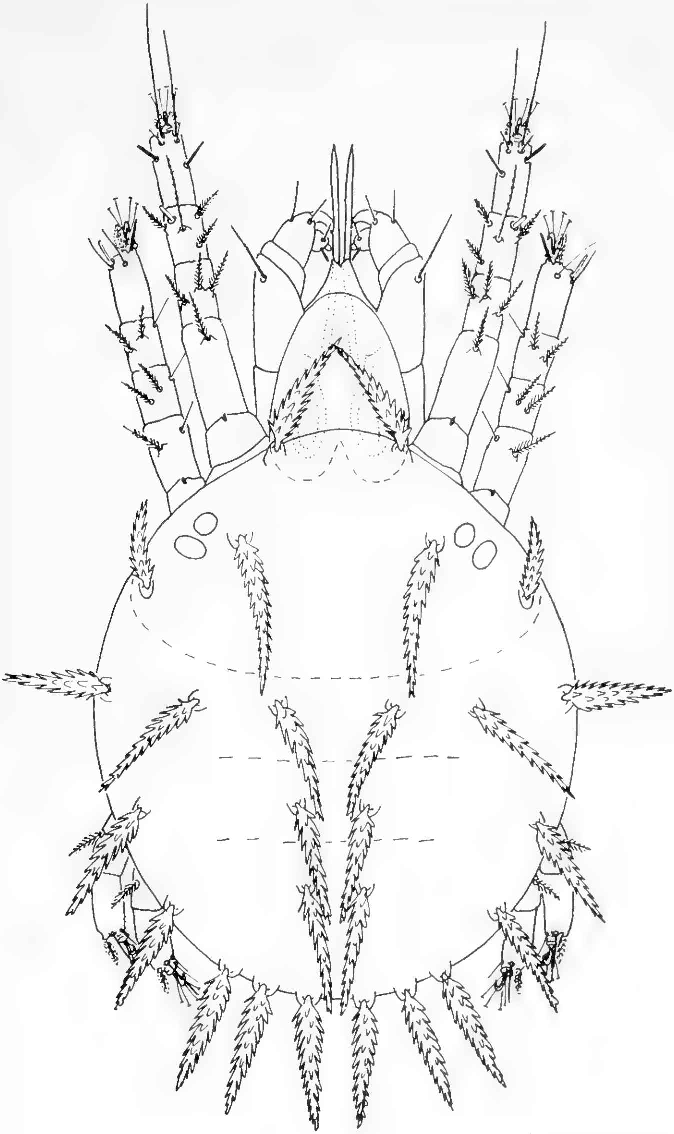

Fig. 5

FIG. 5. *Tenuipalpoides dorychaeta.* Dorsal aspect of deutonymph.

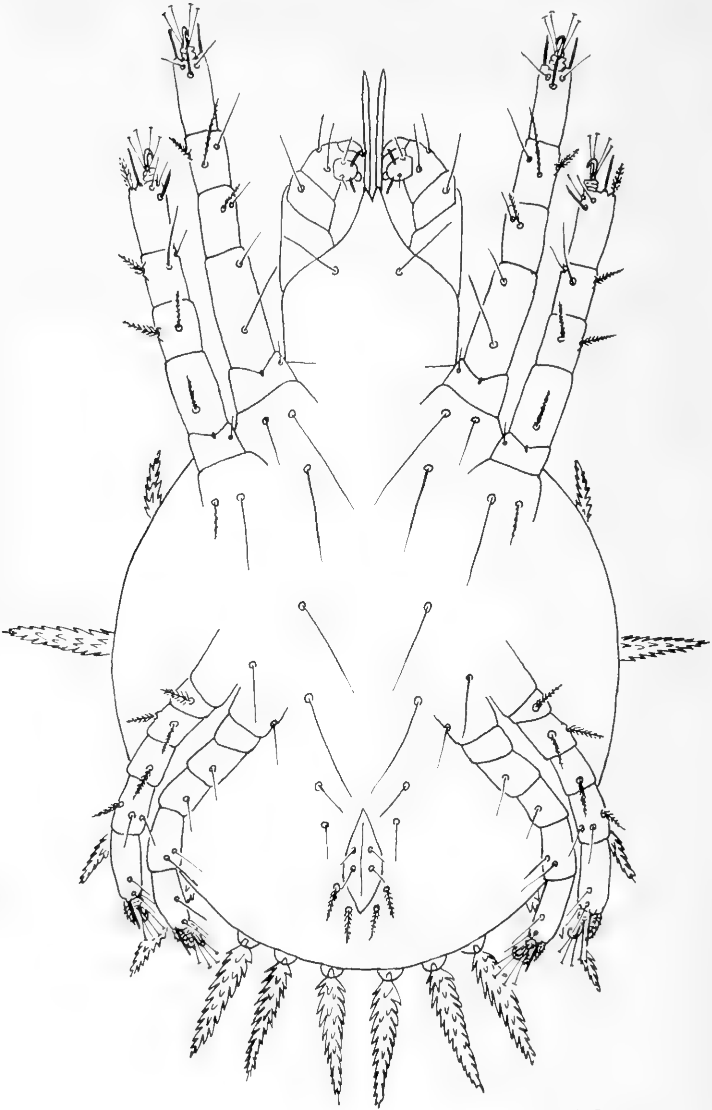

Fig. 6

FIG. 6. *Tenuipalpoides dorychaeta.* Ventral aspect of deutonymph.

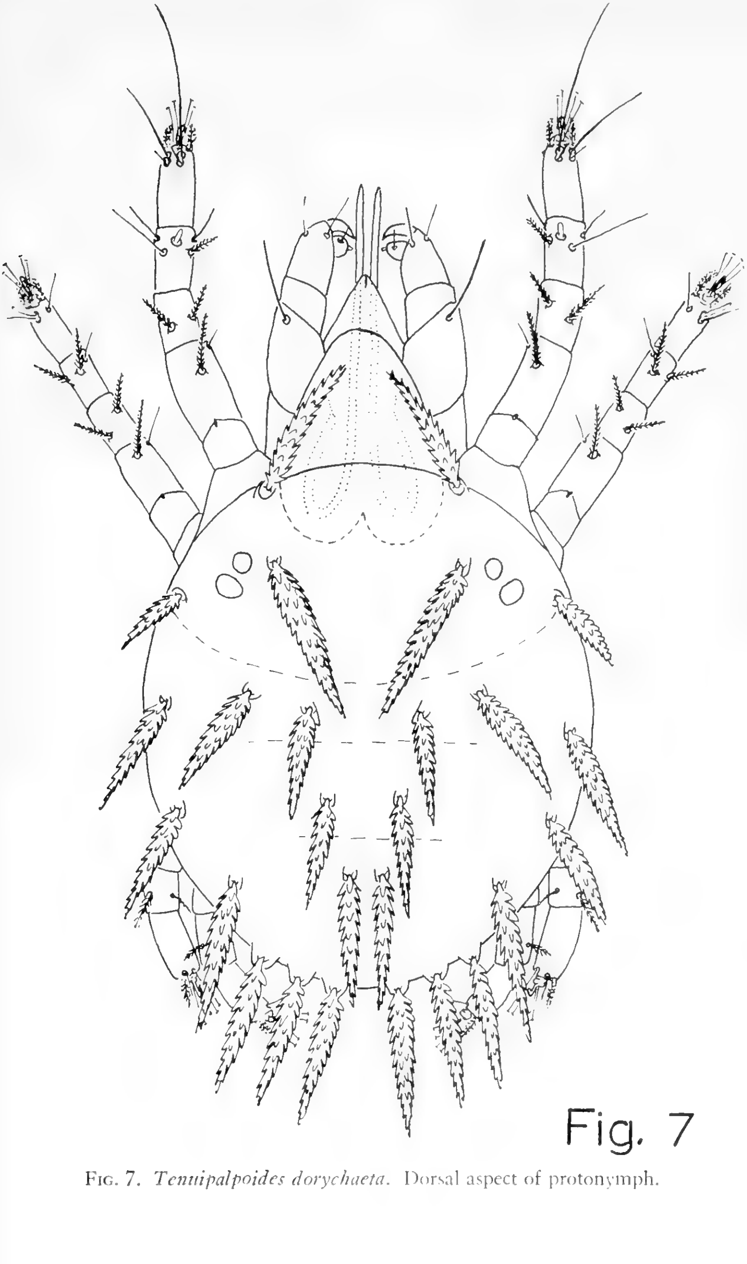

Fig. 7

FIG. 7. *Tenuipalpoides dorychaeta*. Dorsal aspect of protonymph.

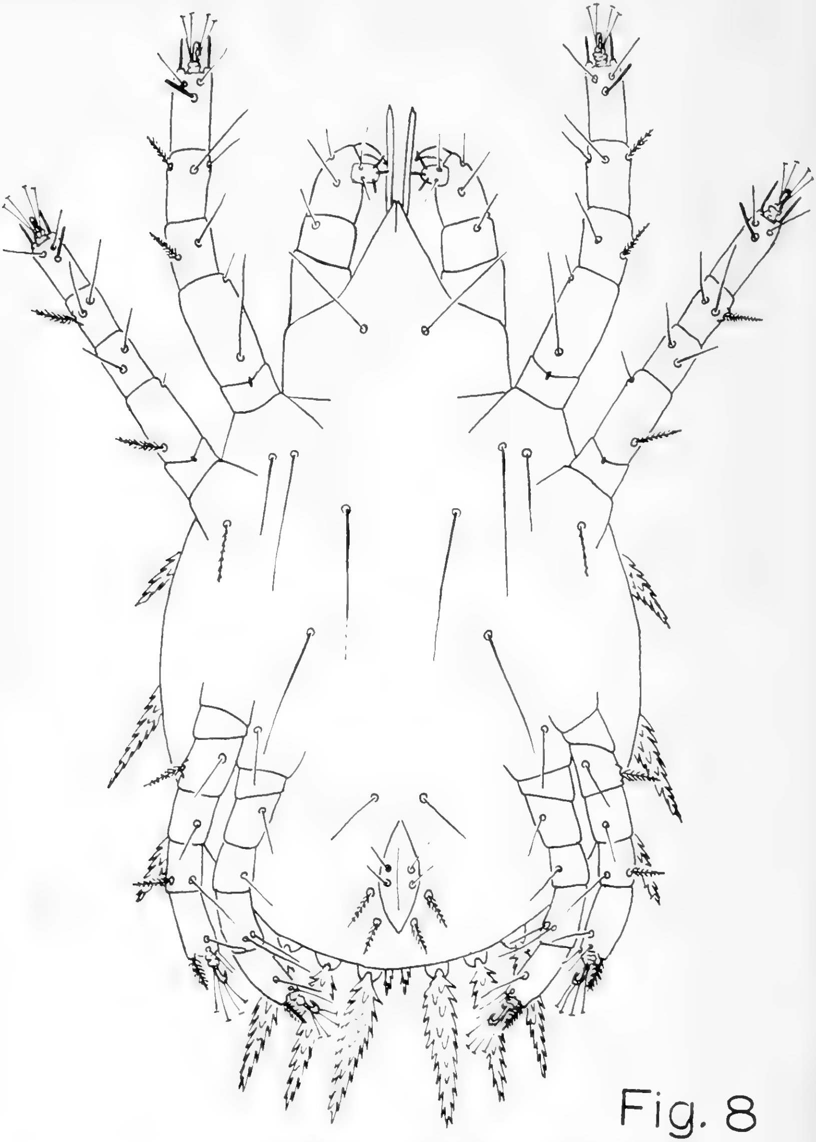

FIG. 8. *Tenuipalpoides dorychaeta.* Ventral aspect of protonymph.

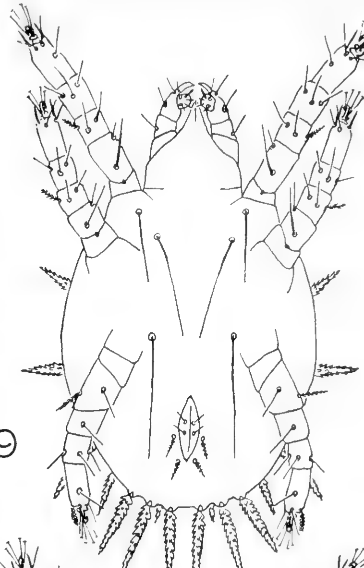

Fig. 9

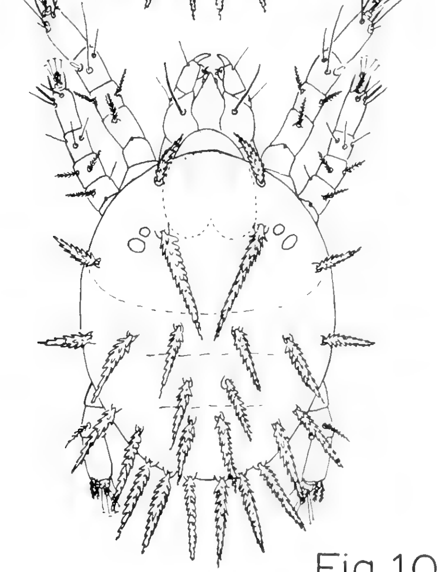

Fig.10

FIG. 9 & 10. *Tenuipalpoides dorychaeta.* Ventral (Fig. 9) and dorsal (Fig. 10) aspects of larva.

THE UNIVERSITY OF KANSAS
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A REVISION OF THE GENUS *EXEMA* OF AMERICA, NORTH OF MEXICO (CHRYSOMELIDAE, COLEOPTERA)

By

Jay B. Karren

Vol. XLVI Pages 647-695 December 2, 1966 No. 18

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A Revision Of The Genus *Exema* Of America, North Of Mexico (Chrysomelidae, Coleoptera)[1]

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ABSTRACT

In this revision of the genus *Exema* of America, north of Mexico, nine species are recognized and separated into three well-defined groups of one, five, and three species. A key to the species of this area is included. Three new species, *Exema mormona, E. elliptica,* and *E. byersi* are described and neotypes are designated for *E. gibber* Fabricius and *E. dispar* Lacordaire. Seven names are placed in synonymy for the first time. Although primarily taxonomic, this work brings together available data concerning variation, distribution, host plants, and parasites of a few species. A total of 6,296 specimens were included in this study.

INTRODUCTION

The object of this paper is to redefine the genus *Exema* and to make recognizable its species from America, north of Mexico. Fourteen specific and two subspecific names have been proposed for the genus in this area. Ten of these names are suppressed as junior synonyms. The nine species recognized in this paper can be separated into three groups. These groups have not been given formal names; the divisions are made only to show the relationships of the species within the genus.

Exema and its close relatives are noteworthy for their cryptic form and color, giving them a remarkable resemblance to caterpillar droppings, mouse feces, or other types of debris. The genus is closely related to *Chlamisus,* and some authors synonymize the two. The two genera are distinct, however, in North America; therefore, *Exema* is treated here as a separate genus. Species of *Exema* are found throughout the United States and in southern Canada from Manitoba eastward. Several of the southwestern species extend into Mexico and Central America.

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[1] Contribution number 1314 from the Department of Entomology, The University of Kansas, Lawrence, Kansas.

Brown (1943) indicated that species of *Exema* and *Chlamisus* of Canada have strong monophagous tendencies. In correspondence, he suggested that I undertake a study of the species of *Exema* and their food-plant relationships. Thereafter, in collecting *Exema* I took special note of plants on which the beetles were feeding. My field observations indicate that a given species feeds on one or on a limited variety of plants. Two or more species have seldom been collected on the same food plant in the same locality. In a few cases I have collected two or three specimens on "wrong" plants along with a considerable series of each species on the respective host plants. By study of a series of beetles from the same species of food plant in a locality, one is also able to obtain an indication of the degree of variability within a species.

Of the nine species in this study, *nodulosa, mormona, byersi,* and *canadensis* definitely have monophagous tendencies. The other five have wider preferences, but four of them are restricted to composites.

Few specimens in museum collections have host labels, but the information obtained from those has been of value. Some such host records seem to disprove the idea of monophagy; however, since larvae often leave the food plants to pupate and adults may wander to other species of plants, records unsupported by observations of feeding may not represent actual hosts. A large series collected from a single plant species represents a fairly reliable host record. A list of plants on which *Exema* has been collected is given for each species. These lists may contain true host plants as well as those that are not.

MATERIALS AND METHODS

This study is based upon my personal collections, those of the Snow Entomological Museum, and those of 48 museums listed in the acknowledgments. A total of 6,296 specimens were examined and their distribution was recorded. County names are placed in parentheses when they do not appear on specimen labels. Complete label data are given for primary types. The symbols in parentheses following the label data indicate the institutions where type material is deposited.

Six species were observed in the field before collection. Three of these were observed through a complete life cycle in the laboratory. Voucher specimens of these are in my collection and that of the Snow Entomological Museum.

The types of all species and synonyms were examined except those of *Chlamys rugulosa* Motschulsky, *Exema dispar* Lacordaire, and *Clythra gibber* Fabricius. Attempts to locate the type of *rugolosa* was unsuccessful. Its synonymy with *conspersa* is quite certain because it is the only species on the Pacific Coast, and the only one common in California. To clear up some confusion and create greater stability, neotypes have been designated for the other two species.

Representatives of several species were compared with a specimen (not the type) of *Clythra gibber* Fabricius in the collection of this authority by Sv. G. Larsson of the Universitetets Zoologiske Museum of Copenhagen, Denmark. The comparison made by Larsson indicates a species different from that of my understanding. Considering the Fabrician description and type locality, a neotype is designated for that species.

Specimens were studied at 15, 60, and 120 magnifications. Drawings and measurements were made with an ocular grid. Overall length was measured from the front of the head, when recessed within the pronotum, to the tips of the elytra. Width was measured between the outer edges of the humeral umbones. Drawings of genitalia were made after clearing them in KOH. The genitalia were removed by placing dried specimens in KOH which was brought to a boil, after which the specimens were immediately transferred to 95% alcohol. After a few seconds in alcohol, they were removed and held beneath the microscope between the thumb and index finger, and the pygidium was raised with a fine needle or forceps, the latter being used to remove the parts and to place them in hot KOH for a few minutes to clear. The genitalia were then immersed in alcohol for about a minute and transferred to a drop of glycerine in a small dish. All drawings of the dorsal aspect of the male genitalia were made with the apical half as nearly horizontal as possible. Female parts were prepared for drawing by spreading in glycerine between two cover-slips. The terminology used for the female parts is that used by Pierce (1940).

All *Exema* studied have a similar pattern of tubercles to which names are assigned to facilitate description. *Exema gibber* is illustrated (Fig. 1) for the purpose of indicating this terminology. All descriptions were made from the holotype or neotype. Variation is treated in the discussion.

Collecting specimens individually in the field was more successful than sweeping. After sweeping an area to determine which kind of plants had beetles, a methodical examination of the plants was made to procure a maximum number of them. A net was useful under the leaf or plant to catch beetles that dropped. When sweeping was the only method used, many beetles fell to the ground as soon as the plant was disturbed and were impossible to locate. The ability to fold appendages compactly enables these beetles to roll into ground litter and debris and disappear easily. Needless to say, all "caterpillar droppings" and similar objects should be examined whenever these beetles are being collected. Both adults and larvae occur on the same plants. All larvae collected were taken to the laboratory and fed with leaves of the plant from which they had been removed. Eventually they pupated and emerged as adults. Sometimes parasitic Ichneumonidae, Chalcidoidea, and Chalcidae emerged from the pupal cases.

The following list of abbreviations is used throughout this paper in parentheses to indicate the individual, museum or University in which the types are housed.

AMNH	American Museum of Natural History
ANSP	Academy of Natural Sciences of Philadelphia
BYU	Brigham Young University
CAS	California Academy of Sciences
CDA	Canada Department of Agriculture
CM	Carnegie Museum
CU	Cornell University
FDA	Florida Department of Agriculture
ISU	Iowa State University
JAW	J. A. Wilcox collection
JBK	Jay B. Karren collection
KSU	Kansas State University
LACM	Los Angeles County Museum
MCZ	Museum of Comparative Zoology, Harvard
MICH	Michigan State University
MSC	Montana State College
MSU	Montana State University
MZU	Museum Zoologicum Universitatis, Helsinki
NYSM	New York State Museum
OSU	Ohio State University
PU	Purdue University
RU	Rutgers University
SCU	Snow College, Utah
UA	University of Arizona
UCB	University of California, Berkeley
UCR	University of California, Riverside
UK	University of Kansas
UM	University of Missouri
UMIN	University of Minnesota
UN	University of Nebraska
USNM	United States National Museum

HISTORY OF THE GENUS *EXEMA* IN NORTH AMERICA

The generic name *Exema* was first used by Lacordaire (1848) for 16 species, mostly South American. In his key he used the character, antennae dentate from the sixth segment, to distinguish *Exema* from *Chlamys* (now *Chlamisus*). This character has since been used by various authors even though it is not reliable in some species. For example, if this character alone is used, *Exema gibber* males (Fig. 4) would be placed in the genus *Chlamisus* while the females (Fig. 3) would remain in *Exema*. A few species show an enlarged fifth antennal segment, making it difficult to decide in which genus they belong. In all cases the fifth segment is smaller than the sixth, and, with the additional characters of the shape of the aedeagus and ejaculatory guide and spines or spinulae on the male sternum and tibiae, it appears wise to retain the name *Exema* for this group in North America.

Of the 16 species treated by Lacordaire, ten were described as new. The other six had appeared earlier in the literature under the generic names *Chlamys* or *Clythra*. Only two of his species are North American.

The earliest description of an *Exema* is that by Fabricius (1798), for *gibber* in the genus *Clythra*. Olivier (1808) transferred this species to the genus *Chlamys* and emended the specific name, making it *gibbera*. From 1808 until the erection of the genus *Exema*, the species remained in the genus *Chlamys*.

Two other names were proposed for North American species prior to Lacordaire's work but were not recognized by him as belonging to the genus. The first was *Chlamys conspersa* Mannerheim (1843), the other *Chlamys rugulosa* Motschulsky (1845), both of which Lacordaire included in the genus *Chlamys* on the basis of the original descriptions.

Chapuis (1874) recognized the 16 species of Lacordaire and one additional species, *Exema malayana* Baly (1865). Other than giving another description of the genus and general distributions of the species, Chapuis' work added little to the knowledge of *Exema*.

In 1914, Achard summarized available information on the sub-family "Chlamydinae" and published the names, synonyms, and distributions of the species. He listed 27 species, mostly South American, but two North American.

Chlamys nodulosa Blatchley (1913) and *Exema neglecta* Blatchley (1920) were the next names proposed for North American species of *Exema*. The genus then remained unchanged until 1940, when Pierce proposed seven new species and two subspecies. Most of these are variations of the two western species.

Since 1848, no one has redefined the genus, but authors have repeated the description given by Lacordaire. Many workers have felt that since the antennal character varies, the genus should be synonymized under *Chlamisus* (*Chlamys* of earlier authors). In fact, Chûjô (1940) published such a proposal except that he recognized *Chlamys* as the synonym of *Exema*. He later (1955) changed this to *Chlamisus* with *Exema* as the synonym. In studying the North American species, I find the two genera quite distinct though closely related. Although the antennal character varies among the species of *Exema*, other characters that are more constant help to define the genus, and the two genera can be recognized easily as separate taxa in North America. More study on a world-wide basis is needed for a better understanding of *Exema* and its relationships to the other genera in the Chlamisinae.

THE GENUS *EXEMA*

Exema Lacordaire; 1848:844; Chapuis, 1874:204; Jacoby, 1881:89; 1908:278; Achard 1914:16-17; Pierce, 1940:7. Type species: *Chlamys intricata* Kollar, 1824 (designation by Jacoby, 1908).

Description: 2.1-3.5 mm long. Black to dark brown, usually marked with yellow on head, pronotum, elytra, and legs, sometimes coppery metallic. Body subquadrate or subpentagonal as seen from above, distinctly convex dorsally and ventrally. Head deeply inserted into prothorax, front inflexed ventrally; face flat, coarsely punctate, each puncture with a small hair which may be obscure. Antenna held in deep groove on side of prosternum in preserved specimens, scape slightly curved, large, as long as next 4 segments combined, ridged on outer side; pedicel globular, larger than next 2 segments; segments 3 and 4 subequal in length; segment 5 larger, sometimes nearly as large as each of the remaining segments; segments 6-10 strongly transverse, subequal in size, serrate, segment 11 longer, subtriangular, rounded at apex. Labrum slightly emarginate at apex, smooth, with a transverse row of hairs; clypeus not separated from frons, ventral margin shallowly emarginate. Eyes large, at sides of face, strongly emarginate at middle of inner margin. Pronotum strongly narrowed anteriorly, with more or less rounded sides; all margins closely paralleled by a continuous sulcus containing a row of punctures; gibbose (elevated median disc); tuberculate, carinate, or both, depending on species; strongly rugose to punctate. Elytra elongate, tuberculate and ridged; sutural margin completely dentate, humeral umbone prominent, less punctate and tuberculate than disc of elytron. Legs short, robust, gently compressed, drawn into excavations on sides of thorax and abdomen in preserved specimens; front tibia of male with short apical spine on inner side, usually a similar spine on middle tibia; tarsomeres padded beneath, tarsal claws simple or toothed (described as appendiculate by many authors). Prosternum (called basisternite by Pierce) large, narrowed posteriorly, highly variable in shape; prosternal process fits into notch in mesosternum. Metasternum large and prominent, with large, round punctures. Abdomen with 5 visible sterna, 1st with a median longitudinal carina, deeply hollowed on each side, with a pair of spines or many spinulae; 5th (last) sternum much longer than 3 preceding combined but smaller than 1st and generally with a median fovea in both sexes, flatter in males; many hairs associated with foveal area in both sexes. Male aedeagus pistol shaped in lateral view (Fig. 9); tegmen (Fig. 9) Y-shaped in apical view; dorsal median orifice near middle of aedeagus; tip flanged, truncate, or rounded, curved ventrally; ejaculatory guide short, torso-shaped (Fig. 11) with a mid-ventral and apical orifice through which flagellum passes.

Female genitalia used for covering egg with excrement, not developed into an ovipositor; 8th tergum with apical groove; 9th and 10th segments each represented by a pair of tergites and sternites in addition to pleura; auxiliary sclerite associated with each 9th sternite; 11th segment mostly membranous.

Comparisons: The small third to fifth antennal segments serve for most species to distinguish *Exema* from its near relatives in *Chlamisus.* In all cases the fifth segment is smaller than the sixth. Only one species of *Exema* is distinctly metallic, another slightly so, while many of *Chlamisus* are metallic. The elytral serration is always complete in *Exema* but complete or incomplete in *Chlamisus*. Species of *Exema* are usually smaller than those of *Chlamisus*. Males of *Exema* have front tibial and middle tibial (lacking in *gibber*) spines; females have neither. In *Chlamisus* some species have the spines in pairs, some single, and some have spines on the female tibiae. North American species of *Exema* have either spines or spinulae on the first and second abdominal sterna of the males. These spines are lacking on all *Chlamisus* that I have examined. The general shape of the aedeagus is constant in *Exema*, and the shape of the ejaculatory guide (called flagellum by Brown) is distinctive. It is a short, tubular, sclerotized structure as compared with the elongate, paired structure found in *Chlamisus* (see Figs. by Brown, 1943:126). More study is needed to determine the taxonomic value of the female structures.

KEY TO THE NORTH AMERICAN SPECIES OF *EXEMA*

1. Tarsal claws simple; cuticle all or in part black, not or only slightly metallic; pronotum at least in part rugose or striopunctate, tip of aedeagus rounded or slightly flanged 2
   Tarsal claws toothed; cuticle yellow, marked with black, or metallic; pronotum punctate; tip of aedeagus round, truncate or highly flanged 6
2. Frons in emargination of eye yellow; face of male mostly yellow; frontal slope of male pronotum always yellow; pronotum in part striopunctate 3
   Frons in emargination of eye black; face of male black with a yellow pattern (Fig. 20); frontal slope of male pronotum black or with reduced yellow markings; entire pronotum highly rugose or striopunctate 5
3. Nontubercular surface of pronotum rough, coarsely punctate anteriorly, punctures round and deep, especially on yellow areas of male; punctures elongate posteriorly .... *neglecta*
   Nontubercular surface of pronotum not rough, striopunctate throughout, punctures oval to elliptical 4
4. Cuticle slightly metallic; pronotal punctures elliptical, tubercles numerous, large; gibbosity high, flat in dorsal outline .... *elliptica* n. sp.
   Cuticle dull or shiny black; pronotal punctures oval to elliptical, tubercles sparse, small; gibbosity evenly rounded .... *byersi* n. sp.
5. Sutural tubercle 3a (Fig. 1, su-3a) and some spots on pronotum always bright yellow; bend of aedeagus smooth, tip truncate .... *mormona* n. sp.
   Sutural tubercle 3a and the rare pronotal spots usually black, never both yellow; bend of aedeagus rugose, tip flanged .... *canadensis*

6. Cuticle coppery to dark brown or black with coppery reflections; tip of aedeagus greatly flanged laterally and truncate with a dorsal, transverse row of long hairs; male with front tibial spine only; female with large auxiliary sclerites (Fig. 7, aux) .... *gibber*

   Cuticle not coppery but yellow and black; tip of aedeagus truncate or rounded, with lateral and ventral hairs only; male with front and middle tibial spines; female with small auxiliary sclerites, sometimes inconspicuous 7

7. Tooth of tarsal claw either small or blunt (Figs. 53-55); tubercles on pronotum and elytra usually small and blunt .... *deserti*

   Tooth and tarsal claw large and acute (Fig. 56); tubercles on pronotum and elytra usually large and distinct 8

8. Punctures distinctly setigerous; third tarsal segment about 0.5 as long as fourth; tarsomeres usually brown, more yellow in specimens from the Pacific Coast .... *conspersa*

   Punctures not or only faintly setigerous, especially on head and pronotum; third tarsal segment 0.7 as long as fourth or more; tarsomeres yellow .... *dispar*

Exema gibber (Fabricius)

Clythra gibber Fabricius, 1798:112; 1801:33; Zimsen, 1964:120

Clytra gibber Fabricius; Coquebert, 1804:129.

Chlamys gibber (Fabricius); Illiger, 1804a:126; 1804b:164; Schoenherr, 1808:343; Klug, 1824:116-117; Dejean, 1837:439 (listed).

Chlamys gibbera (Fabricius); Olivier, 1808:876.

Chlamys nodulosa Blatchley, 1913:22-23; 1930:37, 52 (lectotype designation as *Exema nodulosa*).

Chlamisus nodulosus (Blatchley); Brown, 1961:971 (note on name change).

Exema gibber (Fabricius); Lacordaire, 1848:849-852; Crotch, 1873: 30; Beutenmüller, 1890:175 (biology); Blatchley, 1910:1116; 1920:69-70; Chagnon, 1937-228 (misidentification); Pierce, 1940:12; Brown, 1943:124 (of Canadian authors=*E. canadensis* Pierce); Wilcox, 1954:394-395.

Exema gibber (Olivier; Dury, 1879-11 (probably *canadensis*); Henshaw, 1885:106; Smith, 1889:215 (distribution); Linell, 1879-480; Leng, 1918:208 (synonymizes *nodulosa* with *gibber*); 1920:288 (listed); Blatchley, 1924:50 (note on synonymy and biology); Fattig, 1948:8 (distribution).

Exema gibbera (Fabricius); Gemminger and Harold, 1874:3308 (listed); Clavareau, 1913:222; Achard, 1914:17 (listed).

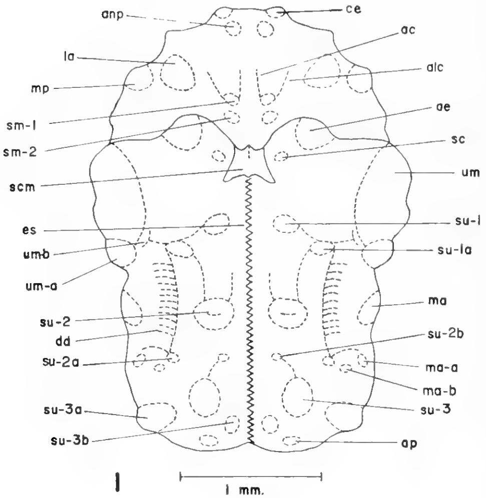
Exema nodulosa (Blatchley); Dekle, 1957:331-333 (biology).

Diagnosis: This is the easiest of the North American forms to identify. The males are unique in having spinulae on the first and fifth abdominal sterna (Fig. 2). This is the only species which lacks a spine on the apex of the middle tibia. This species is more punctate and tuberculate than any of the others. Like *conspersa* and related taxa, it lacks striate or rugose lines on the pronotum, as opposed to *canadensis* and related species which have at least a few on the posterior half. This species is found throughout most of the southern states (Fig. 58) on oak and a few other plant genera.

Type: Clythra gibber Fabricius, "Carolina" (probably near Charleston, South Carolina), Dom Bosc. The Paris museum staff is unable to locate this type. Blake did not find it in 1951.

According to Blake (1952) the Bosc specimens came from near Charleston, South Carolina between 1798 and 1800 and were taken to France and described by Fabricius and Olivier. Zimsen (1964:16) states that Bosc collected in and around New York. Upon his death, the Bosc collection was placed in the Museum National d'Histoire Naturelle, Paris. The type has not been located in that museum. The British Museum has a specimen labeled "*Exema gibber* type" which R. D. Pope (correspondence) feels is not the type but one sent to Olivier by Bosc and assumed to be the same as the one described by Fabricius in 1798. This specimen is the same as my *canadensis*. A speciman in the Fabrician collection, not the type according to Sv. Larsson of Copenhagen's Universitetets Zoologiske Museum, is similar to my *byersi*. Because of so much confusion with regard to this species, and because I feel the true type is lost, I am designating as a neotype a male collected in South Carolina (UK). I am assuming that the published record by Fabricius is the type locality. My study of *byersi* indicated that it is not found near South Carolina. Both Olivier and Lacordaire speak of the coppery color of which *gibber* is quite distinctive. There is some evidence that the type of Fabricius was used by these men in their descriptions. Also the darker forms of *gibber* agree better with the original description than does *byersi* or *canadensis*. Although the distribution of *gibber* is more extensive in Florida, it is found also in South Carolina. The species is somewhat variable in color but quite distinctive. The one that Blatchley described as *nodulosa* from Florida is a synonym of *gibber*.

Description: Male neotype: 2.6 mm long; 1.8 mm wide. Dark brownish bronze; antennal scape pale; remaining segments becoming darker at apex; yellow, smooth spot on frons between eyes; yellow triangle between antennae above clypeus; tubercles pale and shiny; tarsomeres brown. Entire cuticle minutely granulate, irregularly punctate. Head coarsely punctate; large punctures with recurved hairs; depressed area between antennal bases; antenna sparsely clothed with short hair; segments 3, 4, and 5 subequal, segment 6 triangular, segments 7-11 subequal; labrum smooth, slightly emarginate at apex, with a few ventrally projecting hairs. Pronotal gibbosity with rounded and acute tubercles; cephalic small and round; anterior larger and connected feebly to summit-1 by a small acute carina; summit-1 with carina extending anterior to large, round lateral tubercle; summit-2 acute; marginal small; entire pronotum highly irregular and tuberculate; scutellum with rounded lateral wings; median carina small. Elytra coarsely punctate; umbone large and prominent; large tubercles: anterior, sutural-1, 1a, 2, 3, 3a, and marginal; small tubercles: sutural-2a, 2b, 3b, umbonal-a, marginal-a, marginal-b, and apical; other tubercles faintly developed; sutural-1a carinate to umbonal-b.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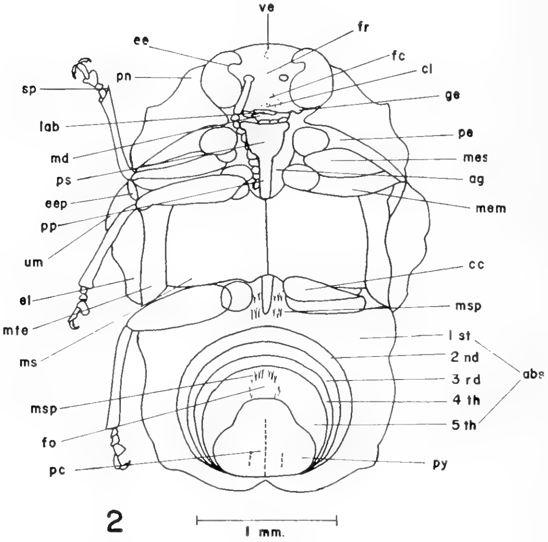
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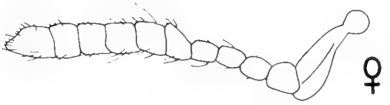
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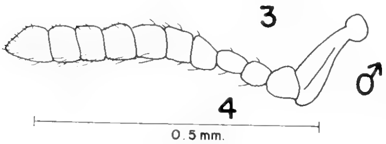
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0.5 mm.

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Legs shallowly punctate; tarsal claws broadly toothed; no spines on tibia or sterna. Prosternum coarsely punctate, concave; prosternal process broad, curved very slightly dorsally at tip; equal in length to concaved portion. Metasternal punctures large and deep, especially laterally. First abdominal sternum with a longitudinal carina between coxae, lateral side of sternum highly punctate with 1 large and 2 smaller tubercles; midventral area of 5th sternum flat and hairy. Pygidium gibbose with a pair of central, 2 elongate lateral, and 4 basal depressions; highly punctate, hairs in punctures. Aedeagus (Figs. 9, 10) greatly flanged at apex, with a heavy row of long, dorsal hairs.

Female: 3.2 mm long; 2.1 mm wide. Similar to male except lacks yellow on head. Tubercles are slightly less distinct. Midventral area of 5th sternum foveolate surrounded by hairs. Central pygidial carina less distinct. Genitalia as in Figs. 6-8.

Discussion: Blatchley listed this species as 4-4.5 mm long, but males are 2.5-3.2 mm and females 2.8-3.5 mm long. The form of the tarsal claws and the metallic appearance of the cuticle indicate this species' close relationship to the genus *Chlamisus*. The males would be identified as *Chlamisus* by use of previous keys, while the females would key out to *Exema*. This is because of the dimorphism of the antennae (Figs. 3-4). The species was described in *Chlamys* and placed in *Chlamisus* by Brown (1961). I have returned it to *Exema* for several reasons. First, the sculpturing of the pronotum and elytra is very similar to that of the other members of the genus. Second, the shape of the ejaculatory guide (Fig. 11) is similar to that in the rest of the genus and differs radically from that of any *Chlamisus* I have seen, including all species figured by Brown (1943). The shape of the aedeagus differs somewhat from the rest of *Exema*, but it differs equally from shapes seen in *Chlamisus*. Third, the elytral serration continues forward to the scutellum as in *Exema;* however, most *Chlamisus* have this same character. Considering these and other

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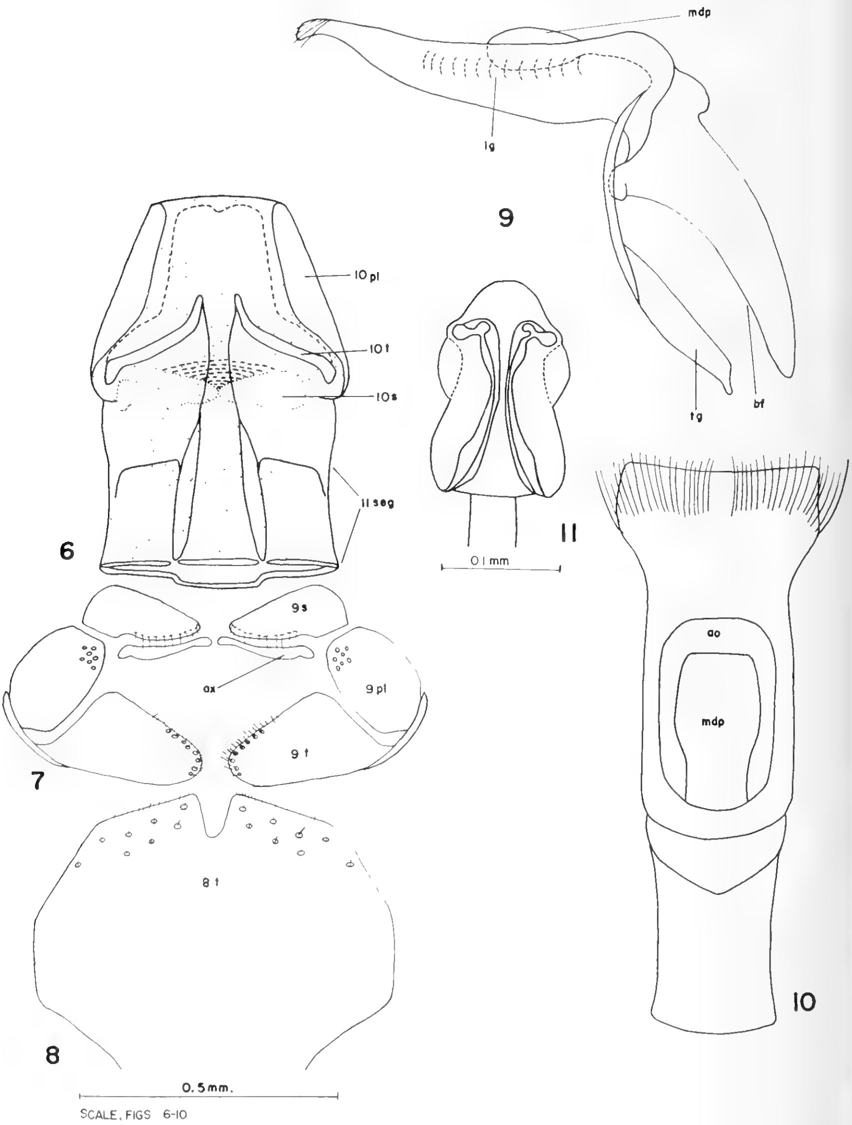
FIG. 1. Dorsal pattern of sculpturing of *Exema gibber:* ac—anterior carina, ae—anterior elytral, alc—anterolateral carina, anp—anterior pronotal, ap—apical, ce—cephalic, dd—discal depression, es—elytral serration, la—lateral, ma—marginal, ma-a—marginal-a, ma-b—marginal-b, mp—marginal pronotal, sc—scutellar, scm—scutellum, sm-1—summit-1, sm-2—summit-2, su-1—sutural-1, su-1a—sutural-1a, su-2—sutural-2, su-2a—sutural-2a, su-2b—sutural-2b, su-3—sutural-3, su-3a—sutural-3a, su-3b—sutural-3b, um—umbone, um-a—umbonal-a, um-b—umbonal-b.

FIG. 2. Ventral aspect of *Exema gibber,* male: abs—abdominal sterna, ag—antennal groove, cc—coxal cavity, cl—clypeus, ee—eye emargination, eep—elytral epipleuron, el—elytron, fc—frontal carina, fo—fovea, fr—frons, ge—gena, lab—labrum, md—mandible, mem—mesoepimeron, mes—mesoepisternum, ms—metasternum, msp—male spinula, mte—metaepisternum, pc—pygidial carina, pe—proepisternum, pn—pronotum, pp—prosternal process, ps—prosternum, py—pygidium, sp—spine of male protibia, um—umbone, ve—vertex.

FIG. 3. Antenna of female *Exema gibber.*

FIG. 4. Antenna of male *Exema gibber.*

FIG. 5. Tarsal claw of *Exema gibber.*



FIGS. 6-8. Dorsal aspect of *Exema gibber,* female abdominal segments eight to eleven; ax—auxiliary sclerite, pl—pleurite, s—sternite, seg—segment, t—tergite.

FIGS. 9-11. *Exema gibber,* male genitalia; 9—lateral aspect; 10—dorsal aspect; 11—ejaculatory guide; ao—apical orifice, bf—basal foramen, ejd—ejaculatory duct, fg—flagellum, lg—lateral groove, mdp—median dorsal plate, tg—tegmen.

characters, *gibber* shows affinities to *Chlamisus,* but it is more closely related to the genus *Exema.* For this reason it occupies a unique position in the genus as compared to the other 2 groups, which are represented by 5 and 3 species respectively.

Plant records: Quercus sp., *Myrica cerifer, Crataegus,* pecan, and *Lichi chinensis.* Dekle (1957) also records *Baccharis halimifolia, Rubus* spp. (blackberry and dewberry), and *Salix* sp.

Specimens examined: (92 males and 100 females). FLORIDA: Alachua Co., 13 Apr.-2 Oct.; Bevard Co., Mar.; Dade Co., 6-12 May; DeSoto Co., 9 Apr.; Duval Co., 19 Apr.-9 May; Hardee Co., 20 Mar.-3 Apr.; Highlands Co., 19 Apr.-31 May; Hillsborough Co., 1 Apr.-15 May; Lake Co., 1-11 Mar.; Lee Co., 6 May; Levy Co., 4 Apr.; Liberty Co., 24 Apr.; Manatee Co., 25-26 Mar.; Monroe Co., Apr.-13 May; Okaloosa Co., 16 May; Orange Co., Apr.-6 May; Palm Beach Co., 7-10 Apr.; Pasco Co., 16 Apr.; Pinellas Co., 15 Apr.-26 Aug.; Putnam Co., 3-26 Apr.; Sarasota Co., 11 May; Seminole Co., 28 Mar.-7 May; Taylor Co., 22 Apr.; Volusia Co., 15 Apr.-25 May; "Gunntown," Apr.; "Haulover," 3-17 Mar. GEORGIA: Chatham Co., 2 Apr.-27 May; Decatur Co., 18-21 May; Tift Co., no date. LOUISIANA: (Parish = county of other states) Caddo Par., 23-27 Mar. MISSISSIPPI: George Co., 7 May. PENNSYLVANIA: Philadelphia Co., 15 June. SOUTH CAROLINA: Beaufort Co., no date. TEXAS: Brazos Co., 1 Apr.; Colorado Co., 24 Apr.; Goliad Co., 18 Apr.; Harrison Co., 25 Mar.; Houston Co., 2 Apr.; Jefferson Co., 27 Apr.; Marion Co., no date; Trinity Co., 20 Mar.

Exema mormona n. sp.

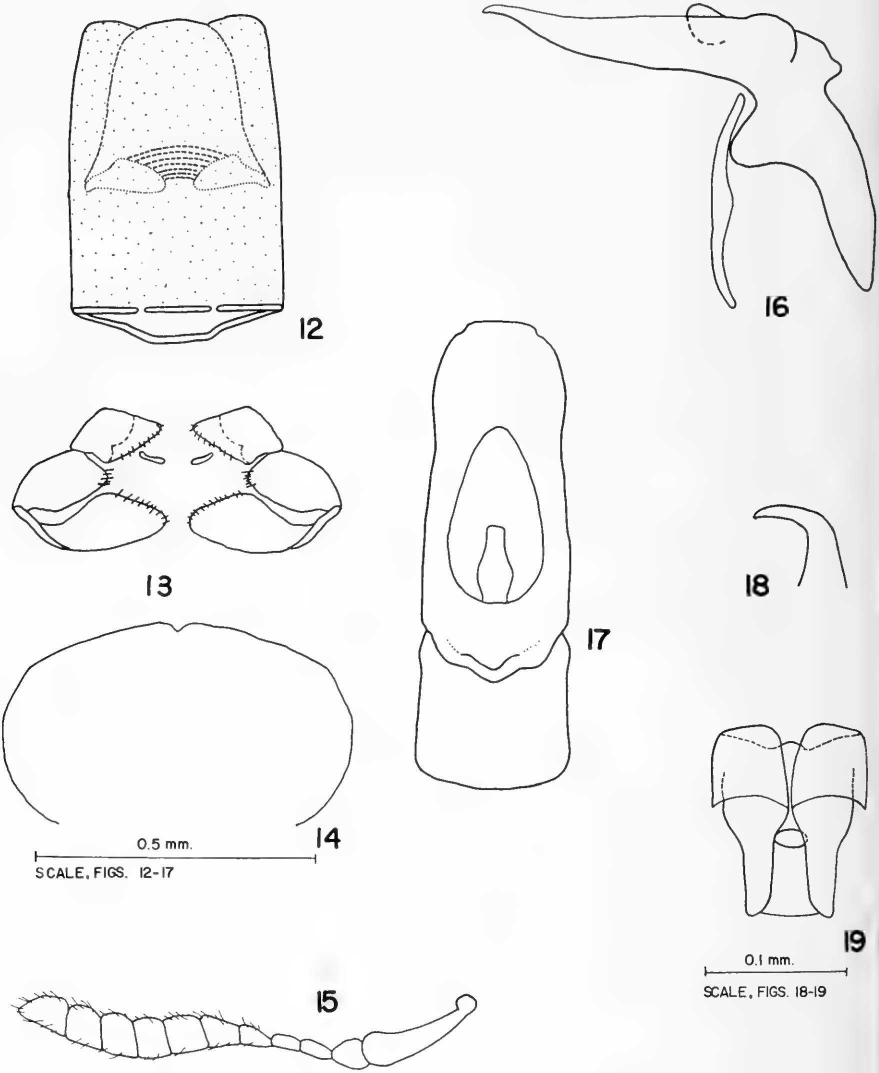
Diagnosis: The posterior slope of the pronotum is highly rugose; the anterodorsal surface is striopunctate. The posterodorsal bend of the aedeagus is smooth (Fig. 17) compared to highly rugose in *canadensis* (Fig. 25). The tip is more truncate and the basal half of the tegmen is much more slender than in *canadensis, neglecta* or *elliptica.*

This species is found most commonly from Texas to Montana, west of the Great Plains and east of the Pacific coast states (Fig. 59) on *Gutierrezia.*

The distribution, unusual color pattern, and host plant of this species first suggested the possibility of its being new. The following description is based upon 53 males and 54 females.

Description: Male: 2.7 mm long; 1.7 mm wide. Shiny black with yellow or yellowish brown markings. Antenna yellow at base, becoming dark brown at apex; mouthparts dark brown, labrum light at apex; face with longitudinal yellow bar next to each eye, transversely connected to central yellow spot which merges with triangular frontal spot covering carinal area. Frontal slope of pronotum with bright yellow inverted V just behind antecostal suture, yellow also extending laterally next to this suture for a short distance on each side (broken on the left side); marginal tubercle prominent, with small reddish yellow spot; yellow spot on anterior pronotum just behind eyes. Sutural tubercle 3a bright yellow. All tibiae with subbasal and subapical yellow rings; tarsomeres dark brown, nearly black; femora black.

Cuticle minutely granulate, coarsely punctate, more sparsely so on yellow than on black areas; head punctures large, mostly shallow, some deep ones in frons of emargination of eye; hairs in large punctures inconspicuous; antenna clothed with many short and a few long hairs, especially toward apex; segment 5 slightly larger than 3 or 4; labrum smooth, emarginate at apex, with



FIGS. 12-19. *Exema mormona* n. sp.; 12—female tenth and eleventh abdominal segments, 13—female ninth abdominal segment, 14—female eighth abdominal segment, 15—antenna, 16—lateral aspect of male aedeagus, 17—dorsal aspect of male aedeagus, 18—claw, 19—male ejaculatory guide.

transverse row of ventrally projecting long hairs. Pronotal gibbosity with rounded tubercles, cephalic and anterior pair missing, anterior carinae present, summit-2 present and separated from corresponding tubercle by a very broad U-shaped space; marginal tubercle small but prominent; entire pronotum with large elliptical punctures, largest posteriorly, giving a highly rugose effect on posterior slope; areas between tubercles minutely granulate. Scutellum finely punctate with lateral wings reflexed and almost acute. Elytra coarsely punctate, punctures large and deep, each with a short curved hair; smaller punctures on tubercles; umbone large and prominent; large tubercles: anterior, sutural-1, 2, 3, and 3a; small tubercles: scutellar, sutural-1a, 2a, 2b, umbonal-a, umbonal-b, marginal and marginal-b; other tubercles very small or lacking; faint carina developed on mesal side between sutural-1 and 2. Legs coarsely punctate, tarsal claws simple; apical spine on front and middle tibiae. Prosternum coarsely punctate, with transverse groove on cephalic end; prosternal process long and narrow. Metasternal punctures large and deep, especially laterally. First abdominal sternum with a longitudinal carina between coxal cavities, carina dividing near midlength into a faint Y-shape and terminating in 2 ventrally projecting spines on posterior margin of segment; 2nd segment with similar but smaller spines; punctures of 1st sternum large, round, shallow medially to deep on lateral margins; midventral area of 5th sternum flat to slightly concave, covered with long recurved hairs; lateral punctures large and oblong, nearly rugose. Pygidium centrally convex, faintly tricarinate, lateral carinae more distinct than medial, diverging ventrally. Aedeagus broadly truncate at tip which is narrower than the rest of structure; tegmen slim on the basal half.

Female: 2.8 mm long, 1.8 mm wide; similar to male except facial yellow reduced, longitudinal bars next to eyes broken, and small central spot only other yellow on head; pronotum with several irregular yellow spots on anterior slope. Punctation, sculpturing, and vestiture similar to those of male except front and middle tibial spines absent, spines on 1st and 2nd abdominal sterna absent, and fewer hairs on 5th sternum; a few long straight hairs situated on periphery of a slightly concave fovea bearing a few very short hairs. Pygidium distinctly tricarinate with lateral carinae larger than median one.

Types: Male holotype, Hobble Creek Canyon, Uinta National Forest, (Utah Co.), Utah, 16 Aug. 1961, on *Gutierrezia sarothrae*, S. L. Wood and J. B. Karren (UK). Same data on female allotype, 15 ♂ and 15 ♀ paratypes (UK, JBK, CDA, BYU).

Additional paratypes: UTAH 6 ♂ and 3 ♀, Diamond Fork Canyon, Utah Co., Aug. 1958, T. B. Moore (JBK, SCU); 3 ♂ and 3 ♀, Palmyra Forest Camp, Utah Co., 2 Aug. 1958, on *Artemisia tridentata*, T. B. Moore (JBK); 1 ♂ and 2 ♀, Honeyville, Utah Co., 18 May 1947, G. F. Knowlton (OSU); 1 ♂ and 1 ♀, Utah Co., 2 Sept. 1956, G. F. Knowlton (OSU); 1 ♀, Far West (Weber Co.), C. J. D. Brown (BYU); 2 ♂ and 1 ♀ labeled "Ut." (MSU). ARIZONA: 1 ♀, Grand Canyon, South Rim, about 7,000 ft. (Coconino Co.), D. Rockefeller (AMNH); 1 ♀, Oak Creek Canyon, Cochise Co., 2 Oct. 1955, Truxal and Freeman (LACM). COLORADO: 1 ♂, Walsenburg (Huerfano Co.), 14 June 1919 (AMNH); 1 ♂, labeled "Colo." (UM); 1 ♂, Greeley (Weld Co.), 1933, Wickham Collection (USNM); 1 ♀, Colorado Springs, 6000-7000 ft. (El Paso Co.), 15 June 1930, H. F. Wickham (USNM); 1 ♀, labeled "Colo.", Wickham Collection (USNM). KANSAS: 2 ♀, labeled "Kans.", Williston, R. M. Moore collection (NYSM). MINNESOTA: 1 ♂, Traverse Co., O. W. Oestland collection (MSC). MISSISSIPPI: 1 ♂, Wiggins (Stone Co.), 15 Aug. 1936, H. H. Harris (ISU). MONTANA: 1 ♀, 15 mi. E. Miles City, Custer Co., 20 June 1956, R. C. Froeschner (MSU); 1 ♀, Glendive, Dawson Co., 21 June 1956, R. C. Froeschner (MSU); 4 ♀, labeled "Mon.", Horn collection (ANSP); 1 ♂ and 1 ♀, labeled

"Mon.", Holland collection (CM). NEBRASKA: 1 ♂, Glen, (Sioux Co.), Aug. 1903 (AMNH); 1 ♂, Pine Ridge (Dawes Co.), July (UN). NEW MEXICO: 4 ♂, Santa Fe, (Santa Fe Co.), 14 July 1934, E. L. Bell (AMNH); 1 ♂, Vaughn (Guadalupe Co.), 5 June 1933, R. H. Beamer (UK); 1 ♂ and 2 ♀, Maxwell (Colfax Co.), 27 June 1916 (RU); 1 ♂, Upton (Roosevelt Co.), 19 Aug. 1949, on *Gutierrezia* sp., J. H. Russell (USNM). TEXAS: 1 ♀, Frio Co., 20 May 1948, D. J. & J. M. Knull (OSU); 1 ♂, Marathon, (Brewster Co.), 1-2 July 1916 (AMNH); 1 ♂ and 1 ♀, Flatonia (Fayette Co.), July 1903, J. W. Green (CAS); 7 ♂ and 7 ♀, 10 mi. N. Pyote (Ward Co.), 8 July 1945, with larvae on *Gutierrezia,* J. H. Russell (USNM, KU, JBK).

Discussion: This species varies little in sculpturing, but in coloration no two individuals are the same. The yellow on the head my be reduced to several spots in the females (Fig. 26). Males, however, always show more yellow than females (Fig. 20), and the pattern is more constant than in *canadensis.* Males always have more yellow on the pronotum than females in which the yellow may be reduced to faint spots. The yellow is quite irregular, and one side of an individual may have a different pattern from the other. The yellow tubercle may be reduced to just a yellow tip but is usually bright and distinct. The body oils cause some of this yellow color to become dark in older specimens. In one female from Texas the umbonal-a and marginal tubercle are also yellow.

The shape of the prosternum is flat to concave and the process narrow to wide. The pygidium also varies in punctation, shape, and size of the carinae.

Specimens of *mormona* show certain affinities with *byersi, neglecta,* and *canadensis.* The males of *canadensis* and *mormona* have similar yellow facial patterns, but the latter seldom has yellow on the pronotum or yellow tubercle 3a. In a few specimens, tubercle 3a is very faintly yellow, and in others there are a few yellow spots on the pronotum, but the two characters never occur together in *canadensis.* Specimens of *mormona* can easily be distinguished from *neglecta* by the elongated punctures and less yellow on the frontal slope of the pronotum. The frons in the emargination of the eye is always yellow in neglecta and black in *mormona.* The aedeagus closely resembles that of *neglecta.* One might think that *mormona* is a hybrid between *neglecta* and *canadensis,* except for its distribution and entirely different host plants. A similar situation exists for *byersi,* discussed later.

Plant records: Gutierrezia sarothrae and *Artemisia tridentata.*

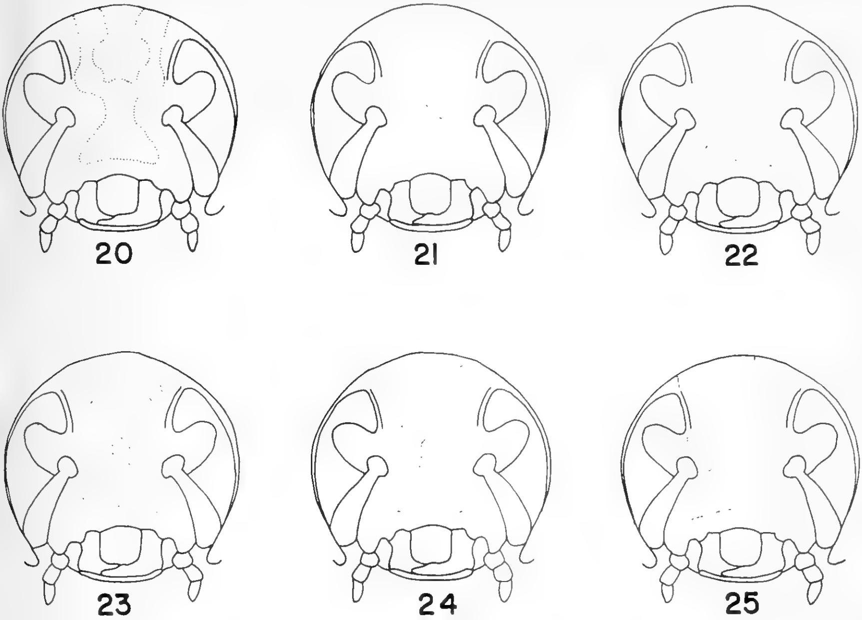
Parasites: Catolaccus aeneoviridis and *Tetrastichus chlamytis.*

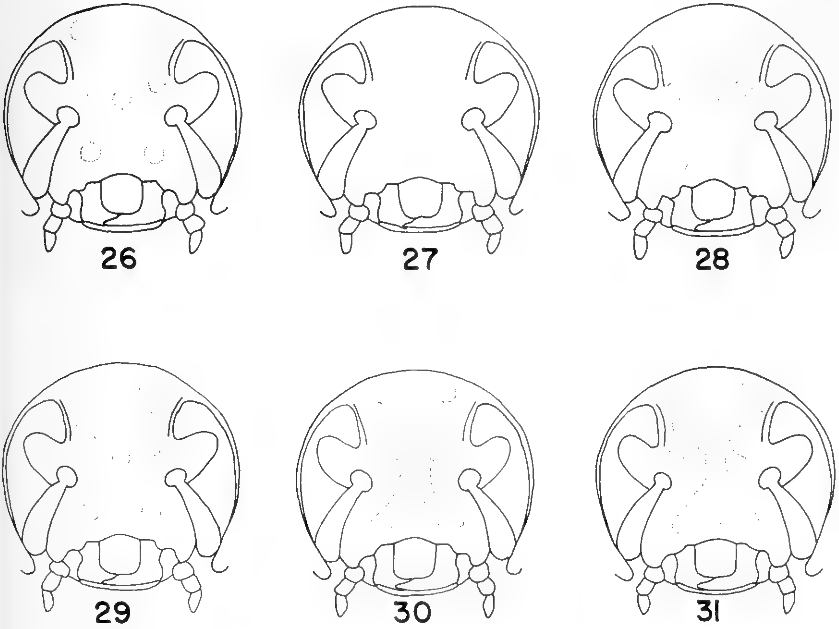
Exema canadensis Pierce

Exema dispar canadensis Pierce, 1940:10-12; Proctor, 1946:187; Blackwelder and Blackwelder, 1948:42 (listed).

Exema canadensis Pierce; Brown, 1943:124; Blackwelder and Blackwelder, 1948-42 (listed); Dillon and Dillon, 1961:670; Wilcox, 1954:394-395.

Diagnosis: Specimens of *canadensis* differ from *neglecta* in having long, slender punctures on the pronotum, giving it the most highly rugose appearance in the genus. The recurved hairs on the foveal area of the male are larger





Figs. 20-25. Variation in yellow pattern of face of male *Exema canadensis*.

Figs. 26-31. Variation in yellow pattern of face of female *Exema canadensis*.

and more numerous than in *byersi*. This species is commonly found east of the Great Plains from Florida into southern Canada (Fig. 60) on *Solidago*.

Description: Male: 2.4 mm long; 1.6 mm wide. Shiny black with yellow or yellowish black markings. Antennal scape yellow, flagellum becoming dark brown at apex; mouthparts dark brown; face with longitudinal yellow bar next to each eye, transversely connected to central yellow spot which merges with triangular frontal spot covering carinal area. Frontal slope of pronotum black. All tibiae with subbasal and subapical yellow rings, anterior femur with basal yellow ring; tarsomeres dark brown. Entire cuticle minutely granulate, punctate. Head coarsely punctate, deeper in frons of emargination of eye; hairs in large punctures inconspicuous; antenna clothed with many long and a few short hairs; segment 5 larger than 3 or 4; labrum smooth with transverse row of ventrally projecting long hairs. Pronotal gibbosity rounded, tubercles and carinae rounded; cephalic and anterior missing, anterior carinae, summit-2, marginal, and lateral tubercles present; entire pronotum with large elliptical punctures, largest posteriorly, giving a highly rugose effect on posterior slope. Scutellum feebly carinate, with lateral wings almost acute. Elytra coarsely punctate, each puncture with a short curved hair; umbone large and prominent; large tubercles: anterior, sutural-1, 1a, 2, 3, 3a, marginal, marginal-b, umbonal-b; small tubercles: scutellar, sutural-2a, 2b, 3b, and apical. Legs with shallow setigerous punctures; tarsal claws simple; apical spine on front and middle tibiae. Prosternum concave, coarsely punctate, with slight transverse groove on cephalic end; prosternal process long, narrow, curved dorsally. Metasternal punctures large and deep, especially laterally. First abdominal sternum with a longitudinal carina between coxae, carina dividing near midlength into a faint Y-shape and terminating into 2 ventrally projecting spines on posterior margin of segment; 2nd segment with similar but smaller spines; punctures of 1st sternum large and round, shallow medially to deep on lateral margins; lateral area of sternum feebly carinate; midventral area of 5th sternum flat to slightly concave, covered with long recurved hairs; lateral punctures large and oblong. Pygidium slightly convex, median carina distinct, lateral carinae obsolete. Aedeagus narrowly flanged at tip, tegmen expanded, dorsal bend of aedeagus rugose.

Female: 2.7 mm long; 1.8 mm wide. Similar to male except for facial yellow reduced to spots, 4 next to eyes, 1 central, 2 on carinal area; never yellow on anterior slope of pronotum. Punctation, sculpturing, and vestiture similar to those of male except front and middle tibial spines absent, spines on sterna absent, and fewer hairs on a deeper fovea of 5th sternum. Pygidium distinctly tricarinate with lateral carinae larger than median one.

Types: The male holotype, female allotype, 3 male and 2 female paratypes, from Montreal, Quebec (LACM) comprise the type series.

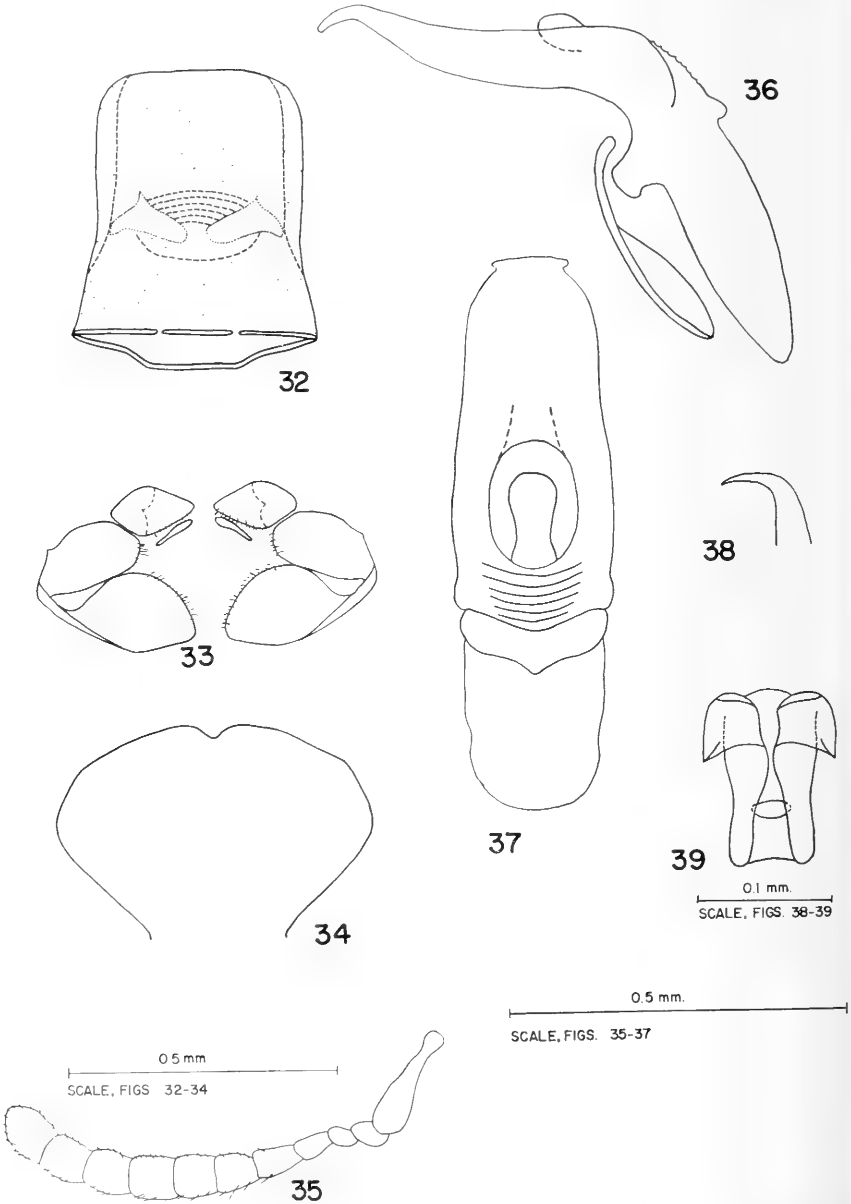
I have examined the holotype, allotype, male paratypes 3 and 4, and female paratypes 6 (CAS) and 7. All agree quite well with the description.

Discussion: This the most abundant and wide-spread species of *Exema*. It appears to feed most frequently on *Solidago*, but occasionally it is found on other composites. The wide distribution, attributable in part to the distribution of *Solidago*, may contribute to the variability of the species. I have several specimens that have the elytral tubercle 3a faintly yellow. Some have a yellow spot or two on the pronotum. Usually the femora are black with subapical and subbasal rings of yellow. Specimens from Pennsylvania, Ohio, and New York, tend to be darker than others in the species. The tibiae are darker; in some they are even black. The pronotal tubercles and carinae are broadly rounded, but larger and more numerous in specimens from the southern states, especially Florida. Some of these southern forms have no yellow markings on the face and the rugose nature of the aedeagus is also very faint, but there are too many intermediates to consider these forms a separate species. There is a general pattern of yellow on the face, which may be several combinations of spots and bars or the complete pattern with the broad Y-shape (Figs. 20-31). Very few of the extreme individuals are found, but they do exist and cause some difficulty in distinguishing males from females by color alone. In most cases the two ventral spots are lacking in the female pattern, but in a few these spots are faint to distinct. The yellow carina always seems to be present in males, but the other yellow areas may be lacking in darker specimens. The prosternum is concave to convex. The carinae on the pygidium vary from highly tricarinate to very smooth, males usually being smoother than females.

Plant records: Solidago altissima, S. neglecta, Corylus, Sambucus canadensis, chokecherry blossoms, elm, ragweed and ironweed?, *Salix* sp., birch, strawberry, *Cornus* sp., *Haplopappus phydocephalus, Erigeron quercifolius,* and blackberry foliage.

Parasites: Spilochalcis delumbis and *Perilampus fulvicornis.*

Specimens examined: (568 males and 784 females). One female specimen from Blatchley's collection, among those indicated as *neglecta,* is labeled as a "lectoparatype" of that species. ALABAMA: Houston Co., 18 June; Limestone Co., 27-28 June; Macon Co., 19 July; Mobile Co., 23 Apr.-21 Sept. ARKANSAS: Clay Co., June-6 Nov. (?); Garland Co., no date. CONNECTICUT: Fairfield Co., 24 June-2 July; Litchfield Co., 21 May-28 Aug.; New Haven Co., 25 May-7 June; Tolland Co., 6 June-2 Oct. DISTRICT OF COLUMBIA: Washington, 23 June. FLORIDA: Alachua Co., 30 Mar.-21 Apr.; Charlotte Co., 25 Apr.; Citrus Co., 23 May; Dade Co., 14 Apr.-11 June; Dixie Co., 20 Apr.; Duval Co., 9 May; Gadsden Co., 1 May-12 July; Hendry Co., 19 Apr.-26 Feb.; Highlands Co., 6 Mar.-10 May; Lafayette Co., 16 May; Lake Co., 21 Oct.; Lee Co., 31 Mar.; Levy Co., 13 Apr.-31 July; Pinellas Co., 2 Apr.-26 Aug.; Polk Co., 6 May-13 Aug.; Putnam Co., 24 Apr.; Seminole Co., 3 May; Volusia Co., Apr.; "Gunntown," no date. GEORGIA: State record, no date. ILLINOIS: Cook Co., 18 May-5 Aug.; Jackson Co., 3 June; Kankakee Co., 4 July; Lake Co., 19 Aug.; LaSalle Co., 15 May-29 July; Will Co., 13 June. INDIANA: DeKalb Co., 13 June; Dubois Co., 14 May; Elkart Co., no date; Knox Co., 18 Sept.; Kosciusko Co., 21 May-24 June; Lake Co., 11 May-22 Sept.; Lawrence Co., 21 May-9 June; Orange Co., 28 May-9 June; Porter Co., 30 May. IOWA: Dickinson Co., 22 Aug.; Mahaska Co., 6 Aug.; Monona Co., 6 June; KANSAS: Anderson Co., 1 July; Crawford Co., no date; Douglas Co., 4 May-11 July; Jefferson Co., 27 May-8 July; Labette Co., no date; Miami Co., no date; Montgomery Co., 23



Figs. 32-39. *Exema canadensis;* 32—female tenth and eleventh abdominal segments, 33—female ninth abdominal segment, 34—female eighth abdominal segment, 35—antenna, 36—lateral aspect of male aedeagus, 37—dorsal aspect of male aedeagus, 38—claw, 39—male ejaculatory guide.

May; Riley Co., 21 June-July; Sedgwick Co., 16 Aug. KENTUCKY: Bullitt County, 9 Mar.; Jefferson Co., 10 Aug.; LOUISIANA: (Parish=county of other states) Natchitoches Par., 16 Aug.; St. Charles Par., 14 Apr.; St. James Par., 7 June; St. Landry Par., June; St. Tammany Par., 25 May-June; "Doeville," 6 May. MAINE: Cumberland Co., 11-15 Aug.; Hancock Co., 26 Aug.; Kennebec Co., 12 July; Lincoln Co., 18 June-27 Aug.; Oxford Co., 10 July; Washington Co., June. MARYLAND: Baltimore Co., 17 May-30 July; Charles Co., 25 May; Montgomery Co., 30 May; Prince Georges Co., 22 May-9 July; "Glover," no date. MASSACHUSETTS: Hampden Co., 28 June-24 Aug.; Hampshire Co., 9 June; Middlesex Co., 25 May-10 Oct.; Norfolk Co., 2 Sept.; Suffolk Co., 17 May; Worcester Co., 19 June-5 Sept. MICHIGAN: Allegan Co., 1 June; Barry Co., 10 July; Bay Co., 1 June; Cheboygan Co., 18 June-18 July; Clinton Co., 31 Aug.; Ingham Co., 4-27 Sept.; Kent Co., 5 Aug.; Midland Co., 29 May-12 Aug.; Washtenaw Co., 1 Aug.; Wayne Co., no date. MINNESOTA: Anoka Co., 14-27 Aug.; Big Stone Co., no date; Clearwater Co., 25 July; Hennepin Co., 28 June-24 Aug.; Ottertail Co., no date; Ramsey Co., no date; Red Lake Co., 20 June; Traverse Co., no date; Washington Co., 7 Aug. or 8 July. MISSISSIPPI: George Co., 5-22 June; Green Co., 23 May-13 Sept.; Grenada Co., 11 June; Jackson Co., 12 July; Montgomery Co., 7 May; Perry Co., 23 Mar.-2 Oct. MISSOURI: Boone Co., 4-16 May; Howard Co., 12 May; Miller Co., 16 May; Morgan Co., 13 May; Ozark Co., 9 June; Pettis Co., 10 June; Pike Co., 20 Apr.-28 June; St. Louis Co., no date. MONTANA: "Assinbne," 29 Aug. NEBRASKA: Antelope Co., 21-22 June; Douglas Co., 20 Sept.; Holt Co., 9 Sept.; Lancaster Co., 6 July-2 Oct. NEW BRUNSWICK: French Lake, 2 June. NEW HAMPSHIRE: Strafford Co., no date. NEW JERSEY: Atlantic Co., 15 June; Bergen Co., 20 June-1 Aug.; Camden Co., no date; Cape May Co., June; Cumberland Co., 30 Sept.; Essex Co., 4 June-27 Sept.; Gloucester Co., 31 May; Middlesex Co., 2 June-2 Aug.; Hudson Co., no date; Passaic Co., 26 June-27 July; Somerset Co., no date; Sussex Co., 24 May; Union Co., no date. NEW YORK: Albany Co., 26 May-5 July; Bronx Co., 30 May-3 July; Cortland Co., 18 May; Erie Co., 28 June-10 Aug.; Essex Co., 11 May-2 June; Herkimer Co., no date; Livingston Co., 29 Aug.; Monroe Co., 30 May-9 Sept.; Orange Co., 26-30 May; Orleans Co., 10 June; Oswego Co., 1 Aug.-15 Oct.; Putnam Co., 29 May-June; Queens Co., 15 June-July; Richmond Co., 20 May-1 Oct.; Rockland Co., 30 May-28 June; Saint Lawrence Co., 12 June-18 Aug.; Suffolk Co., 25 Aug.; Tompkins Co., 8 May-25 Sept.; Westchester Co., 5 May-25 Aug. NORTH CAROLINA: Guilford Co., 21 June; Moore Co., Aug.; Wake Co., no date. NORTH DAKOTA: Bottineau Co., 30 July; Traill Co., 7 Aug. OHIO: Champaign Co., 22 May-6 June; Delaware Co., 2 May; Franklin Co., 5 June-5 Sept.; Hocking Co., 2 July-9 Aug.; Jackson Co., 3-6 July; Lake Co., 3 June; Lorain Co., 13 June-4 Sept.; Ross Co., 22 May; Scioto Co., 10 June; Summit Co., 2 July-11 Aug.; Williams Co., no date. OKLAHOMA; Jefferson Co., 18 May. ONTARIO: Arnprior, July 23 Aug.; Blackburn, 31 July; Delhi, 3 June; Fisher Glen, 12 June; Leamington, 6 July; Ojibway, 29 Aug.; Rich Edward Co., 24 May-6 Oct.; Simcoe, 13 June; Toronto, 16 May; Turkey Point, 1-8 June; Walsingham, 1 June. PENNSYLVANIA: Bucks Co., 30 May; Dauphin Co., 17 June-27 Aug.; Delaware Co., 28 May-16 June; Juniata Co., 14 Sept.; Monroe Co., 21 Sept.; Northampton Co., 31 May-18 June; Philadelphia Co., 25 May-21 Aug.; Pike Co., 20 May-15 Aug. QUEBEC: Hemmingford, 7 Sept.; Longueuil, 18 Aug.; Montreal, 10 May-20 Oct.; Outremont, 25 Aug.; Rigaud, 12 Aug. SOUTH CAROLINA: Jasper Co., 14 June. SOUTH DAKOTA: Auroro Co., 23 Aug.; Fall River Co., 11 Sept.; Marshal Co., 7 Sept. TENNESSEE: Hamilton Co., 6 May. TEXAS: Brazos Co., 18 May-27 Sept.; Cameron Co., 30 July; Dallas Co., 27 Apr.-3 Nov.; Ellis Co., 21 Sept.; Harris Co., 3 Aug.; Navarro Co., 7 June; Tarrant Co., 2 May. VERMONT: Windham Co., Spring. VIRGINIA: Alexandria, 2 June-July; Arlington Co., 30 May-14 July; Fairfax Co., 6 June-15 July; Montgomery Co., 7 May-30 June; Nottoway Co., 17 May; Prince George Co., 27 July-11 Aug.; Princess Anne Co., 20 July. WEST VIRGINIA: Greenbrier Co., July; Wood Co., 11 June. WISCONSIN: Columbia Co., 31 Aug.; Milwaukee Co., 23 June-21 Aug.; Washington Co., 16 Aug.; Waupaca Co., 7 Aug.

Exema neglecta Blatchley

Exema neglecta Blatchley, 1920:69; 1924:50 (biology note); Leng and Mutchler, 1927:44 (listed); Blatchley, 1930:52 (lectotype designation); Pierce, 1940:19 (keyed); Brown, 1943:124 (note).

Diagnosis: This species is the most highly punctate of those with simple claws. There are rugose lines on the posterolateral slopes of the pronotum similar to the other species in this group, but the punctures are larger and more distinct. The males are easy to recognize by the large amount of yellow on the face and pronotum. This yellow is greatly reduced in the females. The flange on the tip of the aedeagus is sharp and distinct. The median dorsal plate is narrow. This species is found in the extreme southeastern part of the United States (Fig. 61) on *Baccharis* and other composites.

Description: Male: 2.7 mm long; 1.8 mm wide. Black except yellow on entire face, anterior half of pronotum, spot on anterior coxa, entire anterior femur, subapical and subbasal rings on middle tibia and middle femur; tarsomeres brownish yellow. Anterior pronotal yellow area spotted irregularly with black and black punctures. Entire cuticle minutely granulate, punctate. Head sparsely punctate; antenna clothed with many short and a few long hairs; segment 5 larger than 3 or 4, 6-11 subequal; labrum smooth and faintly emarginate with a few ventrally projecting hairs. Pronotal gibbosity with rounded tubercles and carinae; marginal present, lateral divided and carinate with summit-2; posterior punctures oblong, anterior punctures round. Scutellum convex, with rounded lateral wings. Elytra coarsely punctate, punctures large and deep, each with a short curved hair; smaller punctures on tubercles; umbone large and prominent; large tubercles: anterior, sutural-1, 1a, 2, 2a, 2b, 3, 3a, marginal, and marginal-b; small tubercles: scutellar, umbonal-a, umbonal-b, sutural-1b, 3b, marginal-a, and apical. Legs shallowly punctate; tarsal claws simple; apical spine on front and middle tibiae. Proternum coarsely punctate; prosternal process narrow and long, curved dorsally. Metasternal punctures large and deep, especially laterally. First abdominal sternum with a longitudinal carina between coxae, carina dividing near midlength into a faint Y-shape terminating in 2 ventrally projecting spines on posterior margin of segment; 2nd segment with similar but smaller spines; sides of 1st sternum irregularly carinate with large, round punctures, shallow medially to deep on lateral areas; midventral area of 5th segment flat with short recurved hairs, lateral punctures large and round. Pygidium distinctly tricarinate, lateral carinae curved and rounded. Aedeagus similar to *canadensis* except with a wider tip.

Female: 2.8 mm long; 1.8 mm wide. Similar to male except yellow usually absent on pronotum and reduced on face, yellow frons of emargination of eye connected to yellow spot near eye, two spots near vertex, and a central spot between eyes; legs with less yellow than male. Punctation, sculpturing, and vestiture similar to that of male except front and middle tibial spines absent, spines on 1st and 2nd sterna absent, and fewer long, straight hairs on 5th sternum.

Types: Male lectotype, Dunedin, Pinellas Co., Florida, 26 Jan. 1913, W. S. Blatchley (PU). 1 ♀ lectoparatype on the same pin as the lectotype.

Other specimens labeled lectoparatype examined from the Blatchley collection (PU): FLORIDA: 1 ♂, Sanford (Seminole Co.), 4 Apr. 1913; 1 ♂, Ormond (Volusia Co.), 22 Mar. 1913; 1 ♂, Dunedin (Pinellas Co.), 22 Mar. 1913; 1 ♀, 13 Jan. 1917; 1 ♂, Ft. Myers (Lee Co.), 31 May 1913; 1 ♀, Dunedin (Pinellas Co.), 5 Apr. 1913; 1 ♀, Kissimee (Osceola Co.), 16 Feb.

1913. Other specimens labeled lectoparatypes but collected after the original description was published (PU): 1 ♂, Chokoloskee (Collier Co.), 17 Mar. 1921; 1 ♂, Casambas (Collier Co.), 8 Mar. 1921; 1 ♂, Royal Palm Park (Dade Co.), 21 Mar. 1924; 1 ♀, (=*canadensis*), Labelle (Hendry Co.), 26 Feb. 1918. All were collected by W. S. Blatchley. I was able to examine all the types listed above.

Discussion: The yellow areas on the pronotum have a striking, blistered appearance in some specimens from the South. The central Floridian forms have a much smoother pronotum, especially in the yellow areas of males, than do those from any other area. Further north this yellow in the males covers less of the pronotum. More elliptical punctures are found on the pronotum of northern forms, but deep round punctures still persist to distinguish *neglecta* from *canadensis, byersi,* and *elliptica.* The color of the legs is highly variable, from nearly black to completely yellow. The femora and tibiae usually have subbasal and subapical yellow rings so that when the legs are retracted four longitudinal yellow stripes are produced on the venter. There is usually a yellow spot on the procoxa.

The entire face is yellow except for a brownish area around the bases of the antennae and a black spot on the vertex. There may also be a few black or brownish punctures on the front near the vertex.

The male sternal spines are very small and may even be absent on the second and third sterna. The hairs on the foveal area of the male are outwardly recurved and more scattered than in *canadensis.* In the female the hairs around the fovea are straight and more numerous than in *canadensis.*

The species in this group, i.e., *canadensis, mormona, neglecta, byersi,* and *elliptica,* are quite similar, especially in the genitalia, and show very close relationships. For this reason I have omitted separate drawings for *neglecta* and *byersi.* Including them would add little of taxonomic value. The tip of the aedeagus in *neglecta* is wider than that figured for *canadensis* and lacks the rugose lines on the bend. The tegmen, ejaculatory guide, and female genitalia are very similar in the two species. The fifth antennal segment in *neglecta* is smaller than the sixth and similar to the fourth, while this same segment is noticeably larger in *canadensis* but not as large as the sixth segment.

The yellow on the pronotum of males usually makes them easy to distinguish from females. A number of females have a few yellow spots on the pronotum, and one from Carolina Beach, North Carolina, looks like a male in coloration. The most reliable characters to distinguish the sexes are the spines on the tibiae and first abdominal sternum.

In the original description, Blatchley stated that *neglecta* was "common throughout Florida on huckleberry and other low shrubs throughout the winter months." It is not restricted to this plant as can be seen from records. Brown collected and reared a good series on *Baccharis,* suggesting that this may be the preferred host. Several other collectors have taken this species on *Baccharis.*

Plant records: Baccharis halimifolia, Chondrophora virgata, Eupatorium, Arundinaria (cranebrake), *Solidago* sp., and *Strophostyles helvola.*

Specimens examined: (504 males and 376 females). ALABAMA: Baldwin Co., 10 July; FLORIDA: Alachua Co., 8 May-14 Nov.; Baker Co., 3 May-5 Aug.; Bay Co., 7 July; Brevard Co., 11 July-8 Nov.; Charlotte Co., 9 Apr.-13 Nov.; Citrus Co., 23 May; Clay Co., 7 Aug.; Collier Co., 8 Mar.-6 June; Dade Co., 16 Jan.-22 July; DeSoto Co., 9 Apr.; Duval Co., 9 May-16 Nov.; Escambia Co., 13 Mar.; Hardee Co., 12 Apr.-15 July; Hendry Co., 26 Feb.; Hernando Co., 13 Mar.; Highlands Co., 10 Apr.-10 May; Hillsborough Co., 13 Jan.-23 June; Indian River Co., 27 July; Lake Co., 1 Mar.-1 Sept.; Lee Co., 1 Apr.-13 Nov.; Levy Co., 30 June-18 Oct.; Manatee Co., 23 Mar.-3 Sept.; Monroe Co., 28 Mar.; Nassau Co., 31 Aug.; Orange Co., 12 Jan.-19 Nov.; Osceola Co., 4 July; Pasco Co., 15 Apr.-7 July; Pinellas Co., Jan.-Dec.; Polk Co., 26 Mar.-10 Nov.; Putnam Co., 20-22 Apr., 24 Dec.; St. Johns Co., no date; St. Lucie Co., 27 July; Sarasota Co., 28 Mar.-10 Dec.; Seminole Co., 1 Mar.-30 Dec.; Taylor Co., 20 Apr.; Volusia Co., 14-20 Apr.; Wakulla Co., 6 July; "Gunntown," no date. GEORGIA: Charlton Co., 20 June-7 July; Chatham Co., 18 June-22 July; Glynn Co., 12-14 July; Jefferson Co., 3 May; Richmond Co., 5 Oct.; Tift Co., 1-10 Aug. NORTH CAROLINA: Beaufort Co., 16 June; Dare Co., 21 Aug.; Johnston Co., July; Moore Co., 12 May; New Hanover Co., 8-26 July; Onslow Co., 28 July; Scotland Co., 17 Aug.; Wake Co., 7 June. SOUTH CAROLINA: Beaufort Co., 14 Apr.; Charleston Co., 14 June-27 July; Greenwood Co., 1-25 June; Jasper Co., 28 Oct.; Lee Co., 4 May. TEXAS: Runnels Co., 6 June.

Exema byersi n. sp.

Diagnosis: Exema byersi can easily be distinguished by the yellow coloring on the face, which always includes the frons in the emargination of the eye, and many oval to elliptical punctures on the pronotum, especially on the anterior half. The male aedeagus differs from that of *canadensis* in having a narrower flange and being smooth at the bend. This species is found from New York to Kansas and south to Texas (Fig. 61) on *Gutierrezia dracunculoides* and several other genera of plants. It is more common in Kansas and absent in the southeastern states.

Description: Male: 2.6 mm long; 1.7 mm wide. Black with yellow or yellowish brown markings; antenna and labrum yellowish brown, mouthparts darker; head entirely yellow, except black genae, brownish clypeus and antennal sockets, and black punctures on vertex and front; frontal slope of pronotum yellow; wide yellow band extends from summit to antecostal suture laterally along suture as a narrow bar to well below the middle of pronotum then turns posterodorsad for a short distance; front femur and all tibiae with subbasal and subapical yellow rings, middle femur with a wide subbasal ring, hind femur black, tarsomeres yellowish brown, claws black. Body surface finely granulate throughout; head sparsely punctate; labrum smooth, apex emarginate with subapical row of transverse hairs. Antennal segment 5 slightly larger than 3 or 4, but smaller than 6, covered with a few long and many short hairs. Pronotum with summit-1 tubercle developed into rounded carina running irregularly to small anterior pronotal tubercle; lateral tubercle divided into a large dorsal and a small ventral, rounded tubercle; marginal obscure and rounded; posterolateral slope highly rugose; anterolateral pronotum covered with long elliptical punctures; punctures on yellow area oval or round. Scutellum with a central carina on anterior half; posterior scutellar wings reflexed, almost acute. Umbone large and prominent; elytral punctures larger than those on pronotum; large tubercles: anterior, sutural-1, 1a, 2, 3, 3a, and marginal-b; small tubercles: scutellar, sutural-1b, 2a, 2b, 3b, umbonal-a, b, and marginal; marginal-a and apical very small; discal depression shallow; tarsal claws simple; legs coarsely but shallowly punctate. Prosternum coarsely punctate, slightly concave, with transverse anterior groove; prosternal process narrow. Metasternum coarsely punctate, punctures becoming larger laterally. First abdominal sternum with median, inverted Y-shaped carina dividing coxal cavities, extending to 2 small spines on posterior edge of segment, similar pair of very short spines on 2nd sternum; 1st sternum coarsely punctate, laterally tuberculate; punctures of 5th sternum slightly elongate, central spot slightly concave, smooth, covered with short recurved hairs. Pygidium convex, slightly tricarinate, central carina most apparent ventrally; surface coarsely punctate. Aedeagus flanged at tip; basal stem of tegmen as in *canadensis* (Fig. 36).

Female: Facial yellow reduced to 2 broken bars next to eyes, a large central spot, and a small spot on the frons in emargination of each eye; no yellow on pronotum; legs darker than those of male. Front and middle tibiae without apical spine; no spines on 1st and 2nd abdominal sterna, 5th sternum with central, slightly depressed area surrounded by a few long and short hairs; pygidium distinctly tricarinate. Genitalia similar to those of *canadensis.*

Types: Male holotype, 8 miles north of Lawrence, Jefferson Co., Kansas, 27 May 1965, taken on *Gutierrezia dracunculoides,* J. B. Karren (UK). Same data on allotype and 2 ♂ paratypes (UK, JBK). An additional 49 ♂ and 59 ♀ paratypes were collected at the same locality on 7 June, 15 June, and 8 July 1965 by the author (UK, JBK, BYU, RU, ANSP). A few of these specimens were reared from eggs or larvae collected in the field.

Other paratypes, all from Kansas, as follow: 2 ♂ and 2 ♀, 8 miles north of Lawrence, Jefferson Co., 14 June 1964, R. C. Funk (JBK); 2 ♀, Mission, (Johnson Co.), 22 Aug. 1963, H. L. Willis (JBK). 1 ♂, Miami Co., 1915, R. H. Beamer; 1 ♂, Crawford Co., 993 ft., 1915, R. H. Beamer; 1 ♂, Douglas Co., 1926, R. H. Beamer; 2 ♀, Labette Co., 899 ft., R. H. Beamer; 4 ♂ and 2 ♀, Garnett (Anderson Co.), 8 Oct. 1926, R. H. Beamer; 2 ♂ and 2 ♀, Hutchinson (Reno Co.), 27 July 1950, taken on *Echinacea angustifolia,* J. G. Rozen; 2 ♂ and 1 ♀, Anderson Co., R. H. Beamer; 1 ♀, Topeka (Shawnee Co.), Aug., Popenoe; 1 ♀, Haskell, Douglas Co., July 1909 (all UK); 1 ♂, Medora (Reno Co.), 17 Apr. 1932, C. W. Sabrosky (MSU); 1 ♀, Baldwin (Douglas Co.), May, J. C. Bridwell (OSC); 2 ♂ and 1 ♀, Onaga (Pottawatomie Co.), F. Crevecoeur (CDA); 1 ♂ and 1 ♀, Onaga (Pottawatomie Co.), 29 July 1909, F. Crevecoeur (CAS); 3 ♂ and 1 ♀, Onaga (Pottawatomie Co.), 1 Sept. 1929, 20 June 1929, and 5 May 1923, F. Crevecoeur (KSU); 1 ♀, Ashton collection (PU); 4 ♂ and 3 ♀, Topeka (Shawnee Co.), 1 labeled 3 Sept. and 2 labeled Aug., *Fraxinus viridis,* 2 labeled Popenoe (USNM); 2 ♂ and 1 ♀, Riley Co., Popenoe (USNM). The type material represents all of the available specimens from Kansas.

Discussion: This species very closely resembles *neglecta* and *elliptica* except for the elliptical punctures on the pronotum of the former and the shape of the pronotum of the latter. Other differences can be seen, but the above are the most apparent. The face of the male is entirely yellow, but there may be a few scattered black or brown punctures, especially on the vertex. The yellow on the pronotum is more reduced than in *neglecta,* but more extensive than in most *elliptica.* The yellow on the face of the female is reduced approximately as shown in Fig. 21, except that the frons is entirely yellow in the emargination of the eye, and the two ventral spots are usually missing. This pattern varies from the two vertical bars, more common in *neglecta,* to no yellow except for that on the frons in the emargination of each eye.

This species looks very much like *canadensis* in punctation, sculpturing, and size. The shape of the pronotum and the pattern of the tubercles on the elytra are very similar in the two species. Except for the striking difference in coloration, many males of *byersi* might be mistaken for *canadensis.* At first, I felt that this species was a geographical variation of *neglecta,* but as more specimens were examined and additional collections were made in the field, it became apparent that the species was different. At the type locality, specimens of *byersi* were collected along side *canadensis,* the former were almost always found on *Gutierrezia* and the latter on *Solidago.*

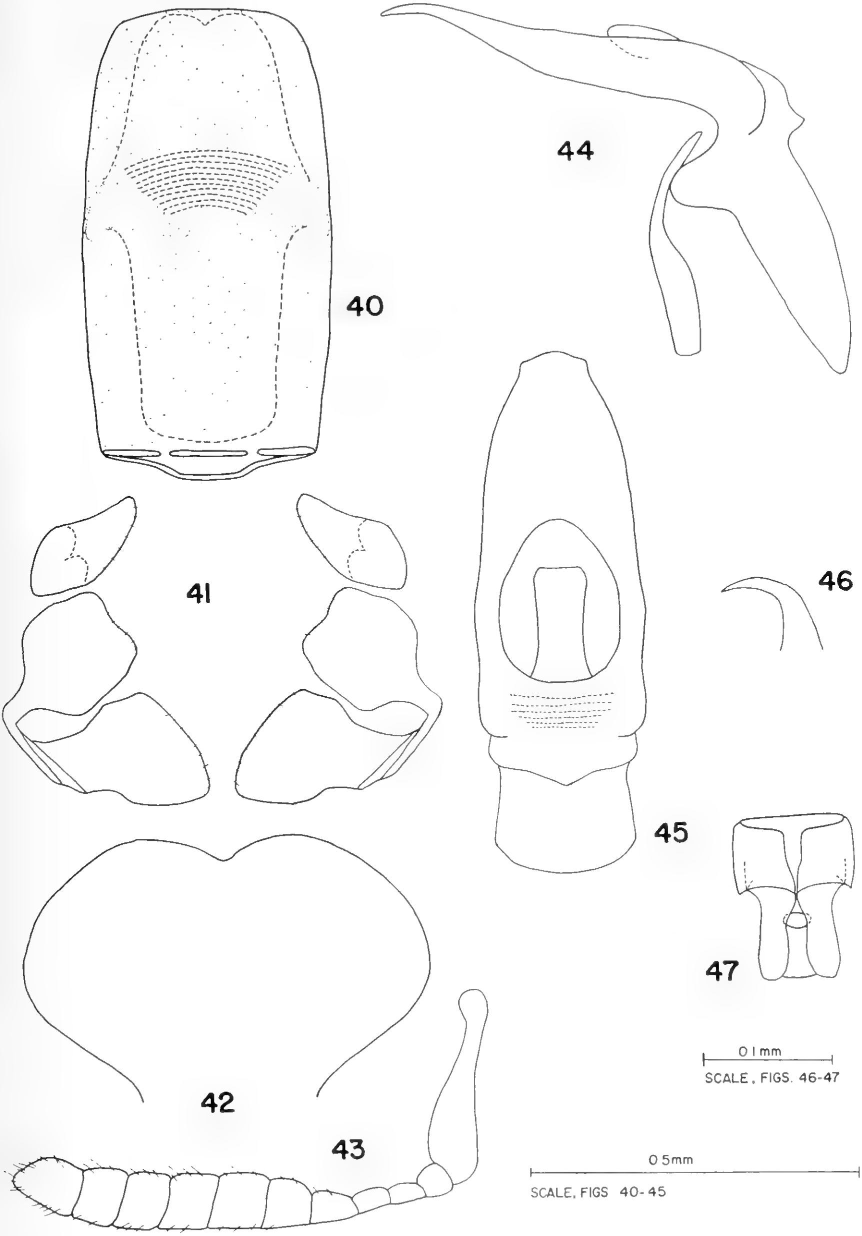
Plant records: Echinacea angustifolia, Fraxinus viridis, Apias tuberosa, and *Gutierrezia dracunculoides.*

Specimens examined: (128 males and 143 females). ALABAMA: Mobile Co., Mar.-15 June. ARIZONA: Cochise Co., 7 Aug. ARKANSAS: State record, 6 Oct. INDIANA: Porter Co., 22 July; Pulaski Co., 16 July. KANSAS: Anderson Co., 8 Oct.; Crawford Co., no date; Douglas Co., May-July; Harvey Co., 22 Aug.; Labette Co., no date; Jefferson Co., 27 May-8 July; Johnson Co., 22 Aug.; Miami Co., no date: Pottawatomie Co., 16 May-29 July; Reno Co., 17 Apr.-27 July; Riley Co., Sept.; Shawnee Co., Aug.-2 Sept. LOUISIANA: (Parish=county of other states) Rapides Par., 14 Oct. MARYLAND: Baltimore Co., 6 June-26 July; Montgomery Co., May; Prince Georges Co., 25 May-29 June. MICHIGAN: Allegan Co., 22 July. MISSISSIPPI: George Co., 13 June; Jackson Co., 24 June-23 Aug. MISSOURI: State record, no date. NEW JERSEY: Cape May Co., June; Camden Co., 27 Aug.; Ocean Co., 31 May-11 Oct. NEW YORK: Nassau Co., 30 June; Suffolk Co., 31 May-25 Aug. OKLAHOMA: Muskogee Co., 6 June-19 Sept. PENNSYLVANIA: Allegheny Co., no date; Lebanon Co., 28 Aug. TEXAS: Brazos Co., 1 May; Colorado Co., 13-14 Apr.; Comal Co., no date; Harris Co., 3 Aug.; San Patricio Co., 15 June. VIRGINIA: Alexandria, 2 June; Campbell Co., 2 June; Fairfax Co., 9 Apr.-6 June.

Exema elliptica n. sp.

Diagnosis: This species is easily recognized by the high carinae. The male aedeagus is distinguished by the slightly flanged, rounded tip (Fig. 45) with very little ventral curve (Fig. 44). The tegmen is expanded on the basal half and truncate at the base. The female structures are also similar except for the highly concave outer edge of the ninth pleurite and tergite (Fig. 41). The following description is based on 20 males and 20 females from nine localities in the southern and eastern states (Fig. 62).

Description: Male: 2.8 mm long; 1.8 mm wide. Shiny black to slightly metallic, except for yellow or yellowish brown markings. Antennae yellow, mouthparts light brown, labrum shiny; face yellow except for light brown antennal bases, genae and basal clypeus; black spot or patch of black punctures on vertex. Frontal slope of pronotum with yellow band one-half width



FIGS. 40-47. *Exema elliptica* n. sp.; 40—female tenth and eleventh abdominal segments, 41—female ninth abdominal segment, 42—female eighth abdominal segment, 43—antenna, 44—lateral aspect of male aedeagus, 45—dorsal aspect of male aedeagus, 46—claw, 47—male ejaculatory guide.

of head including eyes extending from antecostal suture dorsally to anterior carinae; slender band extending ventrally half way along suture; yellow spot opposite lower edge of eye. No yellow on elytra. All femora and tibiae with subbasal and subapical yellow rings, very wide on front and middle femora, leaving only a central black spot; tarsomeres yellowish brown. Head minutely granulate, sparsely punctate; punctures small and shallow, obscure in emargination of eye; hairs in punctures inconspicuous or absent; antennae clothed with many short and a few long hairs, especially toward apex; segments 3 and 4 subequal, segments 5 slightly larger, smaller than 6, 6 smaller than 7, 7-10 subequal, 11 subtriangular; labrum smooth with ventrally projecting hairs. Pronotal gibbosity high, appears flat from lateral aspect, with large, rounded tubercles and carinae, cephalic and anterior missing, anterior carina large, summit-2 represented by outwardly curved carina, lateral tubercle divided; entire pronotum with large elliptical to oval punctures, deeply striopunctate on the flanks giving a highly rugose effect; areas between tubercles minutely granulate. Scutellum finely punctate, feebly carinate, scutellar wings small and blunt. Elytra with large, deep, setigerous punctures, smaller punctures on tubercles; areas between tubercles granulate; umbone large and prominent; large tubercles: anterior, sutural-1, 1a, 2, 3 expanded longitudinally, 3a, and marginal-b; small tubercles: scutellar (faint), umbonal-a, umbonal-b, sutural-2a, 2b, 3b, marginal-a, and apical. Legs with large shallow punctures; Tarsal claws simple; apical spine on front and middle tibiae. Prosternum coarsely punctate, granulate, concave, sides rounded; prosternal process long and narrow. Metasternal punctures large and shallow. First abdominal sternum with a longitudinal carina between coxae, dividing near midlength into a Y-shape; 2 ventrally projecting spines on posterior margin; 2nd sternum with similar but smaller spines; punctures of 1st sternum large and round medially, smaller and deeper on roughly sculptured lateral margin; mid-ventral area of 5th sternum flat to slightly concave, covered with outwardly recurved hairs; lateral punctures oblong; all areas granulate between punctures. Pygidium convex, tricarinate, lateral carinae converging ventrally; entire surface granulate with deep punctures. Aedeagus feebly flanged and rounded at apex, slightly curved ventrally; tegmen expanded and truncate at base.

Female: 2.9-3.1 mm long; 1.9-2.1 mm wide. Similar to that of male except more variable, yellow of face and pronotum reduced, sometimes lacking on pronotum; facial yellow represented by spots on frons in emargination of eye plus those shown in Fig. 30, separate or irregularly connected. Punctation and sculpturing similar to those of male except front and middle tibial spines absent; spines on 1st and 2nd abdominal sterna absent and fewer hairs on 5th sternum, hairs straight, a few long hairs situated on periphery of a slightly concave fovea covered with a very few short hairs. Pygidium distinctly tricarinate, with lateral carinae rounded, much larger than median carina.

Types: Male holotype, Anahuac (Chambers Co.), Texas, 10 Oct. 1918, on *Iva fructescens,* H. S. Barber (USNM). Same date on allotype, 3 ♂ and 3 ♀ paratypes (one female collected 30 Oct.). (USNM, UK, JBK).

Other paratypes as follows: FLORIDA: 2 ♀, Levy Co., no date (ANSP, MCZ). GEORGIA: 1 ♂, Tifton (Tift Co.), no date, Liebeck collection (MCZ). LOUISIANA: 2 ♂ and 1 ♀, Alexandria (Rapides Par.), 14 Oct. 1959, R. E. Woodruff (FDA); 6 ♂ and 5 ♀, Lutcher (St. James Par.), 7 June 1944, on *Baccharis* sp. (USNM, JBK). MARYLAND: 1 ♂, Plummer's Island (Montgomery Co.), 22 Aug. 1943, R. H. Beamer (UK). SOUTH CAROLINA: 1 ♀, Adams Run (Charleston Co.), 25 June 1948, Cartwright (CDA). TEXAS: 1 ♂, Dickinson (Galveston Co.), 20 Apr. 1933 (UCR); 4 ♂ and 5 ♀, Houston (Harris Co.), 25 May 1949, reared from *Baccharis halimifolia,* J. L. Ward (USNM, NYSM, JBK). VIRGINIA: 1 ♂ and 1 ♀, Cape Henry (Princess Anne Co.), 28 May 1927, H. S. Barber (USNM).

Discussion: Only 20 males and 20 females were available for study, and all were made part of the type series. The specimens from the United States National Museum were already labeled as a new species by H. S. Barber, but he had not yet proposed a name for it. This group had the largest series with host data, so I chose the type from among them.

The coloration of the males seems to be constant except for a slight reduction of yellow on the pronotum in some. The females, on the other hand, are quite variable, some having no yellow on the pronotum and others with as much as the males. I suppose that with more collecting the extremes will prove to be rare and the typical forms more common.

This species is very close to *neglecta, elliptica,* and *byersi,* differing from these species in its strikingly elevated pronotum and its distribution. It is probably sympatric with *byersi* in Maryland and New Jersey in the North, and Louisiana, Mississippi and Alabama in the South. It is sympatric with *neglecta* in the southern states and has the same host plant in some cases. This is a species that may have developed in Florida and is now spreading northward. There are Florida forms of *canadensis* and *dispar* that vary from the typical forms of their respective species in much the same way that *elliptica* differs from *neglecta* and *byersi,* but this divergence has not gone far enough for them to be called distinct species. They may be forms in which secondary intergradation has taken place; at least there are too many intermediate forms for them to be called species.

Plant records: Iva fructescens and *Baccharis halimifolia.*

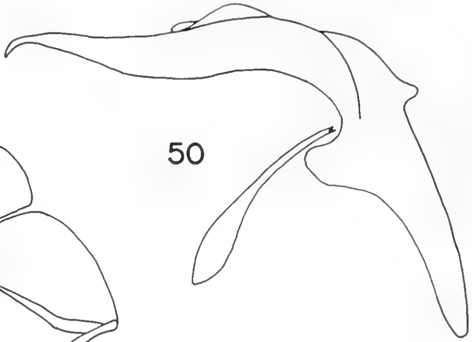
Exema deserti Pierce

Exema deserti Pierce, 1940:20-21; Blackwelder and Blackwelder, 1948:42 (listed).
Exema deserti boregensis Pierce, 1940:21; Blackwelder and Blackwelder, 1948:42 (listed); (NEW SYNONOMY).
Exema globensis Pierce, 1940:21-22; Blackwelder and Blackwelder, 1948:42 (listed); (NEW SYNONOMY).
Exema chiricahuana Pierce, 1940:22-24; Blackwelder and Blackwelder, 1948:42 (listed); (NEW SYNONOMY).
Exema parvisaxi Pierce, 1940:24; Blackwelder and Blackwelder, 1948:42 (listed); (NEW SYNONOMY).

Diagnosis: The pronotum is punctate without any trace of striae or rugose lines. The face of the male is always yellow except as noted in the description. Most specimens are more yellow than any other species in the genus; some are almost completely yellow. Most specimens have small tubercles and carinae. This species is found in the desert regions of the Southwest (Fig. 63) on a variety of plants.

Description: Male: 2.6 mm long; 1.6 mm wide. Yellow marked with black; underside, elytral punctures, and umbone black; a few punctures on head and many on posterior half of pronotum black; antennal socket, condyle of scape, and a narrow clypeal band black; scape of antenna yellow, flagellum becoming brown at apex; mouthparts brown, labrum yellowish brown; face mostly yellow including vertex. Prothorax yellow with a few black punctures and black spots on the posterior half; prosternum with a small central yellow spot. Front femur mostly yellow, hind femur black with subapical yellow ring; all tibiae black with wide subbasal and subapical yellow rings; tarsomeres dark brown. Pygidium black with two lateral, yellow spots associated with yellow spots on the 5th sternum. Entire cuticle minutely granulate, irregularly punctate. Head with large, deep punctures, deepest in middle of vertex and frons, hairs in punctures inconspicuous; antenna clothed with many short and a few long hairs, especially toward apex; segment 5 slightly larger than 3 or 4; labrum smooth slightly emarginate. Pronotum gibbose with low, rounded tubercles, marginal broadly rounded; lateral, summit-1, and 2 feebly carinate; anterior carinae present; entire pronotum covered with deep to shallow, rounded punctures. Scutellar wings reflexed and almost acute, distinctly carinate. Elytra coarsely punctate, shallower punctures on rounded tubercles, punctures setigerous; umbone large and prominent; large tubercles: anterior, sutural-1a, 2, 2a, 3, 3a, marginal, and marginal-b; small tubercles: scutellar, sutural-1, 2b, 3b, and umbonal-b; other tubercles lacking. Legs feebly and shallowly punctate, tarsal claw feebly toothed; apical spine on front and middle tibiae. Prosternum concave and deeply punctate; prosternal punctures large and deep, smaller laterally. First abdominal sternum with a longitudinal carina between coxal cavities, carina dividing near midlength into a faint Y-shape and terminating in 2 large ventrally projecting spines on posterior margin of segment; spine feebly developed on 2nd and 3rd segments; large, round punctures of 1st sternum setigerous, shallow medially to deep on lateral margins; lateral punctures of 5th sternum large, oblong, nearly rugose; midventral area flat, covered with long recurved hairs. Pygidium centrally convex, medial carina distinct, depressed areas near lateral edge. Aedeagus truncate at tip; tegmen expanded at base.

Female: 2.8 mm long; 1.8 mm wide. Similar to male except darker cuticle in most specimens. Punctation, sculpturing, and vestiture similar to those of male except front and middle tibial spines absent, spines on sterna absent, and



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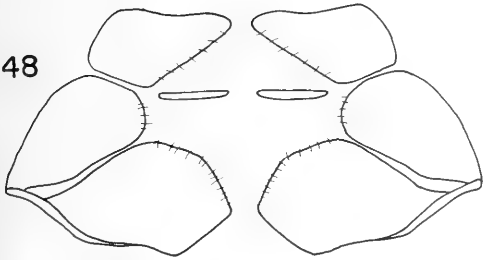

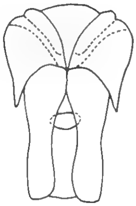

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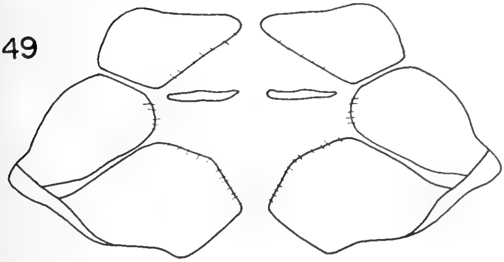

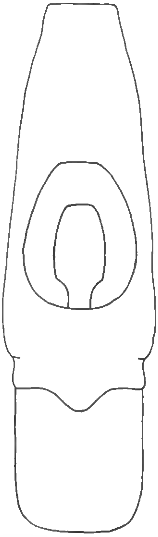

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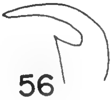

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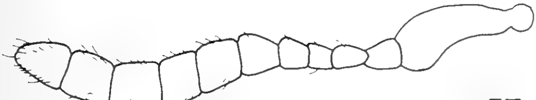

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FIG. 48. *Exema deserti;* female ninth abdominal segment, yellow form.

FIG. 49. *Exema deserti;* female ninth abdominal segment, black form.

FIG. 50. *Exema deserti;* male aedeagus, lateral aspect.

FIG. 51. *Exema deserti;* male ejaculatory guide.

FIG. 52. *Exema deserti;* male aedeagus, dorsal aspect.

FIGS. 53-55. *Exema deserti;* variation in tarsal claws.

FIG. 56. *Exema conspersa;* tarsal claw.

FIG. 57. *Exema deserti;* antenna.

midventral area of 5th sternum concave, surrounded with a few long hairs. Pygidium feebly tricarinate with lateral carinae large and rounded.

Type material: The species was described from a single male specimen from Victorville, San Bernardino Co., California, on the Mojave Desert, collected by G. P. Mackenzie, 20 May 1939 (LACM). All types of synonyms were examined along with most of the paratypes of Pierce's species. The determination labels on the types and paratypes of *parvisaxi, chiricahuana, globensis,* and *deserti* (LACM) indicates that they are subspecies of *deserti,* yet Pierce (1940) treated all but *boregensis* as species.

Discussion: This species shows wide variation in color and sculpturing. Normally, specimens have small or indistinct tubercles, but the size can vary as mentioned below. There is some variability in the shape of the tooth of the tarsal claws, the diagnostic character used in the key; however, the tooth is always small. The prosternum is variable in shape and sculpturing and may vary in color from completely yellow to black, the intermediate individuals having a central yellow spot of variable size. The same is true for the pygidium and the scutellum. The most diagnostic character is the tooth of the tarsal claws (Fig. 54).

The color of this species is variegated yellow and black with variation ranging from mostly yellow to mostly black. Most populations are made up of specimens with more yellow than black. Several California and three Utah specimens, which are almost entirely yellow, have only a faint tooth on the tarsal claws. It is so small that it appears to be missing, giving the claws a shape similar to that seen in specimens of *Exema* with a striate or rugose pronotum. There are also specimens of *deserti* with typical claws. These specimens are as yellow as those mentioned above from Utah. All of these yellow forms lack the dark central punctures near the vertex that are so common in the typical forms. The bases of the antennae and the ventral part of the clypeus and the genae are colored brownish yellow rather than black, and the sculpturing is smoother than in the typical form. Many intermediate characters are present in the larger series and in individual specimens from scattered populations.

The three largest samples examined were one from Sabino Canyon, Arizona, and two from west of Superior, Arizona. The two Superior samples were collected at about the same time of the year, one in 1960 on *Franseria ambrosioides,* a plant that grows along dry stream beds and the other on *Bebbia juncea.* In 1962, I tried collecting from *Franseria,* but the plants were dried up and no *Exema* were present; however, I found the beetles quite abundant on the roadside weed, *Bebbia juncea.* I cannot detect any morphological difference between specimens of these two populations, but rather suspect that the beetles moved to the roadside weeds because of the drying up of the other host plant. Both populations show a large degree of variation, especially in characters used by Pierce to distinguish his species. It is from these two populations and the one from Sabino Canyon that I gain evidence for synonymizing Pierce's *parvisaxi, chiricahuana, deserti, boregensis,* and *globensis* with *deserti*. For example, the yellow coloring on the pygidium varies from black to almost completely yellow. The pygidium varies from smooth and punctate to highly tricarinate. This condition is common in the darker forms, those that Pierce called *chiricahuana* and *parvisaxi.*

This dark form has most of its yellow coloring on the face and anterior half of the pronotum and only a few spots on the elytra and other parts of the insect. For a time I felt that the dark form was a distinct species, but further study revealed too many intermediate forms, too many mixed samples, and a very irregular distribution. Many samples had approximately equal numbers of both dark and yellow forms. Three collections made near Sedona and Globe, Arizona, and one from the Jemez Mountains of New Mexico, contained dark, yellow and intermediate forms. Collections from a great many more localities contained only the intermediates. Such variation occurs irregularly over the entire range of the species, although dark specimens are more abundant in collections from eastern Arizona and New Mexico.

There seems to be a slight difference in the female genital structures of dark forms found on *Gutierrezia* and the yellow ones on *Franseria* and *Bebbia;* therefore, I have figured both types (Figs. 48-49). Other samples contain many intermediate individuals, and it would be impossible to separate them into two distinct groups by this character. The dark form is usually the more roughly sculptured.

Most specimens from a population at Mesilla Dam, New Mexico, have a small acute tooth on the tarsal claw (Fig. 55) as opposed to a rounded tooth (Fig. 53-54). The size of the tooth is within the range of variation of *deserti,* and other characters agree more closely with this species than any other.

Some specimens of *dispar, conspersa* and *deserti* from the southwest are hard to distinguish because of the similarity in color and sculpturing. The variation of these two characters in the three species is so great that a few individuals in each species appear to belong to one of the other species. It is only with the aid of the characters used in the key or several characters used in combination that one can be certain of the identification.

I have illustrated the male and female genitalia of *deserti* but not *conspersa* and *dispar;* all are similar with no apparent taxonomic differences.

It should also be pointed out that in Pierce's paper the description of *parvisaxi* is based on "four males" but that he gives a description of a female. The type proves to be a female, but paratypes 2 and 3 are males.

Plant records: Bebbia juncea, Franseria ambrosioides, Franseria deltoides, Larrea tridentata glutinosa, Gutierrezia sarothrae, Ambrosia psilostachya, *Pluchea sericea, Gutierrezia lucida, Baccharis* sp., *Hymenoclea salsola,* and at black light.

Specimens examined: (740 males and 660 females). ARIZONA: Cochise Co., 18 May-29 Sept.; Coconino Co., 5 Apr.-13 Aug.; Gila Co., 23 Apr.-10 Aug.; Graham Co., 8 July-16 Aug.; Mohave Co., 4 July-26 Aug.; Maricopa Co., 5 June-31 Aug.; Navajo Co., 9 June-24 July; Pima Co., 20 Mar.-25 Sept.; Pinal Co., 23 Feb.-10 Aug.; Santa Cruz Co., 22 July-3 Oct.; Yavapai Co., 14 June-19 Aug.; Yuma Co., 8-21 July. BAJA CALIFORNIA: Catavina, 29 July-2 Aug.; 10 mi. S. Catavina, 29 July; Cedros Island, 4 June; San Quentin, 2 Aug.; San Vincente, 8 July; Socorro, 1 Aug. BAJA CALIFORNIA SUR: 20 mi. N. Comondu, 2 Aug.; Miraflores, 8 July; 45 mi. N. San Ignacio, 27 July; 24 mi. W. Santa Rosalia, 2 Aug.; Todos Santos, 15 July. CALIFORNIA: Imperial Co., 12-16 June; Inyo Co., 3 Apr.-9 Sept.; Kern Co., 14 July-22 Aug.; Los Angeles Co., 9 June-10 Sept.; Monterey Co., 22 July; Riverside Co., Apr.-22 July; San Bernardino Co., 17 Mar.-12 Nov.; San Diego Co., 6 Apr.-23 Sept.; Siskiyou Co., 23 Mar.; "Walker Pass," 9 June. COLORADO: Montezuma Co., 27 July. JALISCO: S.E. slope, Mount Colima, 2 July. NEVADA: Elko Co., no date. NEW MEXICO: Dona Ana Co., 25 Apr.; Lincoln Co., 9 July; Otero Co., 9 May-11 June; Sandoval Co., 4 June-23 Aug.; Socorro Co., Aug. SONORA: 27 mi. N. Guaymas, 16 Mar.-18 June; Pitiquito, 4 July; 20 mi. S.E. Sonoita, 10 June. TEXAS: Brewster Co., 10 June-28 July; Jeff Davis Co., 9 May-4 July; Presidio Co., 20 Feb.-May. UTAH: Emery Co., no date; Grand Co., 25 June; Kane Co., 16 Aug.; Sevier Co., 26 Aug.; Washington Co., 25 Apr.-30Aug.; "Chad's Ranch," 26 July.

Exema conspersa (Mannerheim)

Chlamys conspersa Mannerheim; 1843:311; Lacordaire, 1848:843; LeConte, 1857:24 (distribution).

Chlamys rugulosa Motschulsky; 1845:109; Lacordaire, 1848:844; LeConte, 1857:24 (distribution).

Exema conspersa (Mannerheim); Crotch, 1873:30; Hubbard and Schwartz, 1878:660 (misidentification); Beutenmüller, 1890:175 (biology, probably misidentification); Linell, 1897:480; Clavareau, 1913:221; Achard, 1914:17 (listed); Leng, 1920:288 (listed); Fall, 1927:386 (distribution); Leonard, 1928:463 (distribution); Moore, 1937:93 (distribution and biology); Burks, 1940:336, 354 (parasitized by *Spilochalcis sanguiniventris*); Pierce, 1940:8; Brown, 1943:124 (note on synonymy); Peck, 1963:886, 955.

Exema conspersa (Mannerheim) probably *dispar;* Blatchley, 1920:69; Britton, 1920:273 (distribution); Blatchley, 1924:50 (distribution and hosts); Johnson, 1927:114 (distribution); Proctor, 1938:56 (biology note); 1946:187 (biology note).

Exema jenksi Pierce; 1940:13-18; Blackwelder and Blackwelder, 1948:42 (listed). NEW SYNONYMY).

Exema inyoensis Pierce; 1940:19-20; Blackwelder and Blackwelder, 1948:42 (listed). (NEW SYNONYMY).

Diagnosis: This species is variegated with equal amounts of black and yellow throughout the cuticle with no detectable pattern in most specimens. Specimens of *conspersa* are usually found west of the Rocky Mountains (Fig. 64) on species of *Artemisia* and closely related genera.

Type: The type is in the Museum Zoologicum Universitatis, Helsinki, Finland (MZU). The redescription below was made from this type. The following labels appear on the pin: ♂; Etholén (name of the ship's captain who gave Mannerheim a collection of beetles from California); Coll. Mannerheim; *Conspersa* Mannerh. *Dispar* Dejean; Var. A. Lacord. *Chl. rugulosa* Motsch.; Mus. Zool. Helsinki No. 7722. The specimen was collected by Tschernikh, probably around Bodega, Sonoma Co., California.

The types of *jenksi* and *inyoensis* were also examined (LACM). The first agrees with the type of *conspersa* and the second is an example of a dark form of *conspersa.*

Redescription of male: 2:65 mm long; 1.6 mm wide. Variegated yellow and black or dark brown; face yellow to brownish yellow with many black punctures, antennal bases, genae and ventral clypeus black; labrum yellow, with brown apex; frontal half of pronotum yellow, variegated with black and black punctures, yellow and black about equal over most of body; femur with subapical yellow ring, tibia with subbasal and subapical rings; tarsomeres brown; irregular yellow areas on metaepisternum, 1st and 5th abdominal sterna, and each side of pygidium. Head minutely granulate among large setigerous punctures; upper part of yellow area between antennal bases without punctures; antennae clothed with many short and a few long hairs; segments 3-5 subequal, 6 smaller than 7, 7-10 subequal, 11 subtriangular; labrum smooth, slightly emarginate at apex, with transverse row of about 6 ventrally projecting long hairs. Pronotal gibbosity with poorly defined tubercles, small anterior carina converging posteriorly, separated by 2 rows of punctures, summit-2 developed into a small anterolateral projecting carina; entire pronotum with conspicuously setigerous punctures; areas between punctures granulate. Scutellum finely granulate, lateral scutellar wings small. Elytral punctures conspicuously setigerous, punctures large and deep, areas between tubercles granulate; umbone broad; large tubercles: anterior, sutural-1, 2, 3, 2a, 3a, umbonal-b and marginal-b; all others very small or absent; discal depression well developed; legs feebly punctate, tarsal claws deeply toothed, large apical spines on front and middle tibiae. Anterior edge of prosternum bent ventrally, coarsely punctate, granulate; prosternal process long and narrow. Metasternal punctures large and shallow. First abdominal sternite with a longitudinal carina between coxae, carina dividing near midlength into a Y-shape and terminating in 2 long, ventrally projecting spines on posterior margin of segment; punctures of 1st and 5th sterna large, round, setigerous; midventral area of 5th sternum flat to slightly concave, covered with slightly recurved hairs. Pygidium convex, distinctly carinate, covered with setigerous punctures, surface granulate. Male aedeagus similar to that figured for *deserti*.

Female: Slightly larger than male; yellow on face variegated with black; yellow pattern on pronotum more irregular than in male. Punctation and sculpturing as in males except front and middle tibial spines absent, spines on abdominal sterna absent and fewer hairs on 5th sternum. Hairs surrounding foveal area long and straight. Pygidium tricarinate.

Discussion: The name *conspersa* has been used for most of the species in North America at one time or another. One reason for this is the tremendous variation within the species *conspersa, dispar* and *deserti*. Populations of *dispar* from the east coast and *conspersa* from the west coast are very different from each other, but as samples are taken closer together this difference is less obvious, even though a large area in the great plains region seems to lack both species. All three of the species are difficult to distinguish in areas of the South and Southwest where they are sympatric. Some specimens of all three may look superficially alike, but by the use of the characters cited in the key a proper identification can be made. In some specimens of *dispar* the body oils may, in time, cause the tarsomeres and the yellow pattern on the head and pronotum to look brown, thus causing them to resemble specimens of *conspersa*. The setigerous punctures on the pronotum are sometimes inconspicuous in the Utah specimens of *conspersa*, but are very obvious on the elytra.

As already stated, some forms of *deserti* are very dark and might be confused with either *conspersa* or *dispar*. Such specimens are found in Arizona and Mexico. They have more yellow on the anterior half of the pronotum and face and less on the elytra than do forms from further north. Intermediates are found throughout the range of this species and into Mexico in many localities. All Mexican localities have been placed on a separate distribution list, but included on the map. I have several specimens from Guatemala, Costa Rica and Nicaragua that look like *conspersa*, but more are needed to be certain of the identity. These localities appear in a third distribution list but are omitted from the map.

After looking at the following list of host plants one doubts that there is any host specificity in this species. The problem is complicated by the fact that the larvae may leave the host plant to pupate and be found on any number of nearby plants. The adults, too, seem to wander to plants near the preferred host. Although there are more hosts for the species of *Exema* than I first supposed, I believe that each species has one to several preferred hosts. If the actual host plants could be distinguished in the field from those plants on which the beetles are only incidentally found, specimen labels would be of greater taxonomic importance.

Hosts: Artemisia tridentata, A. douglasiana, A. heterophylla, A. californica, Lipidospartum squamatum, Ambrosia psilostachya, Hymenoclea monogyra, Brickellia californica, Eupatorium adenophorum, Chrysothamus nauseosus, Fransería bipinnatifida, Gnaphalium decurrens, Quercus sp., *Flourensia cernua,* and *Encelia californica. Isocoma veneta* and *Astragalus* are reported as hosts by Moore (1937).

Specimens examined: (517 males and 523 females). *NORTH AMERICA:* ARIZONA: Cochise Co., 5 June-24 Aug.; Navajo Co., 6-20 July; Pima Co., 26 May-28 June; Santa Cruz Co., 2 June-4 Oct.; "Atascosa Mts," 14 July; "Forestdale," 30 June. CALIFORNIA: Alameda Co., 10 Mar.-3 Oct.; Butte Co., 15 July; Calaveras Co., no date; Colusa Co., 15 Aug.; Contra Costa Co., 5 Apr.-19 Aug.; El Dorado Co., 8 Aug.; Fresno Co., 25 July; Inyo Co., 22 July-5 Sept.; Kern Co., 9 July-2 Sept.; Lake Co., 22 June; Lassen Co., 4 July; Los Angeles Co., 26 Jan.-24 Oct.; Merced Co., 30 May; Modoc Co., 20 July; Monterey Co., 4 May-28 Sept.; Orange Co., 4 May-30 July; Plumas Co., 25 June; Riverside Co., 2 June-29 Sept.; Sacramento Co., 7 Mar.-23 Apr.; San Bernardino Co., 24 Apr.-29 July; San Diego Co., 8 Feb.-7 Sept.; San Luis Obispo Co., 4 July; San Mateo Co., 17 Aug.; Santa Barbara Co., 30 Apr.-2 Sept.; Santa Clara Co., 2 Feb.-7 Sept.; Santa Cruz Co., 12 June-16 Aug.; Shasta Co., 2 June-July; Sonoma Co., 30 June-Aug.; Tulare Co., no date; Ventura Co., 14 Feb.; Yolo Co., 24 Mar.-24 Sept.; "Amedae," 20 July; "Newton," 14 July; "Sierra Nevada," no date. COLORADO: State record, no date. IDAHO: Bannock Co., 31 Aug.; Boise Co., no date; Canyon Co., 18 June; Elmore Co., 21-30 July; Franklin Co., 13 July-14 Aug.; Gooding Co., 15 Aug.; Idaho Co., 10 Aug.; Jerome Co., 21 June; Lemhi Co., 6

Sept.; Nez Perce Co., 17 May; Washington Co., 26 July-1 Oct.; "Eureka," 23 June. NEVADA: Humboldt Co., 29 May; Pershing Co., 27 Aug.; Washoe Co., 29 June. NEW MEXICO: State record, no date. OREGON: Baker Co., 6 Sept.; Deschutes Co., 30 July; Grant Co., 14 June-10 July; Harney Co., 18 June-12 Aug.; Jefferson Co., 14 June; Lake Co., 27-28 June; Lane Co., 25 Apr.; Malheur Co., 15-26 June; Union Co., 12 June; Wasco Co., 19 May. TEXAS: Val Verde Co., 14 June. UTAH: Box Elder Co., 29 Sept.; Cache Co., 2 Aug.-18 Nov.; Salt Lake Co., 14 June; Summit Co., 12 June; Tooele Co., no date; Utah Co., 4-19 Aug.; "Raysville," 21 Sept. WASHINGTON: Asotin Co., 20 Apr.; Chelan Co., 4 June; Whitman Co., 1 May; Yakima Co., 26 May. *MEXICO:* BAJA CALIFORNIA: San Felipe, 15 June. BAJA CALIFORNIA SUR: Cape San Lucas, no date; Miraflores, 8 July; San Bartolo, 6 May; 5 mi. W. San Bartolo, 13 July; San Jose del Cabo, no date. COLIMA: Tonila, no date. GUERRERO: Chilpancingo, no date. HIDALGO: Ixmiquilpan, 10 June. JALISCO: El Castillo, 25 Apr.; 22 mi. N.W. La Piedad, 23 July. MICHOACAN: Patzcuaro, 26 Mar. MORELOS: near Alpuyeca, 30 Mar.-19 June; near Cuautla, 8 Aug.; Cuernavaca, Apr.-Nov.; 9 mi. E. Cuernavaca, 23 June; 4 mi. N.W. Cuernavaca, 12 Apr.-17 June; 3 mi. N. Cuernavaca, 14 Mar.-10 Apr.; 3-6 mi. S. Cuernavaca, 17 Apr. NAYARIT: 34 mi. N. Ixtlan, Del Rio, 18 July; Jesus Maria, 26 June-27 July; Tepic, 20 July-24 Sept. OAXACA: Oaxaca, 8 July; Rin Antonio, no date. PUEBLA: Cacaloapan, 26 Apr.; 15 mi. S.W. Peltalcingo, 13 Apr.; 2 mi. N.W. Tehuacan, 25 Apr. SAN LUIS POTOSÍ: 7 mi. E. Valles, 29 May. SONORA: Alamos, 15-16 June; Cocospera Canyon, 8 mi. E. Imuris, no date; La Aduena, 15 Mar.-12 June; 10 mi. E. Navajoa, 13 Aug. *CENTRAL AMERICA:* COSTA RICA: Ciruelas, Heredia, 28 Apr. GUATEMALA: N. of Cabañas, Zacapa, 10 Aug.; Coban, Alta Verapaz, 15 June; Dueñas, Suchitepequez, no date; Guatemala City, Guatemala, no date; Moca, Suchitepequez, 21 June; Purula, Baja Verapaz, 15 June; Santa Clara in interior valley of Sierra de las Niñas, N. of Cabañas, Zacapa, 10 Aug.; S. P. Yepocapa, Chimaltenango, 21 May. NICARAGUA: Chinandego, Chinandego, no date; San Marcos, Carazo, no date.

Exema dispar Lacordaire

Chlamys dispar Dejean; 1836:440 (*nomen nudum*).

Exema dispar Lacordaire; 1848:850-852; Gemminger and Harold, 1874:3308 (listed); Dury, 1879:11 (distribution); Dugès, 1881:5-7, fig. 1-16 (larvae); Jacoby, 1881:89; Hamilton, 1895:339,370; Xambeu, 1899:68-69 (biology); Blatchley, 1910:1116 (distribution and biology); 1920:69; Proctor, 1938:156 (biology); 1946:484, 489 (parasitized by *Spilochalcis albifrons* and *Tetrastrichus chlamytis*); Pierce, 1940:9-10; Muesebeck, et al., 1951:128, 589; Peck, 1963:128, 871-872, 955.

Exema conspersa dispar Lacordaire; Henshaw, 1885:106 (listed); Wickham, 1896-97:153; Leng, 1920:288 (listed); Brisley, 1925:168 (= *conspersa*); Leonard, 1928:462 (distribution); Powell, 1941:156 (male genitalia).

Exema pennsylvanica Pierce; 1940:18-19; Brown, 1943:123-124; Proctor, 1946:187 (distribution and biology); Blackwelder and Blackwelder, 1948:42 (listed); Fattig, 1948:8 (distribution); Wilcox, 1954:395; Dillon and Dillon, 1961:670. (NEY SYNONOMY.)

Diagnosis: This species is black variegated with spots of yellow on most of the body, and large yellow areas on the head and anterior slope of the pronotum. The last tarsomere is short, only about 1/3 longer than the third. It is found from the Great Plains eastward (Fig. 65) on several genera of composites, including *Ambrosia, Helianthus,* and *Eupatorium.*

Types: Exema dispar Lacordaire, United States. This type is unable to be located. *Exema pennsylvanica* Pierce, Allegheny Co., Pennsylvania, Klages (LACM).

Several different species of North American *Exema* have been identified as *dispar*. Although Lacordaire's description is long and detailed, several statements make positive application of this name impossible. Unsuccessful attempts were made to locate the type in various museums in Europe. From these efforts it is believed that the type is lost and it is necessary to designate a neotype for this species in order to avoid confusion and establish stability of names in the genus.

This species was first considered a synonym of *conspersa* (Crotch, 1873). Next is was applied probably to specimens of *canadensis* and *neglecta* (Blatchley, 1920). Other authors have considered it a subspecies of *conspersa* and one used *dispar* in place of *conspersa* (Jacoby, 1890).

The color described for *dispar* could apply equally well to *pennsylvanica, neglecta, byersi,* or *elliptica;* however, the variation described suggests *pennsylvanica.* The size given for *dispar* could also apply to any of the above species. On the basis of the shape of the tarsal claws, all species in the *canadensis* group key out to *Poropleura* in Lacordaire's key; therefore, one would probably consider *pennsylvanica* a synonym of *dispar.* The description fits *pennsylvanica* very well except for the statement "elle est striée sur ses flancs" (it is striate on the flanks). The Latin description states "prothorace rugoso-punctulato" (prothorax rugose-punctate). A striate or rugose pronotum is found only in *neglecta, byersi, canadensis,* and *elliptica.* Lacordaire did not know the shape of the tarsal claw; therefore, one of these four species may be a synonym of *dispar.* Another possibility is that Lacordaire had a mixed series. My study indicates that this must have been the case. Lacordaire himself stated that there was considerable variation in the series; therefore, he designated the most common forms as varieties. I am here designating a neotype for Lacordaire's variety A. His description most nearly agrees with that of *pennsylvanica,* which now must be synonymized with *dispar.*

The neotype is a male collected on Plummer's Island (Montgomery Co.), Maryland, 4 May 1913, by W. L. McAtee (USNM). Maryland is chosen as the type locality for this species since Lacordaire's specimens probably came from someplace on the eastern coast of the United States.

Description: Male: 2.3 mm long; 1.55 mm wide. Shiny black to brown with yellowish or yellowish brown markings. Antenna yellow to 6th segment, segments 7-11 brown; mouthparts dark brown; frons yellow except emargination of eyes and antennal sockets, clypeus, and gena black; central spot on vertex and area next to eyes black (similar to Fig. 25). Frontal slope of pronotum yellow from antecostal suture to summit, yellow also extending laterally on upper 1/4 of pronotum in an irregular pattern; marginal tubercle with a small reddish yellow spot. Sutural tubercles 2b and 3b yellowish brown, faint yellowish brown on marginal tubercle and other irregular spots toward apex. All tibiae with subbasal and subapical yellow rings, reduced to spots on femora; tarsomeres yellow. Entire cuticle minutely granulate, irregularly punctate. Head coarsely punctate, more sparsely so on yellow than black areas; punctures large, deeper on yellow areas of frons and pronotum than black areas; hairs in punctures inconspicuous; antenna clothed with many short and a few long hairs, especially toward apex; segment 5 subequal to 3 and 4, segments 6-11 twice as wide as 5; labrum smooth, feebly emarginate at apex, with ventrally projecting, long hairs. Pronotal gibbosity with rounded tubercles; cephalic and anterior pair missing; anterior carina present, connected to summit-1; summit-2 represented by a broken carina projecting toward lateral tubercle; marginal tubercle short and broad; entire pronotum with large, round, deep punctures inconspicuously setigerous. Scutellum feebly carinate with obtuse lateral wings. Elytra coarsely punctate, punctures large and deep, each with a short curved hair; smaller punctures on tubercles; umbone large and prominent, sparsely punctate but highly granulate; large tubercles: anterior, sutural-1, 1a, 2, 2a, 3, 3a, marginal, and marginal-b; small tubercles: umbonal-a, umbonal-b, sutural-2b, and 3b; discal depression well developed. Legs shallowly punctate; tarsal claws toothed; last visible tarsomere less than 1/3 longer than 3rd; apical spine on front and middle tibiae. Prosternum coarsely punctate, slightly concave; prosternal process long and narrow, curved dorsally. Metasternal punctures large and deep, especially laterally. First abdominal sternum with a longitudinal carina between coxal cavities, carina dividing near midlength into a faint Y-shape and terminating in 2 ventrally projecting spines on posterior margin of segment; 2nd and 3rd segments with similar but much smaller spines; punctures of 1st sternum large and round, shallow medially to deep on lateral margins; midventral area of 5th sternum flat to slightly concave, covered with long recurved hairs; lateral punctures large and round. Pygidium centrally convex; faintly tricarinate, lateral carinae shorter but more distinct than medial, diverging slightly ventrally; entire surface coarsely punctate. Male aedeagus similar to that figured for *deserti*.

Female: 2.4 mm long; 1.6 mm wide. Similar to that of male except facial yellow reduced; black spot on vertex larger and extends to area between eyes; more black on clypeus and around antennal sockets; yellow of frons extends into emargination of eye. Pronotum with similar or reduced yellow areas. Elytra more yellowish brown than males. Punctation, sculpturing, and vestiture similar to those of male except front and middle tibial spines absent; spines on sterna absent and fewer hairs on 5th sternum; a few long straight hairs situated on periphery of a slightly concave fovea bearing a few short hairs. Pygidium distinctly tricarinate with lateral carinae larger than median one.

Discussion: This is one of the species that has been confused with *conspersa* because of the lack of understanding of variation in the two species and in the genus as a whole. Characteristics of *dispar* are fairly constant north of North Carolina, but further south there is a rapid change to a strikingly different Florida form which is smaller and yellower than specimens from the North and in which the pronotum appears to be blistered, because of the large, round, yellow tubercles. Varying degrees of this type can be found in Alabama, Mississippi, Louisiana and Texas. The yellow color persists in some Texas specimens, but the pronotum has only a slightly blistered appearance.

Further north, in Kansas, this blistered appearance is completely lacking and the pronotum has a distinct pattern rather than scattered spots of yellow. The apparent cline from Florida, through the Gulf states to Texas, northeastward to New York, and down the coast to North Carolina, could be the result of intergradation of a Florida form with the northern form, resulting in a highly variable species.

The intermediate Texas forms are similar to the forms of *conspersa* from the eastern edge of its range, making identification of specimens from that area difficult. A combination of characters rather than any single character is necessary to identify specimens. There are similar forms of *deserti* in this same area, but the form of the tarsal claw is a reliable character to separate these from *dispar*.

The male and female genitalia of this species are not sufficiently different taxonomically from *conspersa* and *deserti* to warrant illustrating. The shape of the antenna (Fig. 57) and tooth of the tarsal claws (Fig. 56) are similar to *deserti* and *conspersa*, respectively.

Plant records: Helianthus tuberosus, H. hirsutus, Ambrosia trifida, A. psilostachya, Chrysanthemum sp., *Silphium*, "artichoke," *Achillea, Cercis occidentalis*, strawberry, *Salix* sp., *Verbesina, Quercus virginiana, Bidens pilosa*, cabbage, *Eupatorium drummondii, E. maculatum*, and *E. alba*.

Specimens examined: (550 males and 520 females). ALABAMA: Clay Co., 3 May; Macon Co., 20 June; Mobile Co., 23 Apr.; Tuscaloosa Co., 26 Apr. ARKANSAS: Clay Co., no date; Lee Co., 30 June; Monroe Co., 4 July; Washington Co., 30 May-June. CONNECTICUT: Fairfield Co., 24 June-25 Sept. DISTRICT OF COLUMBIA: Rock Creek, 5 Apr.; Washington, 5-12 June. DURANGO: 10 mi. W. Durango, 12 July. FLORIDA: Alachua Co., 3 Apr.-16 Nov.; Dade Co., 11 June; Duval Co., no date; Jackson Co., 9 July; Lake Co., 1-11 Mar.; Leon Co., 29 Oct.; Manatee Co., 25-29 Mar.; Palm Beach Co., 27 Mar.; Pinellas Co., 28 Jan.-26 Aug.; Seminole Co., 15 Mar-13 June; Suwannee Co., no date; Volusia Co., 15 Apr.-16 May. GEORGIA: Clarke Co., 22 May; De Kalb Co., 3 June; Fulton Co., 2 June; Glynn Co., Aug.; Rabun Co., 15 May. ILLINOIS: Alexander Co., 29 Sept.; Champaign Co., 15 Feb.; Cook Co., 1 June-11 Sept.; La Salle Co., 15 May-2 July; Macon Co., 8 May. INDIANA: Crawford Co., 30 Aug.; Harrison Co., 16 June; Knox Co., 5 July-13 Sept.; Lake Co., 29 May; Lawrence Co., 8 June; Marion Co., 15 May-8 Sept.; Posey Co., 24 Sept.; Putnam Co., 29 May; Starke Co., 18 June; Tippecanoe Co., 17 May; "So. McAlister," no date. IOWA: Dickinson Co., 22 Aug.; Louisa Co., June; Story Co., 18 May-4 Oct. KANSAS: Cherokee Co., 15-31 May; Douglas Co., 23 Apr.-15 Aug.; Jefferson Co., 21 May; Linn Co., 21 May; Montgomery Co., 26 May-2 June; Riley Co., no date; Shawnee Co., 14 May. KENTUCKY: Edmonson Co., no date; Floyd Co., 20 June; Rowan Co., 11 June. LOUISIANA: (Parish=county of other states) Caddo Par., 19 Aug.; Cameron Par., 20 June-14 Aug.; Jefferson Par., June; Natchitoches Par., 16 Aug.; Sabine Par., 16 June; St. Landry Par., 26 Apr.; St. Mary Par., 3 May. MARYLAND: Baltimore Co., 17 June; Charles Co., 25 May; Montgomery Co., 9 Apr.-16 Sept.; Prince Georges Co., 14 May-21 July. MICHIGAN: Kalamazoo Co., 25 June. MINNESOTA: Hennepin Co., 12 June-4 Sept.; Houston Co., 2 June; Olmsted Co., no date. MISSISSIPPI: Adams Co., 27 May; Grenada Co., 21 Apr.-13 May; Montgomery Co., 27 May; Quitman Co., 8 Sept. MISSOURI: Boone Co., 11-22 May; Cooper Co., 21 May; Greene Co., 20 July; Howard Co., 12 May; Morgan Co., 13 May; Pettis Co., 10 June; St. Louis Co., 6 Feb.-9 June; Shannon Co., 28 May; Wayne Co., no date. NEBRASKA: Antelope Co., 22 June; Cuming Co., June; Otoe Co., June; Sarpy Co., 9 May; "Sand Hills," July. NEW JERSEY: Bergen Co., 14 June. NEW YORK: Erie Co., 24 Aug.; Herkimer Co., 23 May-30 June; Livingston Co., 24 May; Monroe Co., 10 June; New York Co., 9 July; Onondaga Co., 23 June-14 Sept.; Rockland Co., 20 Oct. NORTH CAROLINA: Jackson Co., 1 June; McDowell Co., 25 June; Moore Co., 11 May; Transylvania Co., 14 May-16 Aug.; Watauga Co., Aug. OHIO: Champaign Co., 10 May-31 Aug.; Columbiana Co., no date; Delaware Co., 2 May-4 Sept.; Franklin Co., 24 May-6 June; Greene Co., 28 Apr.-19 Sept.; Hocking Co., 8-20 May; Lake Co., no date; Lawrence Co., 22

Mar.-29 May; Lorain Co., July-12 Aug.; Ross Co., 22 May; Seneca Co., 5 Aug.; Summit Co., 12 June; Washington Co., 15 June. OKLAHOMA: Jefferson Co., 18 May; Muskogee Co., 29 May-19 Sept.; Tulsa Co., 21 June. ONTARIO: Fuller, 3 mi. E. Ivanhoe, Hastings Co., 23 July-24 Aug.; "W. Ont.," no date. PENNSYLVANIA: Alleghany Co., 2-4 July; Dauphin Co., 24 May-10 July; Philadelphia Co., no date; Westmoreland Co., 10 June-26 July. SAN LUIS POTOSÍ: Huichihuayan, 25 Aug.; Tamazunchale, 7 Mar. SOUTH CAROLINA: Beaufort Co., 7 July; Charleston Co., 10 July; Greenville Co., 26 Aug.; Orangeburg Co., 27 June; Richland Co., 21 Aug. SOUTH DAKOTA: Union Co., 23 July. TAUMAULIPAS: Rio Guayelajo, Victoria, 25-27 Aug. TEXAS: Bandera Co., 10 Aug.; Bexar Co., 16 June-23 Sept.; Blanco Co., no date; Brazos Co., 18 Mar.-26 Sept.; Brooks Co., 20-25 July; Burleson Co., 5 Feb.; Cameron Co., 4 Apr.-27 Nov.; Colorado Co., 19 May; Comal Co., 9 June-9 Aug.; Dallas Co., 25 Apr.-4 Nov.; Duval Co., 26 May-13 June; Gillespie Co., 2 May-20 June; Harris Co., 6 Aug.; Harrison Co., 7 June; Hays Co., 5 July; Hidalgo Co., 8 May-30 July; Jim Wells Co., 24 July; Karnes Co., 23 July; Kerr Co., 11 Apr.; Lee Co., July; Medina Co., 3 Sept.; Milam Co., 4 Apr.-3 Aug.; Parker Co., 6 May; Red River Co., 10 Apr.; Sabine Co., 25 Mar.; San Patricio Co., 25 Mar.; Uvalde Co., 14 June-11 July; Val Verde Co., 27 Aug.; Victoria Co., 11 Apr.-31 July; Wharton Co., 18 Apr.; Williamson Co., 1 May; Zavala Co., 11 Aug. VIRGINIA: Alexandria, 22 May-9 June; Arlington, 10 May-8 July; Fairfax Co., 22 May-23 Sept.; Henrico Co., 15 May; Nelson Co., 28 June; Nottoway Co., 17 May; Princess Anne Co., July; Rockbridge Co., 5 July; Shenandoah Co., 22 May; Spotsylvania Co., 8 June; Stafford Co., 23 May. WEST VIRGINIA: Mercer Co., 12 June; Monongalia Co., 28 June. WISCONSIN: Dane Co., 16 June; Grant Co., Jan.

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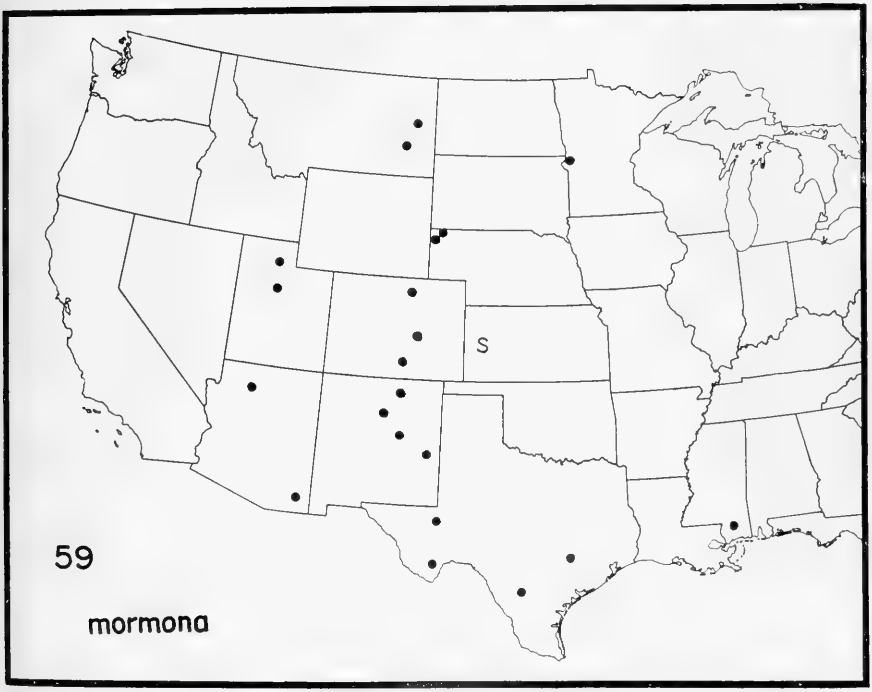
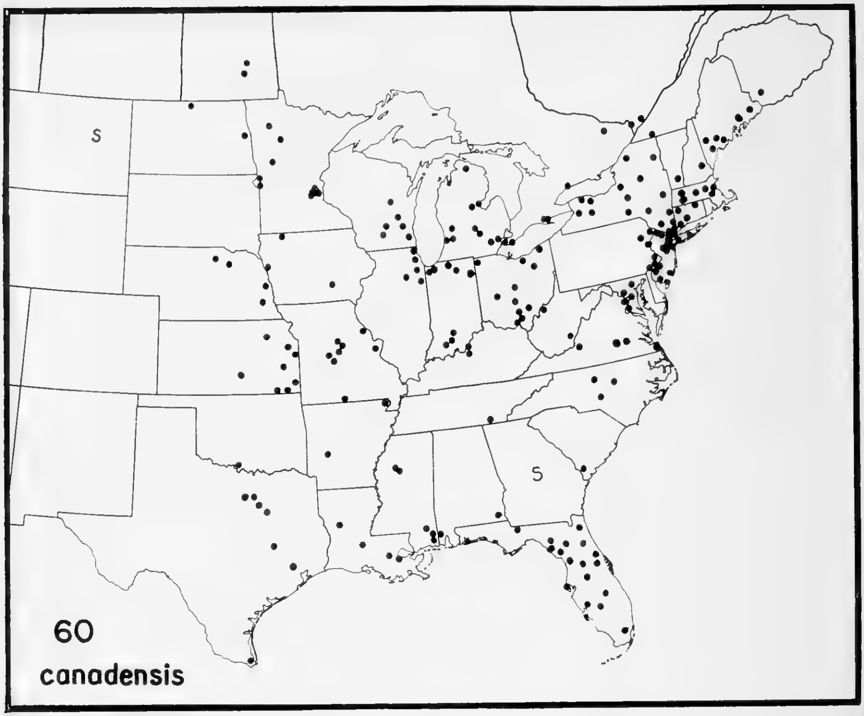


FIG. 58. Range of *Exema gibber*. Each spot represents one or more collections within a county or at a locality.

FIG. 59. Range of *Exema mormona*. Each spot represents one or more collections within a county or at a locality. S=state record.



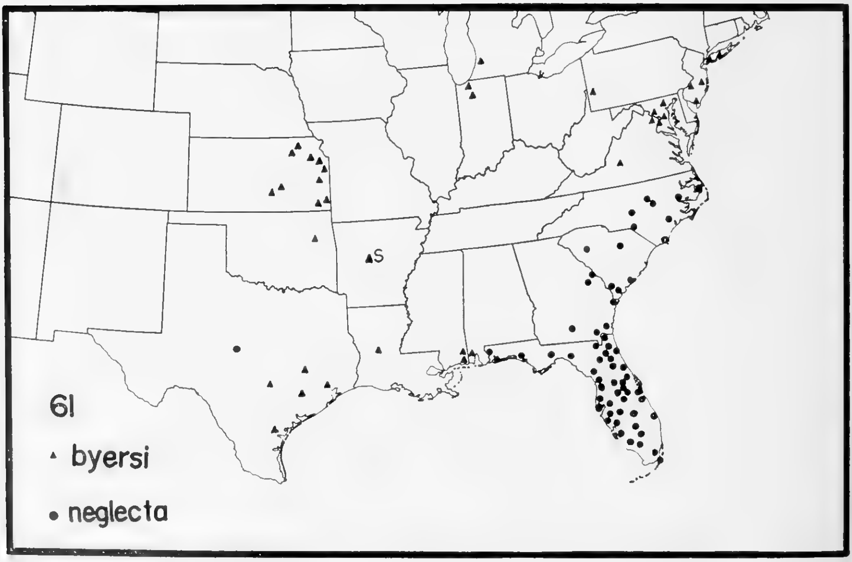
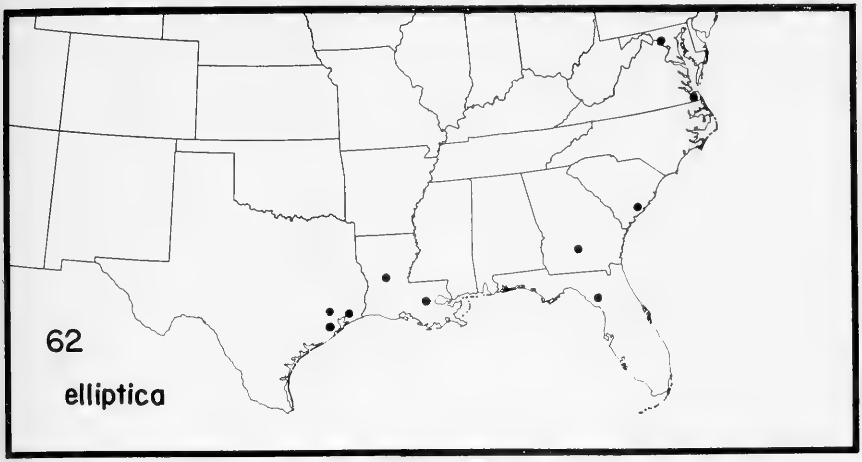


FIG. 60. Range of *Exema canadensis*. Each spot represents one or more collections within a county or at a locality. S=state record.

FIG. 61. Range of *Exema byersi* and *Exema neglecta*. Each spot represents one or more collections within a county or at a locality. S=state record.



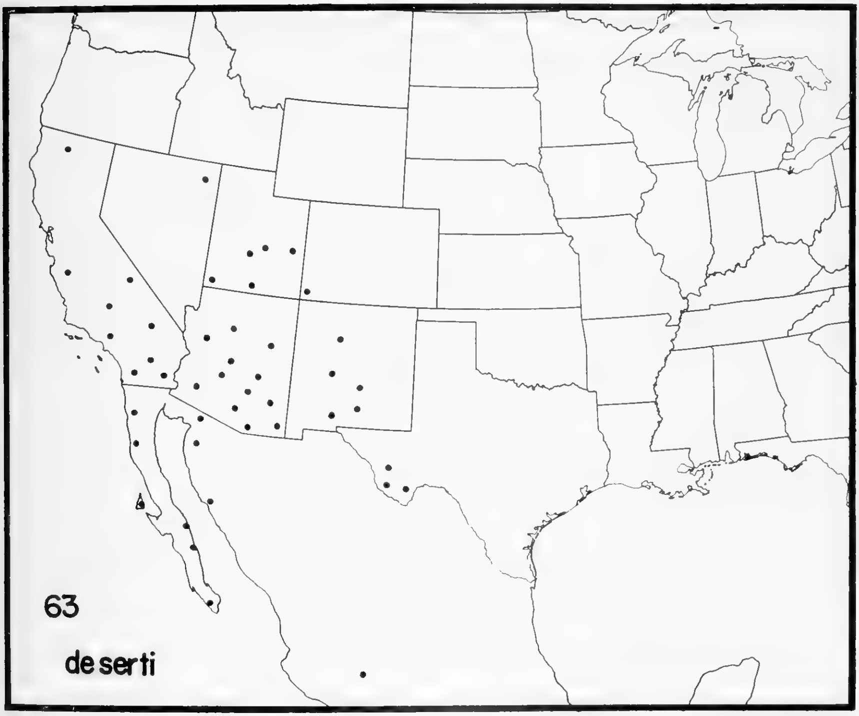


Fig. 62. Range of *Exema elliptica*. Each spot represents one or more collections within a county or at a locality.

Fig. 63. Range of *Exema deserti*. Each spot represents one or more collections within a county or at a locality.

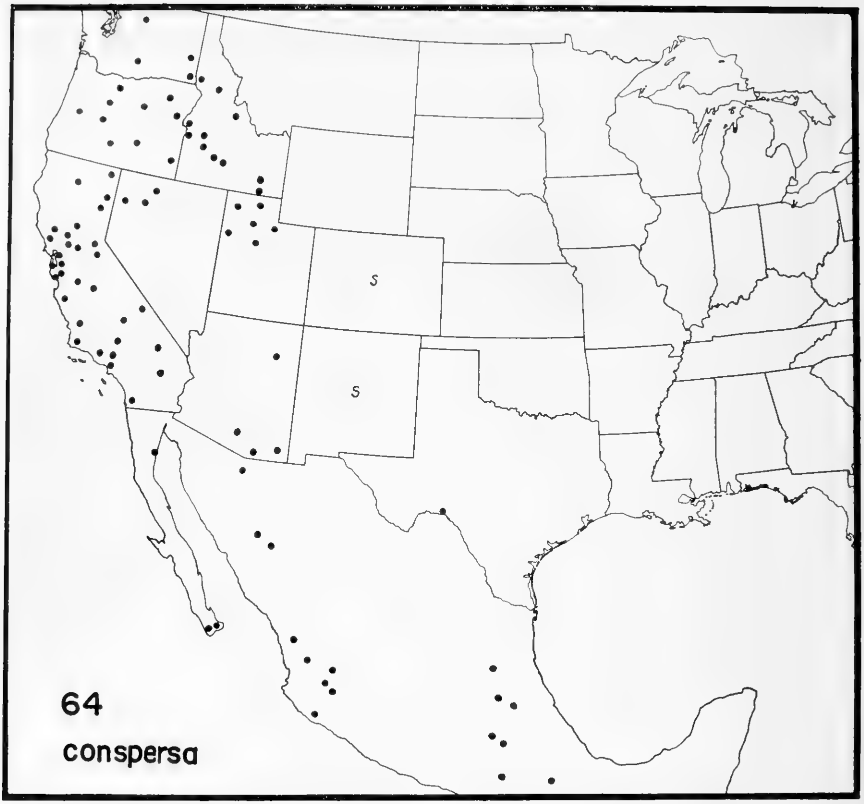


FIG. 64. Range of *Exema conspersa*. Each spot represents one or more collections within a county or at a locality. S=state record.

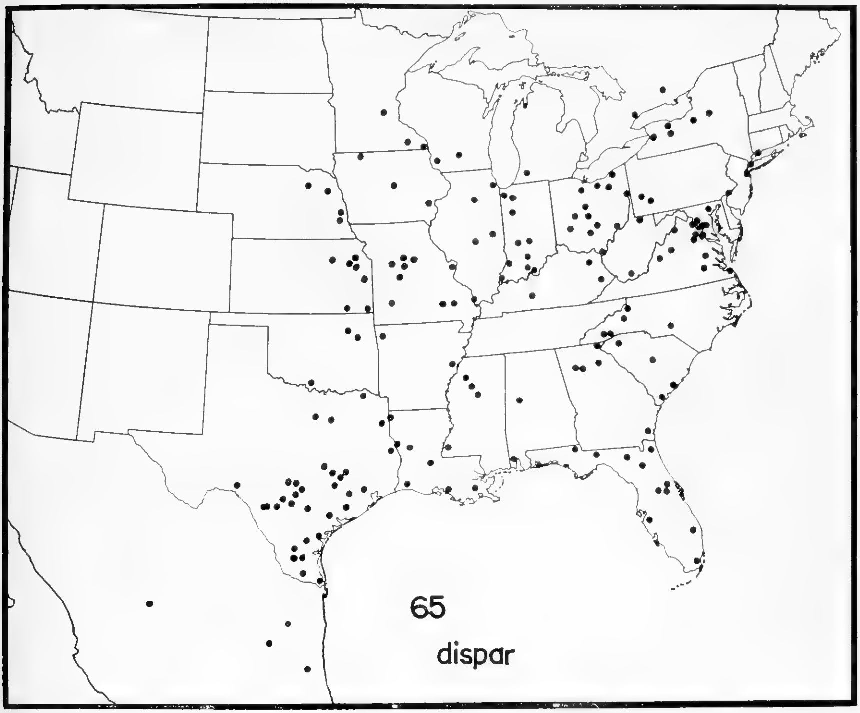


FIG. 65. Range of *Exema dispar*. Each spot represents one or more collections within a county or at a locality.

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PUPATION SITE DIFFERENCES IN *DROSOPHILA MELANOGASTER*

By

Robert R. Sokal

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Pupation Site Differences In *Drosophila melanogaster**

By

Robert R. Sokal
Department of Entomology, The University of Kansas, Lawrence

I. INTRODUCTION

This paper describes an experiment selecting two lines of *Drosophila melanogaster* Meigen for central and peripheral pupation sites, respectively. The account includes the development of differences between the strains, correlated characters and the results of crossing experiments.

The study grew out of an incidental finding in a selection experiment on DDT-resistance of larvae of *D. melanogaster,* i.e., that resistant larvae in control medium without toxicant tended to pupate at the margin of the medium-cylinder or on the wall of shell vials, while susceptible larvae tended to pupate away from the margin (Sokal and Hunter, 1954).

The main purpose of these experiments was to be an investigation of the quantitative inheritance of this newly recognized character of drosophila. However, a number of factors, among them the complexities of measuring this quantal character, and environmentally caused fluctuations in phenotype, made the analysis and interpretation of these data extremely difficult. The results were put aside, but by the time new insights and new techniques would have placed the genetic interpretation of a repeat experiment on a sounder basis, my interests and activities had changed and the necessary stocks or facilities no longer existed in my laboratory. The reason for publishing the following account is, therefore, not as a definitive genetic interpretation of the findings, but because several aspects of this experiment are unique and should, consequently, be of interest to drosophila workers.

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* Contribution No. 966 from the Department of Entomology, The University of Kansas, Lawrence, Kansas. These studies were aided by the Office of Naval Research, Department of the Navy (Contract No. Nonr 171(00)). This investigation also was supported in part by a Public Health Service research career program award (No. 3-K3-GM-22, 021-01S1) from the National Institute of General Medical Sciences.

II. MATERIALS AND METHODS

The flies were reared in six-dram shell vials (height 85 mm, diameter 21 mm) filled with 4.4 cc of corn meal-agar-molasses medium (height of medium column 14 mm). Medium preparation is described in detail in Sokal et al. (1960).

Medium for all lines in any one generation was prepared in one big batch in one pan. Occasionally it was necessary to prepare medium in two pans. In such cases pupation site records were taken separately for each batch, flies of any one line being divided equally into the two batches.

The vials were seeded with ten eggs each from half-pint oviposition bottles, prepared by the method of Gowen and Johnson (1946). Each bottle contained only a single parent pair and the eggs from any one bottle were therefore full sibs. While in general only one vial was prepared from an oviposition bottle, two or more vials were prepared from the same bottle when few flies were available or when the fecundity of a particular generation was unusually low. In these "replicated sibships," vials coming from the same parent pair were identified as such.

Seeded vials were placed in a temperature chamber at 25±0.5°C. Humidity was not controlled, but occasional records indicated a stable R.H. near 40%. During periods of no selection, stocks were kept in the main laboratory at 25±3°C, as were the oviposition bottles.

When all larvae had pupated, pupation sites were recorded for each vial (see Figure 1). All pupae which were not touching the wall of the vial were called "central." Pupae touching the wall, were termed "marginal" if partly submerged in the medium, or "on wall" when cemented to the wall of the vial and entirely free from medium. Since there were relatively few "on wall" pupae they were lumped for computational purposes with the "marginal" pupae, both being called "peripheral" pupae. The percent peripheral pupation,

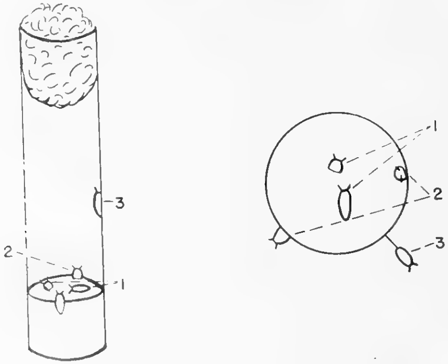

FIGURE 1. Diagram explaining scoring of pupation site. 1-in medium, 2-at margin, 3-on wall; 1 = central, 2 + 3 = peripheral.

the basic variable measured in the study, was computed from the number of peripheral pupae out of the total number of pupae.

Pupation site readings for any one generation were always carried out by the same technician, although over the entire study a number of technicians were employed. Bias in readings among technicians was kept to a minimum by repeated checks. Furthermore, large sections of the study were assayed by the same person so that the fluctuations observed from generation to generation cannot be attributed to differences between technicians.

The lines were selected from the COSU-2 stock, synthesized from the Canton-S, Oregon-R-C, Sweden-C, and Urbana-S strains as described for COSU-1, by Hunter (1959). The COSU-2 stock had been mass mated in six culture bottles for three generations at the start of the present experiment.

For pupation site assays and selection 100 vials of 10 eggs each were prepared. These vials ideally came from 100, but frequently fewer, parent pairs; the lowest number was 22. Each generation was to consist of one thousand individuals, but this figure was rarely reached. In each generation 100 pairs of flies were to serve as the parents of the next generation. Therefore rather more than 200 pupae were selected in the hope of obtaining 100 fertile adult pairs.

Selection for high peripheral pupation (PP line) consisted of securing all pupae from those vials that exhibited 100% peripheral pupation, whether based on 10 or fewer pupae. For additional individuals all vials with a percentage of peripheral pupation above an arbitrary level (say 90%) would be chosen and all central pupae in them destroyed by a pin prick. The selection threshold would be lowered until a satisfactory number of peripheral pupae had been selected.

Selection for central pupation (CP line) was done in an analogous manner. All vials exhibiting zero per cent peripheral pupation were saved in their entirety. Low peripheral percentage vials were selected up to a certain selection threshold, with the peripheral pupae within them killed or disposed of.

Adults emerging from the selected pupae were sexed every eight hours to ensure the virginity of the females and to prevent inbreeding among the full sibs of a vial. Sexed flies were stored in medium vials for several days to permit them to mature. The parents-to-be of the next generation were mated at random. When selection was interrupted for one generation all the flies emerging from the pupation site vials were sexed and mated at random to produce the next generation.

The method of assaying larval resistance to DDT has been reported elsewhere (Sokal, 1959). The analysis of the mortality data was performed by standard probit analysis techniques (Finney, 1952), with maximum likelihood estimates obtained on a digital computer (Sokal, 1958). Length of larval and pupal periods was determined by a technique standard in this laboratory (Hunter, 1959; Neunes, 1962).

To summarize the treatments carried out in the present study: Pupation site was assayed in generations 1-32, 40, 42, 44-55, 60-61, 75-81. Selection in both directions took place in generations 1-14, 16, 18-26, 28-32, 40, 44-45, 48, 51-55, 76-81; for central pupation only in generations 15 and 27 and for peripheral pupation only in generation 17. Replicated sibships for both lines were run in generations 7, 14-15, 20, 28, 45, 48, 77 and 80; for the CP line only in generation 5; and for the PP line only in generations 4, 6, 12, 13, 52, 54 and 79. The generation numbers of successful assays for DDT-resistance can be found in Table 3, those of length of developmental period in Section IV(7), and those of crosses in Section V.

III. PROBLEMS OF SCALE

It seemed proper to weight each percentage peripheral pupation by the number of pupae on which it was based. Moreover, since vials contained ten pupae, the presence or absence of one pupa made the difference between 90 and 100% or 0 and 10% peripherality. Assuming the existence of a continuous distribution of phenotypes, a probability scale would lump all phenotypes beyond 90% and below 10% peripherality into two groups labeled as the most extreme phenotypes.

While a relation between pupation site and density has been found at the higher densities (12 to 50 pupae per vial; Sokal *et al.*, 1960), these authors and Schlager (1959) were unable to demonstrate such a relation in either the COSU-2 or the BS-Canton strain at the lower densities employed in this study. Thus the relation demonstrated below for the CP and PP lines appears to have been acquired by them as a concomitant result of the selection procedure.

After considerable trial and error the probit transformation was found to approximate a normal distribution of pupation sites and a linear regression of pupation site on density more closely than other scales. Furthermore, the problem of bias at the tails of the curve was also solved in this manner, since probit analysis routinely estimates the tails of the distribution during the maximum likelihood method of computation.

Data for all available generations were converted to probit peripheral pupation site and regressed on density, using the method of maximum likelihood (Finney, 1952). In the replicated sibships it was possible to perform an analysis of covariance of the data in addition to probit analysis. In the non-replicated sibships of the CP line only 1 of 48 regression coefficients is positive; the mean regression of probit peripheral pupation on density is -0.0970. Of these 48 regression coefficients only 26 are significant at $P \leqq 0.05$ (mean $= -0.1255$), but none of the significant ones is positive. The PP line did not show as clear a relationship. Of 41 regression coefficients with a mean of -0.0407, 8 are positive. Only 9 of the 41 coefficients are significant (mean $= -0.0778$) and 1 of these is positive. No trend in magnitude of the regression coefficients is evident in either line. In all but 8 of 89 instances there are no significant deviations from linearity ($P \leqq 0.05$). Analyses of covariance for the replicated sibships bear out these findings. Among 10 CP generations the pooled regression within and between sibships averages −0.1181, the pooled significant regression −0.1660. In the PP the pooled regression is −0.0735, the pooled significant regression −0.1188.

On the basis of these findings the average probit pupation sites for each line and generation were corrected by replacing them with the expected probit pupation sites at the (aimed at) density of ten pupae per vial. These estimates were computed from separate regression equations for each line and generation. With the few exceptions of positive regression slopes, the correction resulted in a reduction of the probit peripheral pupation over the uncorrected value. Since the regression coefficient for the PP line was roughly only half that of the CP line the correction of the data also served to differentiate slightly the phenotypic expression of the character in the two selected lines. While the effects of these corrections are only modest, the regression analysis did permit appropriate weighting of each vial and satisfactory statistical treatment of the extreme phenotypes.

The average probit pupation sites, the regression estimates, their 5% fiducial limits and the regression coefficients have been tabulated but are not reproduced here to conserve space. Copies of the table may be obtained from the author.

IV. RESULTS OF SELECTION EXPERIMENT

1. *Over-all Trends*

Figure 2 shows the results of the selection experiment up to and including generation 81. The ordinate is in probits peripheral pupation estimated at densities of 10 pupae per vial. Differences between the two lines are graphed in Figure 3.

There is an appreciable difference between the phenotypes of the two lines in the direction intended by selection (P of null hypothesis infinitesimal). Marked fluctuations in pupation site, often against the direction of selection (as in CP generation 7 and 10 or in PP generations 9 and 11) greatly complicated the evaluation of the results. The partial parallelism of these fluctuations indicates their environmental causation. Schlager (1960) was able to implicate one of the ingredients of the medium, molasses, as responsible for the fluctuations. Regrettably these findings came too late to modify the conduct of the present experiment.

2. *Evidence of Selection Progress*

In spite of the fluctuations between successive generations, increases of differences between line means, *d*, are evident between generations 2 and 32.

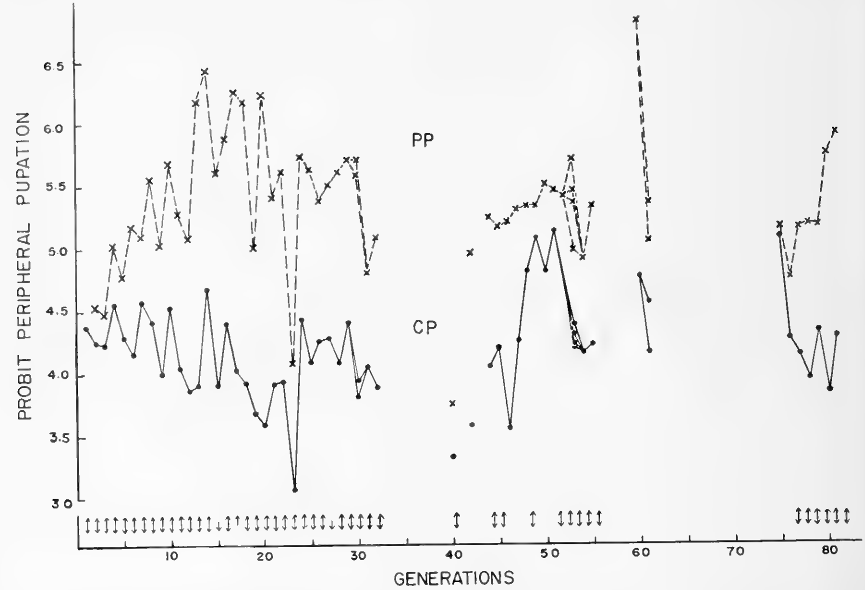

FIGURE 2. Results of selection for peripheral and central pupation sites. Abscissa: generations of selection; ordinate: probit peripheral pupation. The means for each generation have been adjusted to expected values for a density of ten pupae per vial. Missing points for any one generation indicate no pupation site assay for that generation. Multiple points in any one generation represent different series. Only means of consecutive generations are connected by lines. The PP means are connected by broken lines, the CP means by solid lines. The arrows along the abscissa indicate the generations in which selection for pupation site was practiced. A double-headed arrow signifies bidirectional selection, an arrow pointing up selection for peripherality, one pointing down for centrality.

However, Figure 3 shows an end to the increase in the difference at approximately generation 21. The regression coefficient of *d* on generation number from generation 2 to 21 is 0.100 ± 0.0150. Visual inspection suggests a selection limit for the PP line by generation 18. The regression coefficient of estimated pupation sites on generations 2 to 18 is 0.104 ± 0.0157. Figure 2 suggests an end to selection progress in the CP line after generation 23, if not earlier. The regression coefficient of estimated pupation site on generations 1 to 23 is −0.037 ± 0.0090. The response to selection is thus quite asymmetrical, being three times as large for peripherality as for centrality. A substantial number of pupation site assays of the parent COSU-2 stock, both during the course of this experiment and in connection with other experiments, showed no consistent time trend in pupation site, supporting the conclusion of asymmetry of phenotypic response.

3. *Estimation of Heritability*

Since the selection method practiced in the experiment was a combination of individual and family merit selection, the detailed computation of a prop-

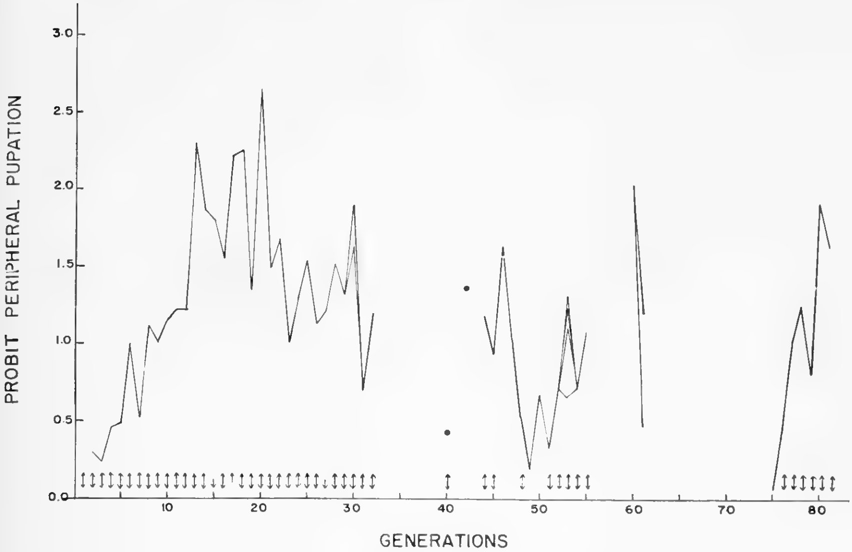

Figure 3. Deviation between PP and CP lines during the selection experiment. Only consecutive generations are connected. Abscissa: generations of selection; ordinate: difference expressed as probit peripheral pupation. Missing points for any one generation indicate no pupation site assay for that generation. Multiple points in any one generation represent different series. The arrows along the abscissa indicate the generations in which selection for pupation site was practiced. A double-headed arrow signifies bidirectional selection, an arrow pointing up selection for peripherality, one pointing down for centrality.

erly weighted standardized selection differential $(\bar{i})$ for each generation would have been an extremely tedious process which, in view of the phenotypic fluctuations, would have introduced an unwarranted element of refinement. Trial values computed for PP, generation 2 based on the two limiting assumptions of mass selection (individual merit) and family merit gave estimates of 0.20 and 0.12, respectively. Equally serious, however, was the problem of estimating the genetic gain, $\triangle G$, between consecutive generations. The phenotypic fluctuations resulted occasionally in $\triangle G$'s with signs opposed to that of their appropriate $\bar{i}$ or, conversely, in $\triangle G > \bar{i}$. The course adopted was to obtain a single estimate of h^2 as the regression coefficient (0.1076 ± 0.0148 for the first 21 generations) of the deviation d on the cumulative selection differential $\bar{i}_c$ (see Figure 4). While such an estimate is of questionable value, it was the only approach feasible here. This h^2 cannot be used for predictive purposes, since such an estimate of realized heritability (Falconer, 1960) is really little more than a function of the success of the selection. Choice of d to indicate genetic gain automatically eliminated the additive portion of the fluctuations.

4. *Components of Variation of Pupation Site*

The replicated sibships in various generations permitted analyses of variance for pupation site and density and analyses of covariance for the two variables (Table 1). Variances among families (sibships) represent genetic and environmental differences among the various families used in each generation. Environmental factors affecting the parents are unlikely to affect pupation site. In the case of density, however, one can easily imagine that frequency and success of mating as well as the environment of the oviposition bottle (which, it will be remembered, contained a single parent pair) will contribute to among-family variance.

Columns 1 and 2 in Table 1 give significance levels and percentages of total variation of variance components among families for density and probit peripheral pupation, respectively. The former show no clear trends and fluctuate markedly, while the latter increases for the first 20 generations of the PP with much reduced values for later generations. The CP line follows this general trend but is less clear, being based on fewer values.

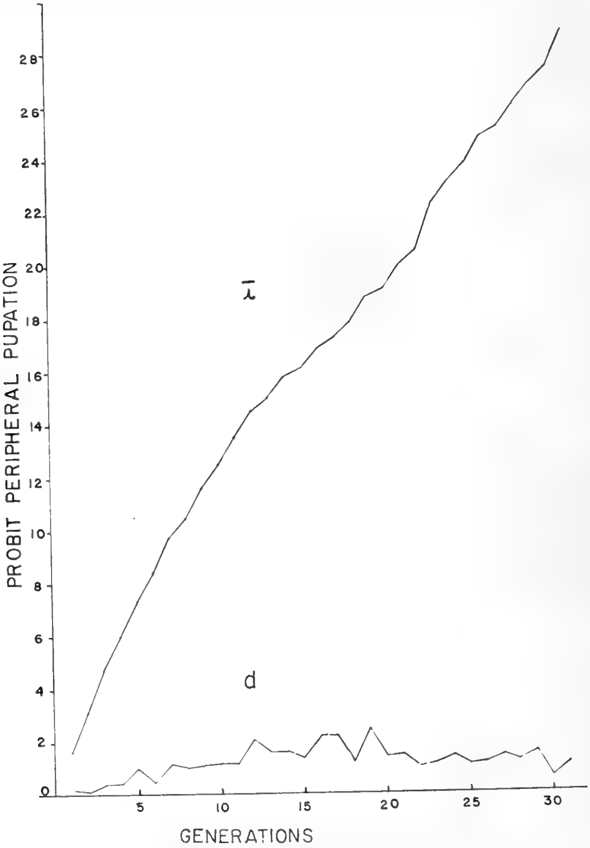

FIGURE 4. Cumulative selection differential, $\bar{i}_c$ compared with difference between means of selected lines, d. Abscissa: generations of selection; ordinate: probit peripheral pupation. Only the first 31 generations are shown.

The analysis of covariance of the replicated sibships yielded a mean square around the average regression of pupation site on density within the families as an estimate of variance among vials of a single family (column 3 of Table 1). It should represent entirely environmental differences between vials with an expected value of 1.0. Most values cluster around unity, with some evidence of underdispersion, especially in the PP, which is difficult to interpret. No trend appears in either selected line. The mean squares of family means (around the regression line; column 4 of Table 1) are in all but one case greater than those within families (column 3), showing the additional effect of genetic as well as environmental differences among families.

Each generation of the non-replicated sibships (where each family is represented by a single vial only) was divided into groups by density and subjected to an analysis of variance testing linear regression, deviations from linearity, densities and vials within densities. The regression coefficients have

TABLE 1. Analysis of Replicated Sibships

CP Generation	density proportion	probit pupation site proportion	among vials within sibship MS	family means from regression MS
5	.062	.117*	.978	1.699
7	.055	.075*	1.042	1.731
14	.327**	.217**	.986	2.327
15	.171*	.160*	.795	2.383
20	.196*	.051	1.165	1.117
28	.045	.103**	.714	1.212
45	.050*	.041*	1.119	1.617
48	.091**	.073**	1.017	1.904
77	.108**	.059	1.057	1.734
80	.119*	.067	1.008	1.113
PP Generation				
4	....	.017	1.148	1.509
6	.114*	.022	.915	1.206
7	.158**	.132*	.749	1.444
12	.115*	.100*	1.317	2.365
13	.290**	.129	1.213	2.412
14	.041	.166	.437	0.873
15	.158	.209	.572	1.301
20	.103	.313**	.297	.940
28	.129*	.080	.800	1.580
45	.069**	.105**	1.161	2.327
48	.140**	.108**	1.083	2.245
52	.047	.183*	.718	1.662
54	.023	.101	.894	1.633
77	.095*	.061	1.482	2.358
79	.081	.066	.542	.895
80	.079	.055	1.085	1.522

Explanation: "Proportion" refers to proportion of total variance represented by variance component among families. Starred proportions indicate significant variance components ($* = 0.01 < P \leqq 0.05$; $** = P \leqq 0.01$).

TABLE 2. Mean Squares among Vials (Sibships) within Densities in Generations without Replicated Sibships

Generation	CP	PP	Generation	CP	PP
2	.879	1.239	32	1.647***	1.595***
3	1.712***	2.078***	40	3.878***	....
4	1.528***	—	42	2.260***	1.977***
5	....	1.538**	44	2.080***	.994
6	1.869***	....	46	1.418	1.987***
8	1.538**	1.343	47	2.449*	2.314***
9	1.362*	1.574**	49	1.620***	1.614***
10	1.382**	.927	50	2.152***	2.070***
11	1.868***	1.618***	51	1.565***	1.350*
12	1.700***	....	52	1.085	....
13	1.604***	....	53 I	1.371	1.297
16	1.705***	1.519***	II	1.894***	1.684*
17	1.964*	2.440***	I	1.178	2.258***
18	1.608***	1.340*	II	.831	2.453***
19	1.163	1.926***	54	1.614***	....
21	1.256	1.653**	55	1.865***	1.524***
22	1.298*	2.507***	60	.342	1.044
23	1.553**	....	61 I	.840	2.503
24	1.718***	1.944***	II	1.462	3.248***
25	1.845***	1.276	75	1.620	.646
26	2.004***	1.619***	76	2.492***	2.636***
27	1.453*	2.474***	78	1.450**	1.907***
29	1.808***	2.235***	79	1.275	....
30			81	1.083	1.829***
I	1.289*	1.305			
II	1.489***	1.108			
31	2.058***	1.574**			

Explanation: Starred mean squares indicate significant heterogeneity among vials within any one density (* = $0.01 < P < 0.05$; ** = $0.001 < P < 0.01$; *** = $P < 0.01$).

already been discussed in Section III. The tests for deviations from linearity are largely non-significant. The mean square among vials within densities (shown in Table 2) corresponds theoretically to the mean square of family means around regression in the analysis of covariance. The actual values for these two types of mean squares show no essential difference. In the non-replicated sibships we cannot partition the vials mean square into environmental and genetic components, but can test the mean square for heterogeneity, i.e. whether it is greater than its expected value of 1.0. Most generations in Table 2 are highly heterogeneous and thus presumably possess an added, largely genetic component among families. There is no consistent difference in magnitude of these mean squares between the CP and PP lines.

5. *Relaxation of Selection*

Removal of selection pressure from generation 32 to 40 resulted in a decrease of the difference in pupation site between the lines. By generation 40, *d* was reduced to the low value of 0.436. However, selection in generations 40 and 51 to 55 increased *d* to values near 1.0. During a second period of relaxation of selection (generation 56 to 75), each line was kept in two half-pint bottles with from 100 to 300 flies per bottle. The considerably more rigorous conditions of existence in these stock bottles should have hastened any genetic changes away from the selected genotype, since the specialized PP and CP flies were likely at a disadvantage in the struggle for survival in the bottle. By generation 75, *d* had declined to a minimal value of 0.079. The difference after yet another generation of relaxed selection was larger again (0.462) but still quite small. The high *d* value of 2.039 for generation 60 is presumably a case of gene-environment interaction, the two lines having responded differentially to the peripheral stimulus of the medium.

Selection applied for six generations starting with generation 76 was immediately effective in restoring the difference between the lines to a very high level ($d = 1.919$ in generation 80). The reversion of the differentiated lines to their original state in the absence of selection, coupled with the speedy re-establishment of the differences upon resumption of selection are substantiated by Schlager (1959) who found a minimal difference ($d = 0.13$) in these same lines in generation 114 after 33 generations without directed selection. By selection of sublines from generation 108, he was able to re-establish an appreciable difference ($d = 1.45$) in a few generations.

6. *Fertility and Larval Survival*

The per cent survival to the pupal stage was obtained as a by-product of the pupation site assays. The percentage was computed only among fertile sibships, since totally infertile vials would, to a large measure, come from unfertilized females. This survival consists of two separate components: fertility in the strict sense (i.e., hatchability of eggs) and survival of larvae to pupation. Separation of these two components was possible only in generations 11, 15, 60 and 61, when separate readings of the number of eggs hatched were taken. On the average, half the loss from egg to pupa represents infertility of eggs and half larval mortality, but the CP line has significantly more egg infertility than larval mortality while the converse relation holds for the PP line.

Figure 5 shows the joint variable (per cent survival to the pupal stage) for the entire study. A marked decline (significant at $P < 0.01$ by means of an ordering test, Quenouille, 1952) for the first 20 generations in the CP and the first 18 generations in the PP line corresponds well with the period of effectiveness of selection. Between approximately generation 22 and generation 32

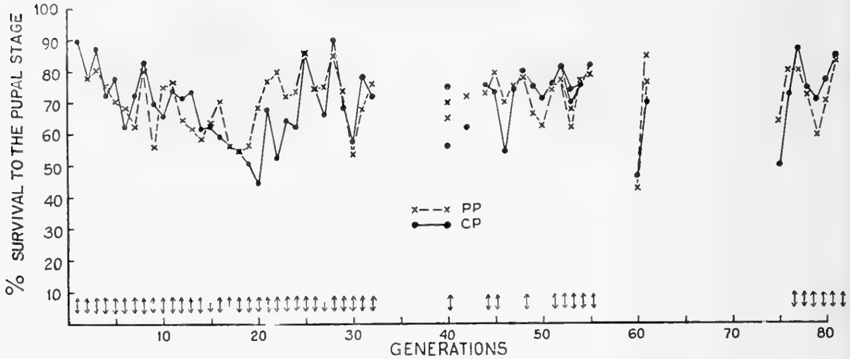

FIGURE 5. Per cent survival to the pupal stage. For a more detailed explanation of this variable see text. Abscissa: generations of selection; ordinate: per cent survival. Means for the PP line are connected by broken lines, means for the CP line by solid lines. Only means involving consecutive generations are connected. The arrows along the abscissa indicate the generations in which selection for pupation site was practiced. A double-headed arrow signifies bidirectional selection, an arrow pointing up selection for peripherality, one pointing down for centrality.

considerable recovery in survival appears to have taken place. In subsequent generations the variable fluctuated markedly.

Significant parallelism occurs in the fluctuations of the two lines (P of the association = 0.05 by the medial test and < 0.01 by Tukey's corner test). This parallelism must be caused by environmental factors common to each generation and is likely to affect larval survival rather than hatchability of eggs. It is unlikely, however, that the decline in fertility observed in the first 20 generations is entirely due to environmental trends. No similar long term trends in either hatchability or larval survival were ever observed in other work in our laboratory and the coincidence between the effective period of selection and the decline in fertility is too great to be coincidental. Attempts to relate the variable to selection differential, phenotypic change or fecundity were not successful.

The variable described above is the same as "density" of pupating larvae. Thus, a density of 8.7 pupae per vial corresponds to a survival of 87 per cent. Two separate terms were retained for the same variable to emphasize that "survival" is a correlated response to selection, while "density" of pupating larvae (a consequence of "fertility" and "survival of larvae") affects the expression of the phenotype.

7. *Other Correlated Characters*

DDT-resistance. Table 3 lists the LD_{50}'s in p.p.m. DDT for the various generations assayed during the experiment. The higher resistance of the PP is established beyond reasonable doubt ($P < 0.006$ on hypothesis of equal resistance for the two lines). Thus, the correlated divergence in pupation site found when selecting for differences in resistance (Sokal and Hunter, 1954;

Sokal, 1959*a*) is matched by the reciprocal correlation. It should be noted, however, that the differences in resistance in this experiment are less than those found in experiments where selection for resistance was practiced.

Length of larval period. Records for generations 11, 15, 60 and 61, suggest that PP flies have a longer larval period but the difference remains not proven (P of overall difference is between 5 and 10% by two separate tests).

Morphological characters. In a morphometric analysis of a number of drosophila strains Sokal (1959) included 14 characters of the two lines at various generations. CP appears to be a generally bigger line of flies. Consistency of the relations found is quite marked.

Ethological observations. The difference between the lines are expressed quite early during larval life. CP and PP eggs of generation 10 were placed in two series of ten vials each at densities of 2 and 20 eggs per vial, respectively. The number of larvae visible on the surface of the medium cylinder was recorded at 24-hour intervals. Figure 6 shows the results of these observations. The general migration away from the surface before hour 72 characteristic of the COSU-2 strain (Sokal et al., 1960) is seen in the selected lines as well. However, the PP line consistently has more larvae on the surface until hour 96 when all larvae are burrowing below the surface. These results were born out by a second study at generation 20. The preference of the PP larvae for the surface was coupled with a generally greater irritability and mobility.

Sokal et al. (1960) were able to show that the first larvae to pupate in a vial tended to do so peripherally, while later pupation tended toward the center of the vial. In the present study (generations 11 and 15) the tendency for

TABLE 3. Resistance Assays of Larvae

Generation	CP LD_{50}	PP LD_{50}	Relative Resistance $\frac{LD_{50}\ PP}{LD_{50}\ CP}$
4	3.33	4.32	1.3
8	2.41	3.75	1.6
10	(4.0)	5.03	1.3
14	3.98	(7.2)	1.8
25	(2.4)	4.78	2.0
31	(4.9)	(5.9)	1.2
32	3.40	(5.3)	1.6
44	4.82	(5.3)	1.1
46	(2.0)	(3.1)	1.6
47	(5.1)	(6.4)	1.3
61	3.18	3.87	1.2

LD_{50}'s are given as p.p.m. DDT in the larval medium. Values in parentheses are eyefit estimates used in cases where the data were too heterogeneous to yield an estimate of the LD_{50} by the maximum likelihood method.

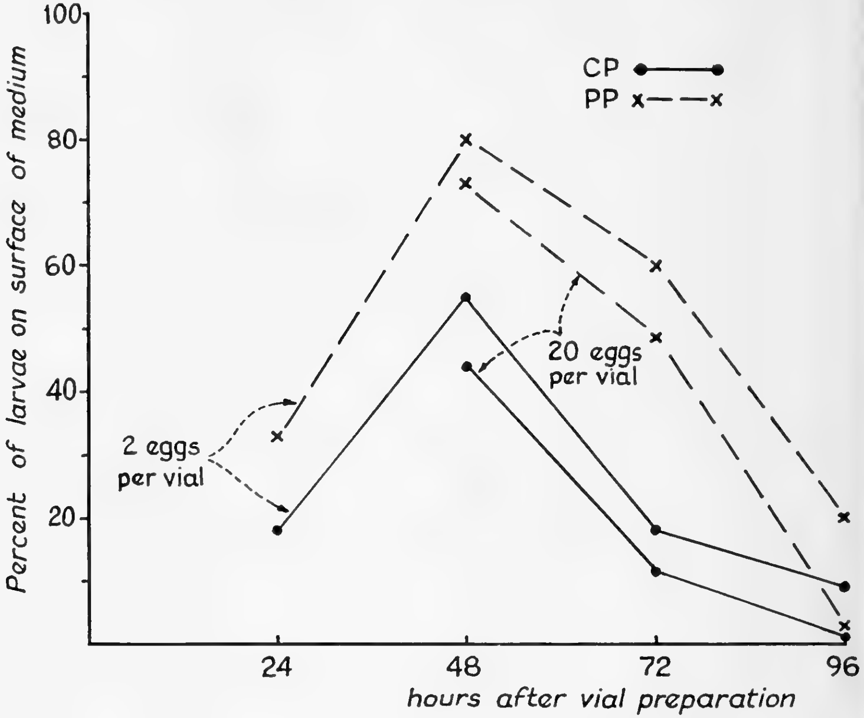

FIGURE 6. Locations of larvae between hatching and pupation. Abscissa: hours after vial preparation; ordinate: per cent of larvae on surface of medium. The graph summarizes experiments at two densities, 2 per vial and 20 per vial. Larvae not on the surface are found in the medium or between wall of vial and medium cylinder.

early larvae to pupate peripherally is present in both lines and the difference between the lines is maintained in both "early" and "late" pupae.

V. RESULTS OF CROSSING EXPERIMENTS

Four crossing experiments were undertaken in generations 16, 29, 45 and 48, respectively. Pupation site assays are based on from 35 to 100 vials (most in excess of 50 per test). The regular assays for the selected lines, run concurrently on the same batch of medium, served as standards of comparison for the various crosses since they were all prepared at the same time. For those populations where all four crosses were assayed, Friedman's two-way analysis of variance yielded $X^2 = 9.3$ and 11.1 ($\chi^2_{.01}$ at 3 d.f. $= 9.21$). We may conclude that the differences among crosses were highly significant. Figure 7 shows the results of the crosses expressed as deviations on a scale where the PP-CP distance equals one, and averaged over the available replicates.

While crosses of the selected lines were generally intermediate between the parental means, several hybrid assays exceeded the phenotypic limits of the

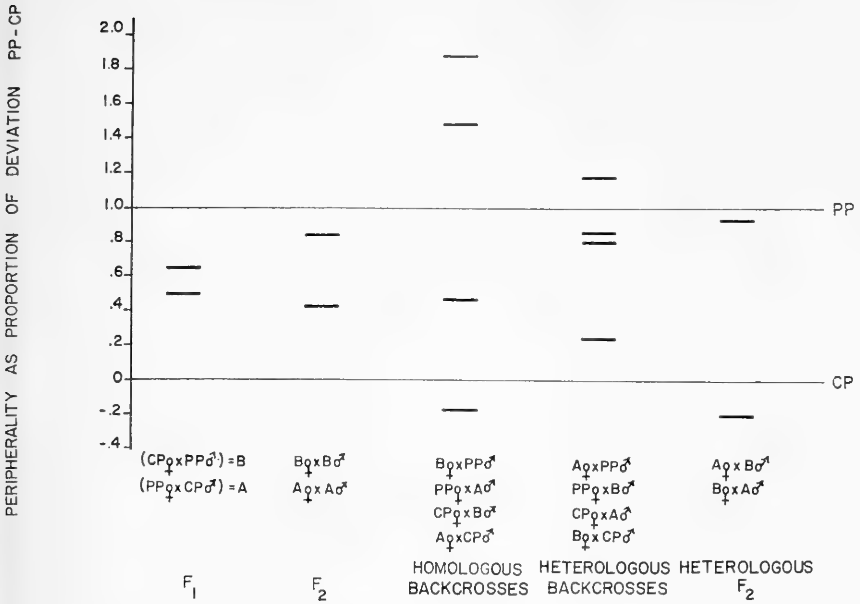

Figure 7. Graphic representation of the results of crosses between lines. The ordinate represents an arbitrary scale expressing the deviation PP-CP as 1.0. This is done because fluctuations from generation to generation made the deviation between these two lines in terms of probit units quite variable. The horizontal lines in the graph represent the average value for a given cross over all its replicates expressed as a proportion of the distance PP-CP. The means of some crosses show higher or lower peripheral pupation than do the PP and CP lines. Labels at the bottom of the graph identify the crosses and are ordered in the same way as the horizontal lines indicating the means. Thus, among the F_2 crosses the upper line represents B♀ × B♂, while the lower horizontal line represents A♀ × A♂.

parents. The position of the hybrid means relative to the midpoint between parental means appears influenced by the general phenohypic level of the given experiment, another example of the environmental fluctuation and gene-environment interaction in this study. The backcrosses resembled the type to which they were backcrossed. Of most interest is an apparent "paternal" influence. Hybrid offspring are more like their fathers than their mothers, and backcrosses to male pure line flies are more effective than backcrosses to females.

VII. DISCUSSION

1. *Pupation Site as a Heritable Trait*

The successful selection for differential pupation sites demonstrates again that few if any phenotypic characters of organisms resist modification under selection. Without careful analysis of any given case it is impossible to ascertain what specific structures or physiological processes of the organisms have been modified to produce results such as are shown in this study.

Humidity content of the medium and of the air surrounding the vials plays an important role in determining pupation site (Sokal et al., 1960), although age of the medium as such (which would be expected to have drying effects) did not produce changes in pupation site. If pupation site were a reaction to the moisture gradient from the drier periphery to the moister center, selection as practiced in this experiment would essentially constitute a shift in the humidity preferendum of the pupating larvae. Since differences in pupation site behavior between the two lines are reflected in earlier behavior of the larvae it is likely, however, that the relations are more complicated.

2. *Limits to Selection*

The asymmetry of the response observed in this experiment could be produced by different rates of response in the two lines as well as by asymmetrical selection limits. Means for the PP line changed two and one-half times as fast as those of the CP line during the period when apparent selection progress was being made. While in part this is due to higher selection intensities in the PP line, these are not sufficient to account for the differences in slope.

Selection limits were apparently reached in both directions. These are roughly symmetrical around the probit value of 5.0, corresponding to 50 per cent peripheral pupation, but since the control strain from which the two lines originated and other control strains tested at different times have a normal pupation site of less than 50 per cent, i.e., a probit peripheral value of less than 5.0, the progress of the lines is asymmetrical. There is some evidence for exhaustion of the genetic variability of the lines in the lowering of the genetic variances after the selection limit had been reached (Table 1). Inter-vial variances in the non-replicated sibships (Table 2) are not similarly lowered, presumably owing to the weak genetic contribution to inter-vial variance. The lowering of genetic variability should be restricted to those loci concerned with pupation site, since the sample sizes employed in this experiment would have precluded more than a very moderate amount of inbreeding.

While there is no reason to assume a physiological limit to the expression of pupation site, some asymmetry is induced by various environmental conditions. For example, Sokal et al. (1960) found that increasing the water content of the medium raised the probit peripheral pupation to approximately 7.0, equivalent to approximately 98 per cent peripheral pupation, while low values of probit peripheral pupation rarely went below 3.5, equivalent to 9 per cent peripheral pupation. Could it be that the peripheral pupation of the earliest pupating larvae (Sokal et al., 1960) is difficult to change while the reactions of the later pupating larvae can be modified by selection?

3. *The Crosses*

A chromosome assay was undertaken to determine the separate contributions of each of the chromosomes and in an attempt to explain the results of the crosses. The results obtained suggested that the paternal effect of the back crosses may be largely due to overdominance of the X-chromosome in the PP line. However, variability among replicates was such that statistical significance of the effects of the assay could not be established. It does not, therefore, seem profitable to pursue the analysis in detail.

4. *Gene Environment Interaction*

The marked fluctuations of pupation site appear due to minor chemical differences in the medium which are largely removed when syrup and molasses were replaced by sucrose as a source of sugar (Schlager, 1960). When the environment increases peripheral pupation, the deviation in pupation site of the CP and PP tends to increase (e.g., generations 24 and 60). Conversely, environmentally caused decreases in peripheral pupation (as in generation 23) result in a diminution of the differences between the selected lines. Schlager (1959) found that the peripherality of the PP line (and of some control strains) responded linearly to increases in water content of the medium, while the CP line showed no such increase. Thus, CP appears to maintain its centrality even under unfavorable environmental conditions. Apparently the PP line did not develop the converse mechanism for protecting itself against centrality in medium containing less water.

Environmentally caused phenotypic fluctuations of this magnitude have interesting implications for evolutionary theory. If natural selection in the field is based on phenotype, then with the effective low heritability the results of selection may be largely due to chance, resulting in a situation resembling drift.

5. *Correlated Characters*

Fertility as measured by survival to pupation decreased for approximately the first 20 generations, concomitant with the effective selection in the study. This is comparable to findings in other *Drosophila* selection studies such as those of Mather and Harrison (1949), Robertson and Reeve (1952) or Prevosti (1956, 1958). An interesting aspect of the present experiment is that in spite of the negative relations between pupation site and density, the peripheral pupating strain did not show lower survival as might have been supposed.

Selection for pupation site differences produced differences in resistance. This is a generally valid observation, having been found in other strains differing in pupation site in this laboratory (unpublished work). Similarly, strains differing in resistance show differences in pupation site (Sokal and Hunter, 1954; and other studies on lines developed in our laboratory and in other laboratories). The nature of this correlation is not clear.

The slight evidence that the PP line has a longer larval period than the CP line would be in agreement with the observations of Hunter (1956) who found strains with longer larval periods to be more resistant than those with shorter periods. However, the CP strain is larger in size than the PP strain. Since the CP larvae buried into the medium considerably earlier than the PP larvae and the latter apparently had a higher metabolic rate, it may be conjectured that the CP larvae are larger since they feed more and earlier and do not use up as much food for energy as do the PP larvae.

VIII. SUMMARY

Drosophila melanogaster reared in shell vials containing cornmeal-molasses-agar medium will pupate at various sites from the center of the medium surface to the wall of the vial above the medium. Ten eggs were placed in each vial. Since mortality of eggs and larvae varied and decreased density raised the percentage of peripheral pupation, pupation site readings were adjusted to a constant density of 10 pupae per vial. The variable measured was transformed to a probit scale. Each generation was based on a large sample size to avoid inbreeding.

Selection for differences in pupation site resulted in a peripherally pupating (PP) and a centrally pupating (CP) line. The PP line responded immediately and strikingly with a plateau reached and maintained by generation 18, while the CP line reacted less sharply but showed selection progress until generation 23. The differences declined during periods of relaxed selection but were quickly re-established when selection was renewed.

Fluctuations in the expression of the character were caused by chemical instability of the larval medium. Gene-environmental interaction made these fluctuations deviate from parallelism.

Fertility and larval survival declined during selection but rose again after the selection limits had been reached. Other characters examined for possible correlation with pupation site were resistance of larvae to DDT in the medium (the PP line is considerably more resistant than the CP line); length of developmental period (the PP possibly have a longer larval period); 14 morphological characters (which showed that on the whole the CP flies were larger than the PP flies); and sex ratio (not significantly different from 50:50 in both strains). The PP larvae took considerably longer to burrow into the medium than the CP larvae.

Crosses between selected lines give intermediate values, but a strong paternal effect was noted in all types of crosses.

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THE UNIVERSITY OF KANSAS
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THE CLASSIFICATION OF THE DIPHAGLOSSINAE AND NORTH AMERICAN SPECIES OF THE GENUS *CAUPOLICANA* (HYMENOPTERA, COLLETIDAE)

By

Charles D. Michener

Vol. XLVI Pages 717-751 December 2, 1966 No. 20

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The Classification of the Diphaglossinae and North American Species of the Genus *Caupolicana* (Hymenoptera, Colletidae)[1]

By

Charles D. Michener

ABSTRACT

This paper describes and provides keys for the tribes of the apoid subfamily Diphaglossinae. One of the tribes, the Caupolicanini, is treated in greater detail, its genera being characterized. The subgenera of one of the genera, *Caupolicana,* are characterized, as are the North and Central American species of the genera *Caupolicana* and *Crawfordapis.* Two new subgenera, *Caupolicanoides* and *Alayoapis,* and one new species, *Caupolicana ocellata,* are described. *Crawfordapis* is given generic rank while *Zikanapis* is reduced to a subgenus of *Caupolicana.*

Most species of the Caupolicanini are active primarily in the early morning and sometimes late evening hours. Some have enlarged ocelli, presumably related to such a time of flight.

This paper consists of (A) brief descriptions of the tribes of the colletid subfamily Diphaglossinae, (B) descriptions of the genera of the tribe Caupolicanini, (C) a subgeneric classification of the genus *Caupolicana,* and (D) an account of the North American (including Central American and Antillian) species of that genus and *Crawfordapis.*

A. THE TRIBES OF DIPHAGLOSSINAE

The Diphaglossinae is a group of large to very large colletid bees limited to the Western Hemisphere. It contains the Diphaglossinae plus the Caupolicanini of Michener (1944); Moure (1945) has united these groups, a viewpoint in which I have agreed (e.g., Michener, 1954). Moure (1945, 1953) divides the subfamily into tribes which may be separated as follows:

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[1] Contribution number 1321 from the Department of Entomology, The University of Kansas, Lawrence, Kansas.

KEY TO THE TRIBES OF DIPHAGLOSSINAE

1. Pre-episternal groove complete; first flagellar segment much longer than others, petiolate, nearly as long as to longer than scape. .... *Caupolicanini*
— Pre-episternal groove absent below scrobal groove; first flagellar segment not greatly longer than others, not petiolate, much shorter than scape. 2
2. Notauli represented by deep grooves in anterior part of mesoscutum; malar space over one third as long as eye. .... Diphaglossini
— Notauli weak or absent; malar space short or absent. 3
3. Arolia present. .... Mydrosomini
— Arolia absent. .... Ptiloglossidiini

TRIBE CAUPOLICANINI

1. Lower part of face short, malar space short or absent. 2. First flagellar segment much longer than other segments of flagellum, nearly as long as to longer than scape, petiolate. 3. Notauli strong. 4. Pre-episternal groove complete. 5. Jugal lobe of hind wing over three fourths as long as vannal lobe and extending beyond cu-v. 6. Second submarginal cell much shorter than 1 or 3; first recurrent vein approximately interstitial with first transverse cubital. 7. Second recurrent vein more or less continued in same direction as Cu_1. 8. Distal parts of wings hairless, strongly papillate, but papillae often ending in slender hairlike points. 9. Arolia present.

This is the most distinctive tribe of the Diphaglossinae, as indicated by characters 2, 4, 5, 6, 7, and 8 above.

Genera included in the Caupolicanini are *Caupolicana, Ptiloglossa,* and *Crawfordapis*. They range from North Carolina, Kansas, and Arizona to Argentina and Chile.

TRIBE DIPHAGLOSSINI

1. Lower part of face elongate, malar space over one third as long as eye. 2. First flagellar segment not greatly longer than others, not as long as scape, not petiolate. 3. Notauli strong. 4. Pre-episternal groove absent below scrobal groove. 5. Jugal lobe of hind wing less than half as long as vannal lobe and not reaching level of cu-v. 6. Submarginal cells decreasing in length from 1 to 3, rarely 2 and 3 equal; first recurrent vein entering second submarginal cell more or less medially. 7. Second recurrent vein at a distinct angle to Cu_1. 8. Distal parts of wings with hairs, not strongly papillate. 9. Arolia present.

This tribe is related to the following tribes as shown by characters 2, 4, 5, 6, 7, and 8; however, it also shows some relations to the Caupolicanini, indicated especially by its similarly large and robust form and by character 3.

Genera included in the Diphaglossini are *Diphaglossa, Cadeguala,* and *Policana,* all of which are Chilean.

TRIBE MYDROSOMINI

1. Lower part of face short, malar space short or absent. 2. First flagellar segment about as long as apical one and less than half as long as scape (female) or much shorter than any others and under one fourth as long as scape (male), not petiolate. 3. Notauli absent. 4. Pre-episternal groove absent below scrobal groove. 5. Jugal lobe of hind wing about half as long as vannal lobe and not reaching level of cu-v. 6. Submarginal cells decreasing in length from 1 to 3 or 2 and 3 about equal; first recurrent vein entering second submarginal cell at base or in basal third. 7. Second recurrent vein at a distinct angle to Cu_1. 8. Distal parts of wing with hairs, not strongly papillate. 9. Arolia present.

Genera included in the Mydrosomini (Moure's Dissoglottini) are *Mydrosoma* (= *Apista* = *Egapista* = *Dissoglotta*) and *Bicornelia*. They occur in tropical America from Mexico to Brazil.

TRIBE PTILOGLOSSIDIINI

I have not seen specimens of this tribe; the following information, organized to parallel that for the other tribes, is from Moure (1953), who gave an excellent account of the group.

1. Lower part of face short, malar space short. 2. First flagellar segment considerably shorter than scape, shorter than (male) or equal to (female) flagellar segments 2 + 3, not petiolate. 3. Notauli practically absent. 4. Pre-episternal groove absent below scrobal groove. 5. Jugal lobe of hind wing over half as long as vannal lobe and nearly reaching level of cu-v. 6. Second submarginal cell shorter than 1 or 3; first recurrent vein entering second submarginal cell almost medially. 8. Distal parts of wings with hairs, not strongly papillate. 9. Arolia absent.

The only genus of Ptiloglossidiini is *Ptiloglossidia* from Argentina. I suspect that it should be included in the Mydrosomini but not having seen specimens, I retain the Ptiloglossidiini for the present. Character 9 is the only strikingly distinctive feature.

B. THE GENERA OF CAUPOLICANINI

The Caupolicanini is divisible into two large genera and one small one, *Crawfordapis,* as shown below.

KEY TO THE GENERA OF CAUPOLICANINI

. Outer hind tibial spur of male immovably fused to tibia; hind basitarsus of female less than twice as long as broad, second hind tarsal segment broader than long; metasomal terga usually weakly metallic bluish or greenish. .... *Ptiloglossa*

— Outer hind tibial spur of male articulated at base; hind basitarsus of female more than twice as long as broad, second hind tarsal segment longer than broad; metasomal terga usually nonmetallic. 2

2. Seventh sternum of male with no paired apical lobes; base of marginal cell prolonged as narrow sinus to apex of stigma. .... *Crawfordapis*

— Seventh sternum of male with paired apical lobes; base of marginal cell not prolonged as narrow sinus. .... *Caupolicana*

Genus Ptiloglossa Smith, 1853

Ptiloglossa (including the subgenus *Ptiloglossodes* Moure, 1945) can be distinguished from the rest by the following combination of characters:

1. Clypeus clearly elevated above level of adjacent parts of face, extending high on face so that in female clypeoantennal distance is usually distinctly less than diameter of antennal socket. 2. Stigma often only half as long as prestigma, sometimes (*Ptiloglossodes*) two thirds as long as prestigma; marginal cell, except in *Ptiloglossodes*, prolonged basally as narrow sinus to apex of stigma. 3. Hind basitarsus of female less than twice as long as broad. Second and third hind tarsal segments of female broadly expanded above, each, or at least second, broader than long. 4. Outer hind tibial spur of male immovably fixed to tibia, its broad base gradually expanding onto the tibia so that sharp line between spur and tibia does not exist (outer spur entirely absent in male *Ptiloglossodes*). 5. Abdominal terga with metallic bluish or greenish tints (except in one Mexican species, *P. wilmattae* Cockerell). 6. Lateral extremities of fourth and fifth terga of male extending ventrally, usually more than other terga, broadly overlapped by sterna of preceding segments, and densely covered by short erect hair of uniform length, these areas under low magnification appearing dull and scarcely punctate in contrast to adjacent areas. 7. Sixth sternum of male with posterior margin thick, thickest medially where there is usually a weak mid-apical angle, a sulcus at each side in margin, facing posteriorly; carina which delimits lower margin of sulcus projecting ventrally at each side as thorn-like spine (except in *Ptiloglossodes*). 8. Seventh sternum of male with two pairs of apical lobes, both large, broad distally, narrowed basally, the upper pair long pedunculate with a process arising near middle of peduncle (for ventral views, see Michener, 1954). 9. Eighth sternum of male with apical process translucent light brown, strongly curved down apically, with long hairs on dorsal surface. 10. Gonoforceps ending bluntly.

Ptiloglossa is a primarily tropical genus, although a few species reach southern Texas and Arizona in the north and Argentina in the south. The genus does not occur in Chile.

Genus Crawfordapis Moure, 1964

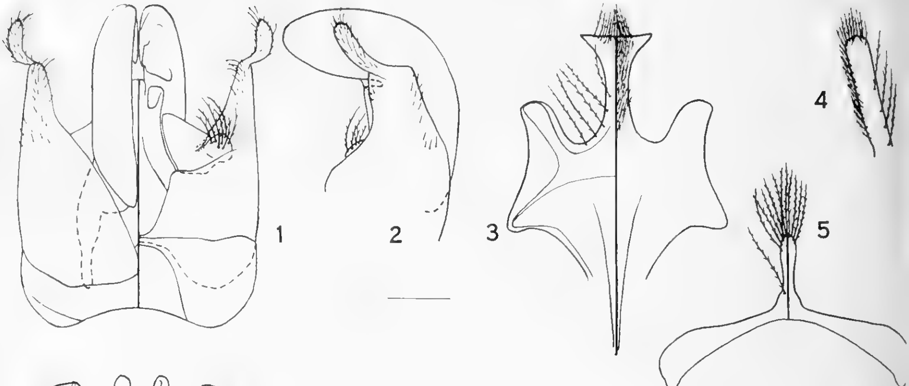
The name *Crawfordapis* was originally proposed as a subgenus of *Zikanapis* but the single Middle American species seems so distinctive that generic rank is warranted for it, even though *Zikanapis* is here considered a subgenus of *Caupolicana, Crawfordapis* is especially distinctive in characters 8 and 10 described below. Characters 1 and 2 are *Ptiloglossa*-like as is part of 3 (expanded second and third tarsal segments of female), and in general, 5. Characters 4, 6, 7, and 9 are more or less *Caupolicana*-like. As shown in the illustrations, there are various other distinctive features of the genitalia and sterna but the external features are very much like those of *Caupolicana.*

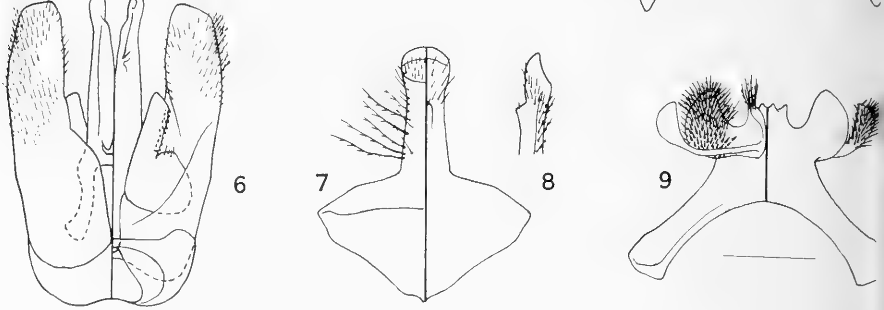
1. Clypeus clearly elevated above level of adjacent parts of face, as in *Ptiloglossa* but more strikingly so. Clypeus extending rather high on face, nearly as in *Ptiloglossa.* 2. Stigma less than half as long as prestigma; marginal cell prolonged basally as a narrow sinus to apex of stigma. 3. Hind basitarsus of female more than twice as long as broad. Second and third hind tarsal segments of female considerably expanded above but longer than broad. 4. Outer hind tibial spur of male normal, articulated at base like inner spur. 5. Abdomen without or with exceedingly weak bluish or greenish tints in male, with distinct blue tints in female. 6. Lateral extremities of terga of male without areas of short, dense, erect hair. 7. Sixth tergum of male with posterior margin not thickened or sulcate, medially produced and slightly bifid as in *Zikanapis.* 8. Seventh sternum of male without paired lobes but with median, apical, slender hairy process. 9. Eighth sternum of male with apical process rather heavily pigmented, not downcurved, hairs of distal half shorter than width of process. 10. Gonoforceps ending in slender styluslike structures, therefore perhaps with distinguishable gonocoxites and gonostyli (Figs. 1-5).

Genus Caupolicana Spinola, 1851

This genus is here interpreted in a broad sense to include the species placed in recent years in *Zikanapis* and *Willinkapis. Zikanapis* in particular is, however, a distinctive group which may well merit generic recognition, as is *Caupolicanoides.* The following characters separate *Caupolicana* from *Ptiloglossa.*

1. Clypeus less elevated above adjacent parts of face than in *Ptiloglossa,* profile of supraclypeal area often a continuation of that of clypeus. Clypeus not extending so high on face as in *Ptiloglossa,* so that in female clypeoantennal distance is at least as great as diameter of antennal socket. 2. Stigma slightly more than half as long as prestigma to as long as prestigma; base of marginal cell not prolonged as a narrow sinus to apex of stigma. 3. Hind basitarsus of female more than twice as long as broad. Second and third hind tarsal segments of female but little expanded above, longer than broad. 4. Outer hind tibial spur of male normal, articulated at base like inner spur. 5. Abdomen without bluish or greenish tints (except in *Willinkapis*). 6. Lateral extremities of terga of male without areas of short, dense, erect hair of uniform length





Figs. 1-5, *Crawfordapis luctuosa,* male (specimen from the type series of *crawfordi* from Costa Rica). 1, genitalia; 2, lateral view of apical part of genitalia; 3, eight metasomal sternum; 4, lateral view of apical process of eighth metasomal sternum; 5, seventh metasomal sternum.

Figs. 6-9, *Caupolicana (Caupolicanoides) pubescens,* male (specimen from Concepción, Chile, labeled as "typus" of *herbsti* by Friese, USNM). 6, genitalia; 7, eighth metasomal sternum; 8, lateral view of apical process of eighth metasomal sternum; 9, seventh metasomal sternum.

The genitalia and sterna are illustrated with the dorsal views at the left, ventral views at the right. The lateral views of genitalia and of the process of the eighth sternum are with the dorsal side at the right. The scale lines for each species represent 1 mm.

except in *Zikanapis,* where such areas are more extensive than in *Ptiloglossa.* 7. Sixth sternum of male with posterior margin not thickened or sulcate, if somewhat thickened, not thickest in middle; no thornlike spines. 8. Seventh sternum of male with upper pair of apical lobes straplike or sometimes broadened distally, without a median process on the peduncle except in *Alayoapis* (of course peduncle not recognizable when lobes are straplike, but no process in any event). Lower pair of apical lobes not or scarcely narrowed basally (except when broadly bifid as in *C. yarrowi*), often reduced so as to be almost unrecognizable or absent. 9. Eighth sternum of male with apical process heavily pigmented, not strongly curved down apically, hairs of distal half of process shorter than width of process. 10. Gonoforceps ending bluntly.

Caupolicana is a genus best represented in warm temperate and subtropical regions of both North and South America but poorly represented or absent in the intervening tropical zone. The majority of the described species are from Chile.

C. SUBGENERA OF CAUPOLICANA

The genus *Caupolicana* can be divided into several groups, as is indicated below.

KEY TO THE SUBGENERA OF CAUPOLICANA

1. Stigma slightly broader subapically than basally; marginal cell large, little over four times as long as wide (Fig. 10). .... *Caupolicanoides*

— Stigma parallel sided or tapering apically; marginal cell slender, five to six times as long as wide (Fig. 12). 2

2. Metasomal terga rather weakly metallic bluish; ventral apical lobe of seventh sternum of male probably represented by broad, apically rounded, laterally directed, heavily sclerotized lateral apical projection which is hairless except mesally. .... *Willinkapis*

— Metasoma nonmetallic; ventral apical lobe of seventh sternum not heavily sclerotized, not hairless, variable in size and shape but not as above, sometimes absent. 3

3. Sixth sternum of male with apex rounded, rarely with broad median, V-shaped notch but no produced region; lateral extremities of terga 2-4 without specialized regions; clypeus of male not over 0.76 times as long as wide. 4

— Sixth sternum of male with weak median apical projection which has a broad median, V-shaped notch; lateral extremities of terga 2-4 of male with large areas of dense short hair of uniform length; clypeus of male about 0.85 times as long as wide. .... *Zikanapis*

4. Inner orbits of male strongly converging above in male, ocellocular distance one fourth of an ocellar diameter or less. .... *Alayoapis*

— Inner orbits not or weakly converging above in male, ocellocular distance over one third of an ocellar diameter and usually nearly equal to an ocellar diameter. .... *Caupolicana s. str.*

Subgenus Caupolicana Spinola

(Figs. 12-29)

Caupolicana Spinola, 1851, *in* Gay, Historia fisica y politica de Chile, Zool., 6:212.
Type species: *Caupolicana gayi* Spinola, 1851, designated by Sandhouse, Proc. U.S. Nat. Mus., 92:534.
Megacilissa Smith, 1853, Catalogue of the hymenopterous insects in the collection of the British Museum, 1:123.
Type species: *Megacilissa superba* Smith, 1853, = *Caupolicana fulvicollis* Spinola, 1851 (monobasic).

1. Inner orbits slightly converging above (subparallel in *ocellata*, rather strongly converging in *mystica*); ocellocular distance usually slightly less than

ocellar diameter (slightly more than in *dimidiata,* about two thirds of an ocellar diameter in *mystica* because of unusually convergent eyes, less than half an ocellar diameter in *ocellata* because of enormous ocelli). 2. Clypeus of male 0.70 to 0.76 times as long as wide. 3. Scape of male usually less than three times as long as wide, about three times as long as wide in *adusta, quadrifasciata,* and *hirsuta.* 4. First basitarsus of male straight to slightly arcuate, as long as or slightly shorter than remaining tarsal segments together. 5. Hind tibia of male straight to arcuate. 6. Basitibial plates of male indicated only on posterior margin, or complete in *adusta, quadrifasciata,* and *hirsuta.* 7. Hind basitarsus of male four to five times as long as wide. 8. All femora of male with abundant long hair except middle and hind femora of *electa, ocellata,* and *yarrowi* which have only sparser, shorter hair; base of middle femur of male with area of short, often rufescent hair (this area absent in *ocellata,* small in *yarrowi,* but unusually large in *electa*). Front femur variable in thickness. 9. Stigma parallel sided or slightly narrower apically than basally, discal area narrower than or as wide as marginal thickenings; first submarginal cell shorter than to longer than second and third together (first on posterior side shorter than or equal to second and third together); marginal cell narrow, five to six times as long as wide; cell 1st M 2.72 to 3.61 times as long as broad; first recurrent vein shorter than or equal to posterior margins of second and third submarginal cells together, the latter shorter than or nearly equal to first abscissa of vein Cu_1 (i.e., posterior margin of cell 2nd M). 10. Pubescence, at least that of metasoma, partially black; terga with apical bands of white hair, sometimes much reduced *(albiventris, adusta, electa)* or absent *(dimidiata,* female of *funebris)*; sterna two to five of male usually with unusually dense long hair (not or scarcely true of North American species). 11. Metasoma nonmetallic. 12. Terga of male without lateral areas of short erect hair. 13. Sixth sternum of male with long hairs or with discal area of short hairs; posterior margin usually rounded, sometimes *(ocellata, hirsuta)* notched medially suggesting *Zikanapis* and *Willinkapis;* some species with a pair of preapical lobes (*gayi, dimidiata, vestita, piurensis; fulvicollis* has weak suggestions of the same lobes); surface hairs reaching posterior margin of sternum. 14. Dorsal apical process of seventh sternum moderately robust (very slender in *yarrowi*), not or only weakly spatulate and usually with only sparse, short hairs (but with long hairs in *quadrifasciata* and *hirsuta*); ventral apical process distinctly projecting, hairy, sometimes quite large (largest in *quadrifasciata* and *hirsuta*).

The subgenus *Caupolicana* proper is the largest unit of the genus. The diversity among the species results in forms closely approaching *Caupolicanoides* and is discussed in connection with that subgenus.

Included species that I have studied are: *adusta* Friese, 1899; *albiventris* Friese, 1904=*malvacearum* Cockerell, 1926; *caudens* Pérez, 1911; *dimidiata*

Herbst, 1917; *electa* (Cresson, 1878); *fulvicollis* Spinola, 1851; *funebris* Smith, 1879=*cana* Herbst, 1917 (male not seen); *gayi* Spinola, 1851; *hirsuta* Spinola, 1851; *lugubris* Smith, 1879; *mendocina* Joergensen, 1909 (male not seen); *mystica* Schrottky, 1902; *ocellata* new species; *piurensis* Cockerell, 1911; *quadrifasciata* Friese, 1898; *ruficollis* Friese, 1906; *vestita* (Smith, 1879); *weyrauchi* Moure, 1953; *yarrowi* (Cresson, 1875).

Species of this subgenus are numerous in temperate South America, especially Chile; in tropical South America they are probably restricted to arid regions and mountains; none are known from Central America but three species occur in the southern United States (north to Kansas) and northern Mexico.

Caupolicanoides new subgenus

(Figs. 6-9, 10, 48)

Type species: *Caupolicana pubescens* Smith, 1879 (=*C. herbsti* Friese, 1904).

The description is based on a male of this species, marked as a "typus" of *herbsti,* in the United States National Museum.

1. Inner orbits moderately converging above in male, ocellocular distance equal to ocellar diameter. 2. Clypeus of male about 0.57 times as long as wide. 3. Scape of male over three times as long as wide. 4. Front basitarsus of male straight, distinctly shorter than remaining tarsal segments. 5. Hind tibia of male straight. 6. Basitibial plate of male complete. 7. Hind basitarsus of male less than four times as long as wide. 8. All femora of male with abundant long hair, base of middle femur of male with area of short erect hair ventrally. Front femur over three times as long as broad. 9. Stigma slightly broader subapically than basally, discal area distinctly broader than marginal thickenings; first submarginal cell distinctly shorter than second and third together; marginal cell broad (as well as unusually long), little over four times as long as wide; cell 1st M about 2.6 times as long as wide; first recurrent vein shorter than posterior margins of second and third submarginal cells which are subequal to first abscissa of Cu_1 (i.e., posterior margin of cell 2nd M). 10. Pubescence ochraceous, on metasomal terga erect and not forming bands, especially long on sterna of male. 11. Metasoma nonmetallic. 12. Terga of male without lateral areas of short erect hair. 13. Sixth sternum of male with long hairs, posterior margin slightly produced medially, the apex of the projection gently concave; surface hairy to apex. 14. Dorsal apical process of seventh sternum of male spatulate, ventral apical process large, broad, hairy above, slightly spatulate.

Caupolicanoides is known to me only from the type species which is from Chile.

The striking features of this subgenus are the large marginal cell and large stigma, presumably primitive features by which *C. pubescens* differs from all other Caupolicanini. Characters 3 and 10 above are the only other features by which *Caupolicanoides* differs from all species of *Caupolicana s. str.*

However, in various other features *Caupolicanoides* falls at one extreme of the variation among the species of *Caupolicana s. str.* Character 6 is especially striking since basitibial plates are often of importance in classification of bees; *C. quadrifasciata* and *hirsuta* have such plates in the male, just as does *Caupolicanoides.* In other species known to me the plates are delimited only posteriorly. In characters 2, 4, 5, and 7 also, as well as in those parts of 9 not dealing with the stigma and marginal cell, *Caupolicanoides* is at one extreme of the variation within *Caupolicana s. str.* or just beyond that extreme; for example in character 4, the basitarsus is slightly shorter than in those species of *Caupolicana s. str.* in which it is shortest. As to character 14, the apical lobes of the seventh sternum are slightly broader, more spatulate, and more hairy than in *Caupolicana* proper, but are only a little different from those of *quadrifasciata* and *hirsuta* which are in turn closely approached by *ruficollis.* In these three species and also in *albiventris* the close connection between the lower apical lobes of this sternum and the bases of the upper ones is obvious, while in other species the lower lobes seem principally connected to the lateral margins of the sternum. The wing of *hirsuta* is illustrated (Fig. 12) to show how unlike *Caupolicanoides* it is in spite of certain other resemblances of that species to that subgenus.

Subgenus Willinkapis Moure

(Figs. 11, 12)

Willinkapis Moure, 1953, Dusenia, 4:66; Moure, 1964, Studia Ent., (n.s.) 7:453.
Type species: *Ptiloglossa chalybea* Friese, 1906, by original designation.

1. Inner orbits moderately converging above in male, ocellocular distance slightly less than ocellar diameter. 2. Clypeus of male about 0.65 times as long as wide. 3. Scape of male less than three times as long as wide. 4. First basi-

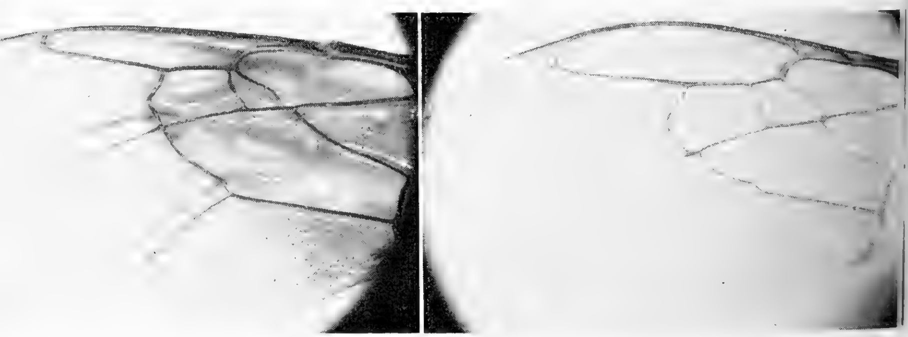


FIG. 10. Forewings of males. Left, *Crawfordapis luctuosa* (specimen from type series of *crawfordi* from Costa Rica). Right, *Caupolicana (Caupolicanoides) pubescens* (specimen from Concepción, Chile, labeled as "typus" of *herbsti* by Friese, USNM).

tarsus of male slightly arcuate, as long as remaining tarsal segments. 5. Hind tibia of male slightly arcuate. 6. Basitibial plate of male indicated only on posterior margin. 7. Hind basitarsus of male less than four times as long as wide. 8. All femora of male with abundant long hair, less long on middle femur than on others; base of middle femur of male with area of short, erect hair ventrally. Front femur over three times as long as broad. 9. Stigma narrower apically than basally, discal area narrower than marginal thickenings; first submarginal cell equal to second and third together (first on posterior margin shorter than second and third); marginal cell narrow, nearly six times as long as wide; cell 1st M about three times as long as wide; first recurrent vein about equal in length to posterior margins of second and third submarginal cells together which are shorter than first abscissa of Cu_1 (i.e., posterior margin of cell 2nd M). 10. Pubescence, at least that of metasoma, largely black, terga with narrow marginal bands of dense hair which is sometimes white; sterna two to five of male with very long hair. 11. Metasoma strongly metallic blue (more metallic than in most *Ptiloglossa*). 12. Terga of male without lateral areas of short erect hair. 13. Sixth sternum of male with hairs short and sparse, posterior margin medially produced, the projection emarginate much as in *Zikanapis* and *Crawfordapis* but projection narrower and shorter; surface with hairs nearly to apex. 14. Dorsal apical process of seventh sternum of male very slender, not at all spatulate; ventral apical process probably represented by a broad, apically rounded, laterally directed, heavily sclerotized, lateral apical projection which is hairless except mesally.

In characters 11 and 14, *Willinkapis* is unique among the subdivisions of *Caupolicana*. Its other features are all more or less duplicated among one or another of the subgenera, although the combination is not found elsewhere.

Willinkapis, which has hitherto been accorded generic rank or placed as a subgenus of *Zikanapis,* is known to me from two species. One is *C. (Willinkapis) chalybea* (Friese) known from the cordilleran region of Argentina (see Moure, 1953). It ranges northward into Peru as shown by a female in the United States National Museum from Huanta, Andes, Peru, 2400 meters, March 24, 1941 (F. W. Woytkowski). From the same locality is a female of another, slightly smaller, species with the pubescence nearly all black.

Subgenus Zikanapis Moure

(Figs. 12, 30-34, 47)

Zikanapis Moure, 1945, Arq. Mus. Paranaense, 4:147; Moure, 1964, Studia Ent., (n.s.) 7:421.
Type species: *Ptiloglossa zikani* Friese, 1925, by original designation.
Foersterapis Moure, 1964, Studia Ent., 7:441 (new synonym).
Type species: *Zikanapis foersteri* Moure and Seabra, 1962, by original designation.

1. Inner orbits moderately to strongly converging above in male, ocellocular distance one third to one half an ocellar diameter. 2. Clypeus of male about 0.85 times as long as wide. 3. Scape of male over three to nearly four times as

long as wide. 4. First basitarsus of male not or scarcely arcuate, distinctly shorter than remaining tarsal segments. 5. Hind tibia of male slightly arcuate. 6. Basitibial plate of male indicated only on posterior margin. 7. Hind basitarsus of male four or five times as long as broad. 8. Front femur of male with abundant long hair beneath, other femora with shorter hair; middle femur of male without area of short erect hair. Front femur three or more times as long as broad. 9. As in *Willinkapis*. 10. Pubescence largely ochraceous or in some South American forms extensively dark, forming apical white bands on metasomal terga of some species. 11. Metasoma nonmetallic. 12. Lateral extremities of terga 2 to 4 and sometimes 5 and 6 of male with large areas densely covered by short erect hair of uniform length, these areas under low magnification appearing dull and scarcely punctate in contrast to adjacent areas. 13. Sixth sternum of male with hairs short, posterior margin medially produced and rather broadly bilobed; surface with hairs nearly to apex. 14. Dorsal apical process of seventh sternum of male spatulate, ventral apical process small and projecting but little from sternal margin.

Characters 1, 2, and 12 are suggestive of *Ptiloglossa*, and Moure (1945) quite properly compared *Zikanapis* with *Ptiloglossa* as well as with *Caupolicana*. However, the majority of the characters indicate placement in *Caupolicana*. One of the characters on which Moure placed special emphasis, the convergence of the eyes in *Zikanapis*, is weak because they are only moderately convergent in *C. (Z.) elegans* and in some of the other forms which he included in *Zikanapis* in 1964.

Zikanapis, which has hitherto been accorded generic rank, contains several species and seems most common in the northern and southern subtropical regions, much less so in the intervening tropics although *modesta* is from Colombia. Included species are: *clypeata* (Smith, 1879); *elegans* Timberlake, 1965; *foersteri* (Moure and Seabra, 1962); *funeraria* (Moure, 1964); *megalopta* (Moure, 1948); *modesta* (Moure, 1964); *seabrai* (Moure, 1953); *tucumana* (Moure, 1945); and *zikani* (Friese, 1925).

The two species, *foersteri* and *tucumana*, which Moure (1964) placed in a subgenus, *Foersterapis*, of *Zikanapis* seem to me too similar to other *Zikanapis* to warrant separation although they do constitute a distinctive group. At the present stage of the development of systematics, there is no objective basis for such decisions and I can only say that I see no obvious advantage in separating *Foersterapis* as a named group.

Alayoapis new subgenus

(Figs. 12, 37-42, 48)

Type species: *Megacilissa nigrescens* Cresson, 1869.

1. Inner orbits strongly converging above in male, ocellocular distance less than one fourth of an ocellar diameter. Posterior margins of posterior ocelli of

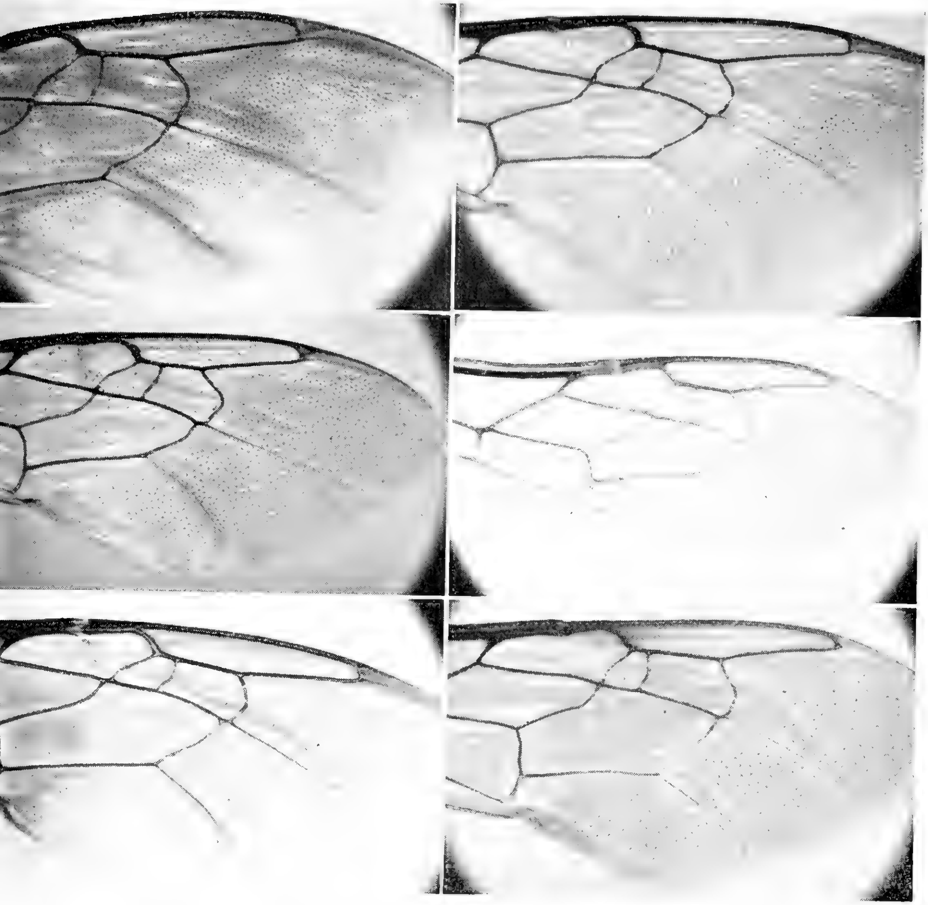


FIG. 12. Forewings. Above left, *Caupolicana (Willinkapis) chalybaea.* Above right, *C. (Caupolicana) yarrowi.* Center left, *C. (C.) hirsuta.* Center right, *C. (C.) ocellata.* Below left, *C. (Alayoapis) nigrescens.* Below right, *C. (Zikanapis) clypeata.*

male well in front of narrowest part of vertex (unlike other subgenera but like *Crawfordapis*). 2. Clypeus of male about or nearly 0.7 times as long as wide. 3. Scape of male about three times as long as wide. 4. First basitarsus of male slightly arcuate, slightly longer than remaining tarsal segments. 5. Hind tibia of male slightly arcuate. 6. As in *Willinkapis* or no indication of basitibial plate in *notabilis*. 7. Hind basitarsus of male nearly five to over five times as long as wide. 8. Hair of femora of male short, not longer than femoral diameter, that of middle femur much shorter except in *notabilis;* base of middle femur of male without area of short erect hair ventrally. Anterior femora thick, not over three times as long as wide. 9. As in *Willinkapis,* but first submarginal cell longer than second and third together (first on posterior margin equal to second and third). 10. Body with considerable dark pubescence, that of metasoma short; terga in some species with apical white fasciae; sterna 2-4 of male with rather long hair. 11. Metasoma nonmetallic. 12. As in *Willinkapis*. 13. Sixth sternum of male with median nearly hairless area or in *notabilis* with short erect hairs; hairs of margin rather dense; posterior margin rounded, with hairs nearly to apex but margin proper a thin hairless translucent flange (doubtful in *notabilis*). 14. Dorsal apical process of seventh sternum of male slightly spatulate with median lobe suggestive of *Ptiloglossa* but shorter; ventral apical process absent.

The combination of characters 1 and 13 (rounded margin of sixth sternum) is not found elsewhere in the genus.

Alayoapis, named after Dr. Pastor Alayo D. of La Habana, Cuba, who has collected more specimens of the subgenus than anyone else and has provided me with useful information about the subgenus. It is known only from the islands of Cuba and Hispaniola.

D. NORTH AMERICAN SPECIES OF THE GENERA *CRAWFORDAPIS* AND *CAUPOLICANA*

This section concerns the species found not only in North America proper but also in Central America and in the Antilles. Probably all of the species are active principally in early morning and late evening, some of them when it seems completely dark to human observers. Nests are made in deep burrows, often and perhaps always in sandy soil. Known details of behavioral matters are indicated under each species.

In the synonymies only major references are given, not mere records or repetitive generic changes.

KEY TO THE SPECIES

1. Metasomal integument red. .... *Caupolicana (Alayoapis) notabilis*
— Metasomal integument dark brown or black. 2
2. Legs largely light red or yellowish. 3
— Legs or at least hind leg reddish brown to black, usually more or less the same color as the body. 5
3. Antenna yellowish red; ocellar diameter nearly twice maximum width of scape. .... *Caupolicana (Caupolicana) ocellata*
— Antenna largely dark brown or black; ocellar diameter little if any greater than maximum width of scape. 4
4. Middle femur of male contorted; head and thorax with some black or dusky and dark tipped hairs. .... *Caupolicana (Alayoapis) subaurata*
— Middle femur of male not contorted; head and thorax with hair entirely ochraceous. .... *Caupolicana (Caupolicana) electa*
5. Male with lateral extremities of terga 2-4 with large areas of short, dense

hair of uniform length, producing a distinctive dull appearance; clypeus of female rather flat with uniform punctation and short hairs over entire surface. 6

— Male with lateral extremities of terga without such specialized areas; clypeus of female more convex with much variation in density of punctation and of hairs. 7

6. Male without metasomal bands; interocellar distance of female slightly more than maximum ocellar diameter. *Caupolicana (Zikanapis) clypeata*

— Male with bands of white hair at least laterally on apices of terga 2-5; interocellar distance of female over twice maximum ocellar diameter. .... *Caupolicana (Zikanapis) elegans*

7. Metasomal terga without bands of pale hair. .... *Crawfordapis luctuosa*

— Metasomal terga with apical bands of white hair. 8

8. Hairs of thorax ochraceous, many of them dark tipped in female. .... *Caupolicana (Caupolicana) yarrowi*

— Hairs of thorax with large areas of black to dark gray. .... *Caupolicana (Alayoapis) nigrescens*

D1. SPECIES OF CRAWFORDAPIS

There is only one recognized species of this genus.

Crawfordapis luctuosa (Smith)

(Figs. 1-5, 10, 11)

Megacilissa luctuosa Smith, 1861, Jour. Entom., 1:150.
Ptiloglossa crawfordi Cockerell, 1919, Proc. U.S. Nat. Mus., 55:178.
Zikanapis (Crawfordapis) luctuosa; Moure, 1964, Studia Entom., (n.s.) 7:449.

Crawfordapis luctuosa is a dusky haired species with light orange hairs at the apex and on the under surface of the metasoma. The femoral and propodeal scopa of the female is largely cream colored. The species was described from Mexico, without other data. The type is in the British Museum (Natural History). The name *crawfordi* was based on material from "Ujurass de Terraba," Costa Rica and the type is in the U.S. National Museum. A series of males in the British Museum (Natural History) is from Cerro Zunil, 4000-5000 feet altitude (Champion). According to Selander and Vaurie (1962) this locality is Volcán Zunil, Quezaltenago, Guatemala.

These Guatemalan males differ from Costa Rican material in being slightly larger with light hair mixed with the black all over the face below the antennae, with a band of light hair across the front of the scutum, with light hair on the posterior surface of the propodeum, the anterior surface of the first metasomal tergum, and the sides of the metasoma anteriorly, and with the whole venter of the metasoma covered with orange hair. Possibly they represent a distinct species or geographical variant. My drawings of genitalia and sterna are based on a specimen in the type series of *crawfordi*

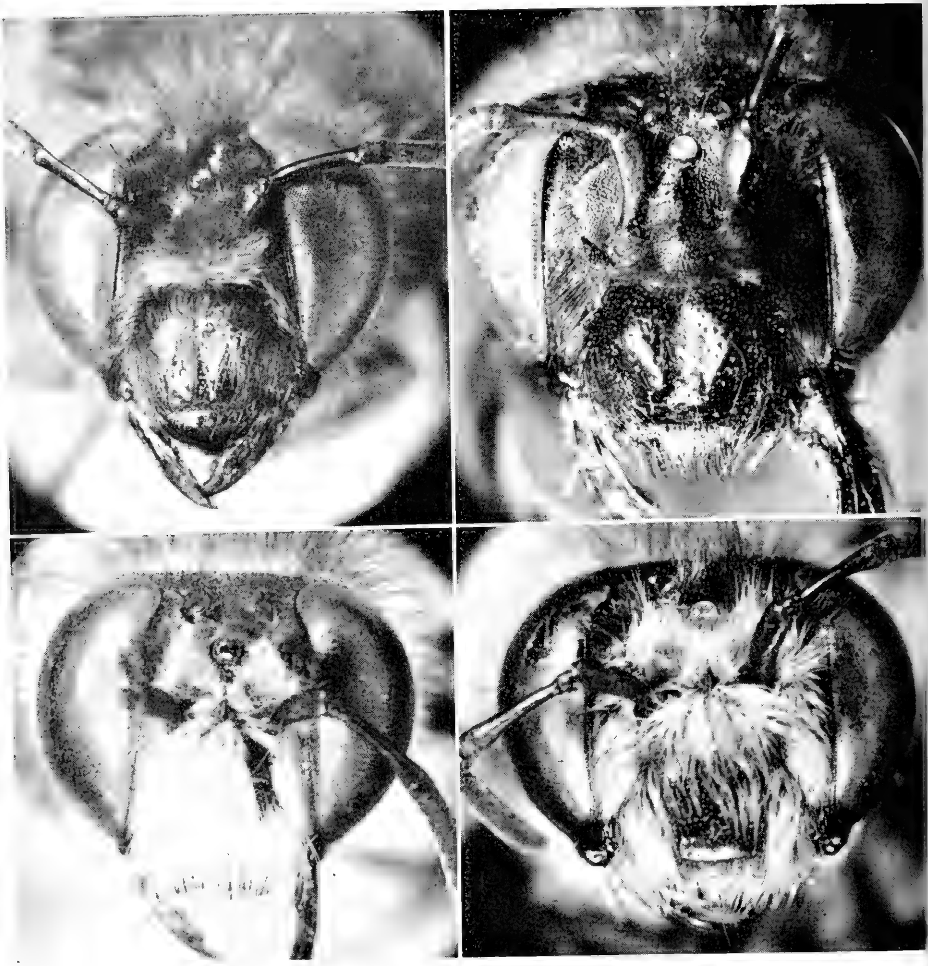


FIG. 11. Faces, males at left, females at right. Above, *Crawfordapis luctuosa*; below, *Caupolicana (Willinkapis) chalybaea.*

from Costa Rica. Moure (1964) reports specimens from Volcán Tacanas, Chiapas, Mexico; the Departamento de Chimaltenango, Guatemala; and Los Planes, El Salvador. Presumably his drawings are based on a specimen from one of these more northern localities and the differences between his drawings and mine may support the idea that different forms are involved.

D2. NORTH AMERICAN SPECIES OF THE SUBGENUS CAUPOLICANA

There are three species of this subgenus in North America, each very different from the others and equally different from the South American species of the subgenus. *C. yarrowi* and *electa,* however, are more similar to one another than either is to *ocellata* or any other species, and *ocellata* is a very isolated form.

Caupolicana (Caupolicana) yarrowi (Cresson)

(Figs. 12, 13-17, 29)

Megacilissa yarrowi Cresson, 1875, Rep. U.S. geogr. survey west of one hundredth meridian, 5:723.

Male: Length 17-21 mm; wing length 14-16½ mm.

1. Inner orbits converging above. Eyes closest on a line that is tangent to posterior margins of posterior ocelli, the latter far in front of posterior margins of eyes; ocellar diameters about equal to maximum width of scape; ocellocular distance more than half of width of ocellus. 2. Basal part of labrum with two distinct longitudinal ridges submedially and weak longitudinal wrinkles laterally. 3. First flagellar segment longer than scape. 4. Anterior femur much thickened, especially broad basally where expanded posteriorly so that it is less than three times as long as broad; middle and hind femora progressively more slender. 5. Anterior femur with rather dense long hairs on lower surface, especially dense near posterobasal angle; other femora with only short sparse hairs ventrally except for small (one fifth as long as femur) basal patch of rufescent hairs on middle femur. 6. Hind basitarsus with apical third distinctly wider than basal third, the basitarsus little over half as long as the slender and distinctly curved tibia. 7. Propodeal triangle without transverse ridges. 8. Posterior margins of sternum 2 and usually 3-4 broadly emarginate. 9. Apex of sternum 6 rounded. 10. Hidden sterna and genitalia as shown in Figures 13 to 17. 11. Integument black, legs brownish black, under side of flagellum brown, tegula yellow brown. Wings light brownish with dark brown veins and stigma. 12. Pubescence of head white, ochraceous on vertex; pubescence of thorax, legs, and first tergum ochreous, paler on venter and on coxae, trochanters, and femora; dorsum of metasomal terga 2 to 7 with hair black, apical white bands on terga 2 to 4, these bands widest laterally and narrowed medially; metasomal sterna 1-4 with white hair, remaining sterna with dusky hair (see comments below on variation).

Female: Length 18-20 mm; wing length 19 mm.

13. Inner orbits subparallel except upper parts. 14. Ocellar diameters about equal to maximum width of scape; ocellocular distance greater than ocellar diameter. 15. First flagellar segment longer than scape, third broader than long and distinctly shorter than following segments. 16. Basal part of clypeus distinctly more shining than supraclypeal area, with distinct punctures. 17. Anterior coxa with apical spine covered with ochreous hair. 18. Propodeal triangle as in male (character 7). 19. Integument colored as in male (character 11). 20. Pubescence of head white with scattered dusky hairs intermixed except on genal area; hair of vertex wholly dusky or black; subapical fringe of

clypeus and lower fringe of mandible rufescent. Hairs of thorax and first tergum ochraceous, whiter laterally, those of dorsum and pronotal tubercles and upper part of mesepisternum dark tipped. Hairs of basal segments of legs whitish or ochraceous except for areas of short reddish dusky hair on lower side of middle trochanter and base of middle femur; hairs of tibiae and tarsi dusky ochreous to almost black except that scopa of under side of hind tibia, like that of femur and trochanter, is white. Dorsum of metasomal terga 2-6 with black hair except for white apical bands, slightly narrowed medially, on 2-4, also on 1. First two sterna with ochraceous hair; sterna 3-4 with similar hair on posterior margins but otherwise with reddish dusky to blackish hair; sterna 5-6 with hair reddish dusky to black.

This species is closest to *C. electa* as is shown by characters 1, 2, 3, 4, 9, 14, 15, and 16 as well as by sternal and genital characters of the male, especially the ventroapical lobes of the seventh sternum. The other characters, as well as some aspects of those listed above, separate *yarrowi* from *electa.*

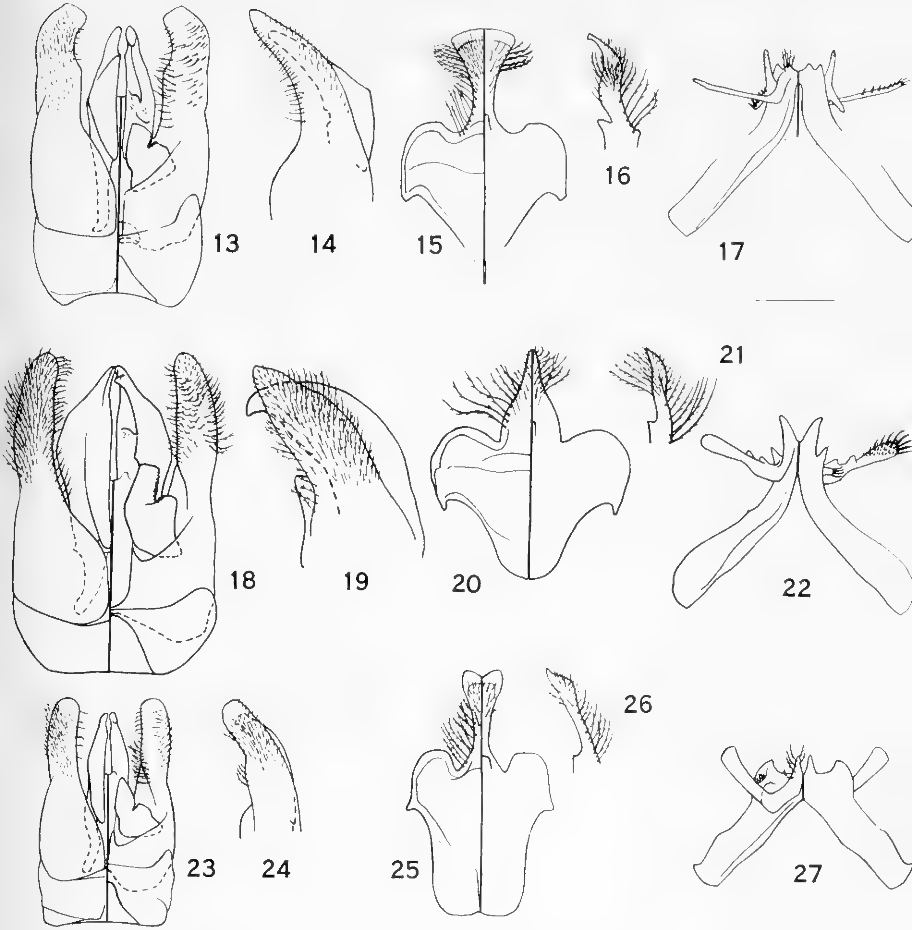
C. yarrowi was described from New Mexico and the type is in the Academy of Natural Sciences of Philadelphia (no. 2141). It occupies a wide range in the desert and semidesert areas of the southwestern United States and Mexico (see Figure 28). Records for Florida (Fox, 1898; Graenicher, 1930) are errors based on specimens of the broad banded southern form of *C. electa.*

Altitude ranges from 4000 feet at Douglas, Arizona, to 5300 feet at LaCueva in the Organ Mountains, New Mexico, and to 6400 feet at El Tascate, Durango, and Zimapán, Hidalgo.

Specimens have been collected as early as June 6 (Huachuca Mountains, Arizona) and June 23 (Tehuacán, Puebla) but most records are in July and August, with one record on September 5 (Organ Mountains, New Mexico).

There is available a single male of a probably distinctive population or species from the southern extremity of the range. The specimen, from the state of Puebla (Tehuacán, June 23, 1951, H. E. Evans), is unusually large with the white metasomal bands reduced; sterna 2-4 (especially 2) are unusually broadly and deeply emarginate; the pubescence of the fourth and part of that of the third sterna is blackish like that of the following sterna instead of pale like that of the preceding sterna; the femora are unusually robust, the anterior one greatly produced posteriorly at the base and not much over twice as long as wide; and the middle basitarsus is broadest medially instead of parallel sided and of uniform width.

Cockerell (1899) records the flight of *C. yarrowi* as from 5:15 to 6:15 a.m. (between dawn and sunrise) on September 4 and 5 in the Organ Mountains, New Mexico. He records a series from flowers of *Datura meteloides,* and two from *Lippia wrightii.* Probably these were nectar sources and Linsley (1960) and Linsley and Hurd (1959) record males of *C. yarrowi* taking nectar from *Melilotus alba* and *Larrea divericata.* At least on the latter plant the bees were



FIGS. 13-17, *Caupolicana (Caupolicana) yarrowi*; 18-22, *C. (C.) electa*; 23-27, *C. (C.) ocellata;* males. For each species structures are genitalia; lateral view of apical part of genitalia, eighth sternum, lateral view of apical process of same, and seventh sternum. For further explanation see Figures 6-9. The scale line represents 1 mm for all three species.

active before dawn. I have also seen the species near Douglas, Arizona, at about sunrise on *Larrea,* not collecting pollen. Specimens collected at Encarnación de Diaz, Jalisco, on *Eysenhardtia polystachya,* had no pollen on the scopa and probably were feeding on nectar.

Linsley and Cazier (1963) treat the pollen collecting, especially on *Solanum,* in some detail, showing, for example, that in mid-August in southern Arizona on a clear morning the activity was from 5:20 to 6:50 while on an overcast morning it was from 5:20 to 8:50 (sunrise both days was at approximately 6:00). Most other pollen collecting bees on the same flowers started later and continued much later, but *Ptiloglossa jonesi* Timberlake, while largely synchronous with *C. yarrowi*, started work perhaps slightly earlier and under overcast conditions stopped its activities considerably earlier than *C. yarrowi*. Pollen collecting, however, is not restricted to *Solanum* and 70% of the females collecting on *Solanum* already carried some *Mentzelia*-like pollen. At the same place where it visits *Solanum* in the morning, *C. yarrowi* collects pollen in the evening (17:50-19:13; sunset at 18:51) from *Mentzelia pumila*, a flower that is not open in the morning. Linsley and Cazier (1963) also give a brief account of the scopal structure.

Linsley (1962) records males of *C. yarrowi* sleeping while grasping *Melilotus* stems with their mandibles, but he observed no aggregations of such bees.

Caupolicana (Caupolicana) electa (Cresson)
(Figs. 18-22, 29)

Megacilissa electa Cresson, 1878, Proc. Acad. Nat. Sci. Philadelphia, p. 221.
Caupolicana electa; Mitchell, 1960, Bees of the Eastern United States, 1:23.
Megacilissa yarrowi; Fox, 1898, Ent. News, 9:128 (misidentification).
Caupolicana (Megacilissa) yarrowi; Graenicher, 1930, Ann. Ent. Soc. Amer., 23:161 (misidentification).

Male: Length 18-20 mm; wing length 15-15½ mm.

1. As in *yarrowi*. 2. Labrum with longitudinal ridges reduced to two gentle submedian convexities; wrinkles absent. 3. As in *yarrowi*. 4. Anterior femur thickened, less than four times as long as broad, not expanded basoposteriorly but thickest shortly before middle; middle and hind femora about equal in thickness, not enlarged. 5. Anterior femur with rather dense long hairs on lower surface; other femora with hairs shorter and sparser ventrally but less short and sparse than in *yarrowi*, basal patch of dense rufescent hairs on middle femur extending beyond middle. 6. Hind basitarsus parallel sided, scarcely over half as long as the slender and distinctly curved tibia. 7. Propodeal triangle with a few transverse ridges, sometimes weak. 8. Posterior margins of sterna 2-4 transverse. 9. As in *yarrowi*. 10. Hidden sterna and genitalia as shown in Figures 18 to 22. 11. Integument black, tegula and legs yellowish brown, infuscated on coxae, trochanters, and femora; under side of flagellum dark brown, lightest apically. Wings colored as in *yarrowi*. 12. Pubescence of head, thorax, legs, first tergum, lateroventral extremities of second tergum, and first two sterna ochreous, most deeply colored on dorsum of thorax; rest of metasoma with pubescence fuscous or black, very narrow apical bands of white pubescence on terga 2-4, sometimes reduced to lateral parts of 2 and absent on 3 and 4; or in specimens from southern Florida, these bands as in *yarrowi*.

Female: Length 17-18 mm; wing length 19 mm.

13. Inner orbits slightly converging below except upper parts which converge above. 14. As in *yarrowi*. 15. First flagellar segment longer than scape,

third slightly longer than broad. 16. As in *yarrowi*. 17. Anterior coxa without spine. 18. Propodeal triangle as in male (character 7). 19. Integument colored as in male (character 11) but legs reddish brown rather than yellowish brown. 20. Pubescence as in male (character 12) but that of tarsi and outer surfaces of tibiae deep ochreous, that of area of basitibial plate brown, that of sterna 2-3 reddish dusky, lateral extremities of sterna 2-4 with long ochraceous hair. The one female studied from the main range of the species has the apical tergal bands present; in southern Florida they are broad as in the male from that area.

This species is most similar to *C. yarrowi*. The similarities and differences are summarized under that species.

Caupolicana electa was described from Georgia and the type (no. 2140) is in the Academy of Natural Sciences of Philadelphia. It is known from sandy areas in the eastern lowlands from North Carolina to Georgia, Alabama, and northwestern Florida (Fig. 28). Localities are Mobile, Alabama; Crestview, Okaloosa County, Florida; Southern Pines and Lakeview, Moore County, North Carolina; and Harnett County, North Carolina. In addition, at least two specimens have also been collected in Dade County, southern Florida (Fox, 1898; Graenicher, 1930).

The specimens from southern Florida have broad white tergal bands and look superficially like *C. yarrowi*, which accounts for their misidentification by Fox and Graenicher. They are also smaller and more slender than typical *electa*. In other features, however, they agree with *electa*. The probable speci-

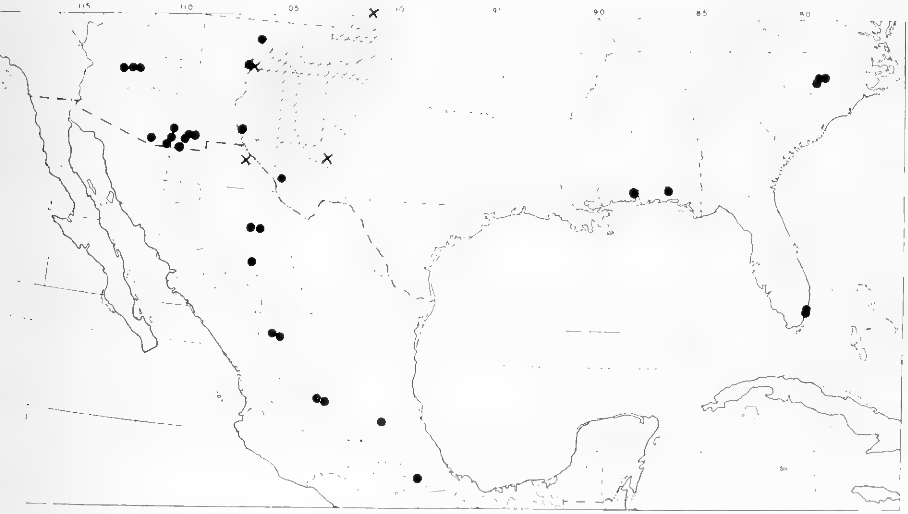


FIG. 28. Map showing distribution of the North American species of *Caupolicana s. str.* Dots in Mexico and the west show records of *C. yarrowi*; dots in the east, *C. electa*; crosses held together by shading, *C. ocellata*.

men (a male) which Fox recorded merely from Florida is in the American Museum of Natural History, labeled as from Biscayne Bay. The specimen taken by Graenicher was from South Miami.

The season of flight seems to be autumnal (September and October). Flower records on specimens seen are yellow *Gerardia* (=*Aureolaria*) and *Trichostemma*. The flight period is reported as "around sunrise" and late afternoon or dusk (Mitchell, 1960; Graenicher, 1930).

Caupolicana (Caupolicana) ocellata new species

(Figs. 12, 23-27, 29)

Male: Length 14-15 mm; wing length 11½-12 mm.

1. Inner orbits parallel except for upper parts which converge. Eyes closest on a line that passes through posterior ocelli, the latter extending back almost as far as posterior margins of eyes; ocelli enormous, diameters much greater than maximum width of scape, ocellocular distance less than half width of ocellus. 2. As described for *yarrowi* but ridges weaker and wrinkles fewer and coarser. 3. First flagellar segment about as long as scape. 4. Femora of about equal thickness, anterior one about four times as long as broad. 5. Anterior femur with rather dense long hair on lower surface, middle and hind femora with ventral vestiture progressively sparser and shorter; patch of rufescent hair at base of middle femur absent. 6. Hind basitarsus parallel sided, distinctly over half as long as tibia. 7. Propodeal triangle as in *yarrowi*. 8. As in *electa*. 9. Apex of sternum 6 with median broadly V-shaped emargination. 10. Hidden sterna and genitalia as shown in Figures 23 to 27. 11. Integument black; labrum, basal half of mandible, antenna, tegula and legs yellow brown or testaceous; coxae, trochanters, and femora darker brown. Wings nearly clear, veins and stigma brown. 12. Pubescence white, slightly ochraceous on dorsum of thorax and on terga 6-7; dorsal surfaces of terga 2-5 with hair black or fuscous except for broad apical white bands, not narrowed medially, on terga 1-5.

Female: Length 15-16 mm; wing length 11-12 mm.

13. As in *electa*. 14. Ocellar diameter much greater than maximum width of scape; ocellocular distance over half ocellar diameter. 15. First flagellar segment shorter than scape, third as broad as long or longer than broad. 16. Basal part of clypeus dull and granular like supraclypeal area. 17. As in *yarrowi*. 18. Propodeal triangle as in male (character 11). 19. Integument as in male (character 11), but pale areas, including lower part of clypeus, reddish brown rather than yellow brown. 20. Pubescence white, slightly ochraceous on dorsum of thorax, on outer surfaces of tibiae and tarsi, on under surface of middle trochanter and base of femur, and on terga 5-6; dorsal surfaces of terga 2-4 with hair dusky except for broad apical white bands on terga 2-4, a narrower one on 1; metasomal sterna with hair ochreous.

Caupolicana ocellata is one of the most strikingly distinct species of *Caupolicana*. Characters 1, 3, 4, 5, 9, 14, and 15, are especially distinctive.

I am pleased to accept the specific name suggested by Padre J. S. Moure when he saw this remarkable species; the name is given in reference to the enormous ocelli.

The species occurs in sandy areas in the southern high plains and adjacent semidesert areas from Kansas to Chihuahua (Fig. 28). Type material is as follows:

Holotype female and five female paratypes: Three miles south of Garden City, Finney County, Kansas, September 3, 1951 (C. D. Michener and W. E. LaBerge). One female paratype, same data but 5 miles south of Garden City. Three female paratypes, type locality (labeled Garden City), August 29, 1952 (W. E. LaBerge). Allotype male and one male paratype: Albuquerque, New Mexico, July 23, 1950 (R. H. Beamer, H. O. Wright). The above are all from the Snow Entomological Museum of The University of Kansas. One female paratype: Samalayuca, Chihuahua, June 24, 1947 (D. Rockefeller Expedition, C. D. Michener), in the American Museum of Natural History. Forty-seven male and 11 female paratypes: 6.7 miles south of Manahans, Ward County, Texas, June 1-2, 1964 (Peter H. Raven) in the collection of the California Insect Survey, University of California, Berkeley.

A paratype taken with the holotype in Kansas is in the collection of Padre J. S. Moure, Curitiba, Brazil; another is in that of Dr. C. A. C. Seabra, Rio de Janeiro.

Females have been recorded only on *Dalea lanata;* those from both Kansas and Texas were on this flower. Males have been taken on another small legume, *Petalostemum flavescens* (in New Mexico) and on an onagraceous flower, *Gaura coccinea* (in Texas).

Specimens from Kansas were taken from early to mid morning and a female was seen to enter her nest after 9:00 a.m. on a sunny day.

In Texas observations are available on the times of day when specimens were collected on June 2, 1964, at flowers of *Dalea lanata,* thanks to Dr. Peter H. Raven of Stanford University. The specimens were collected and thus removed from the population; figures for later in the day might have been higher had this not been the case. However, Table 1 clearly shows that *C. ocellata* was active early in the morning and late in the evening and that the other principal visitors to the same flowers, *Martinapis luteicornis* (Cockerell) and *Agapostemon texana* Cresson, appeared later and disappeared earlier, having little overlap with the *Caupolicana*. Dr. Raven arrived at the site at 5:00, when it was barely light, and found the *Caupolicana* common; they were much rarer by 5:45. He writes that at 20:10 they became abundant again and continued until 20:40 when it was pitch dark and he had to use a flash light to see the bees. After that time the bees were scarce or absent.

TABLE 1. Times of Capture of Principal Visitors to Flowers of *Dalea lanata* at Manahans, Ward Co., Texas, on June 2, 1964, by Dr. Peter H. Raven. Sunrise was about 5:40; sunset at 19:46.

	Caupolicana ocellata		Martinapis luteicornis		Agapostemon texanus		
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	°F
5:30-6:00	22	1	....	....	....	....	58
6:00-7:00	5	3	...	....	....	....	
No observations made							63
7:30-8:00	2	....	5	2	4	1	65
8:00-8:30	1	....	20	3	6	2	68
Discontinuous observations	....	....	....	....	active all day		to 95
18:30-19:00	6	....	7	1	7	1	89
19:00-19:15	....	....	6	1	4	....	88
No observations made							
19:45-20:00	....	4	....	....	....	. .	
20:00-20:30	2	....	....	....	....	....	83

Of the eight males taken on *Gaura coccinea,* four were collected from 7:30 to 8:15, four from 15:45 to 20:30.

Nests were found by me in loose sand of dunes stabilized by vegetation, three miles south of Garden City, Kansas. They entered horizontal surfaces among small plants in the vicinity of the flowering *Dalea lanata*. I dug two nests. One seemed to consist of only a burrow although the bees were badly tattered and no males were taken, suggesting that the season was well advanced (September 3). The other was 60 cm deep, vertical, rather straight. At the bottom it turned sharply to one side, extended laterally for 8 cm to a vertical cell lined with a membrane similar to that of other colletid cells and partially filled with liquid provisions. Another provisioned cell was found about 8 cm in another direction from the bottom of the vertical burrow; the horizontal burrow leading to it had been completely filled with sand. These very scanty data suggest basic nest structure reasonably similar to that of other *Caupolicana* species whose nests have been described.

D3. NORTH AMERICAN SPECIES OF *ZIKANAPIS*

The North American *Zikanapis* are similar to the South American *C. (Z.) megalopta* (Moure), being large bees with largely ochraceous pubescence. They are quite different from the type species, *C. (Z.) zikani* (Friese), which has much black pubescence. The North American species agree in the tufts of long hairs, sigmoidly curved, arising from the lateral extremities of the fifth sternum of the male, and less conspicuously from the fourth. They also agree in the rather flat clypeus of the female (flatter in *elegans*) with abundant, rather uniform punctation, finely roughened and dull surface between punc-

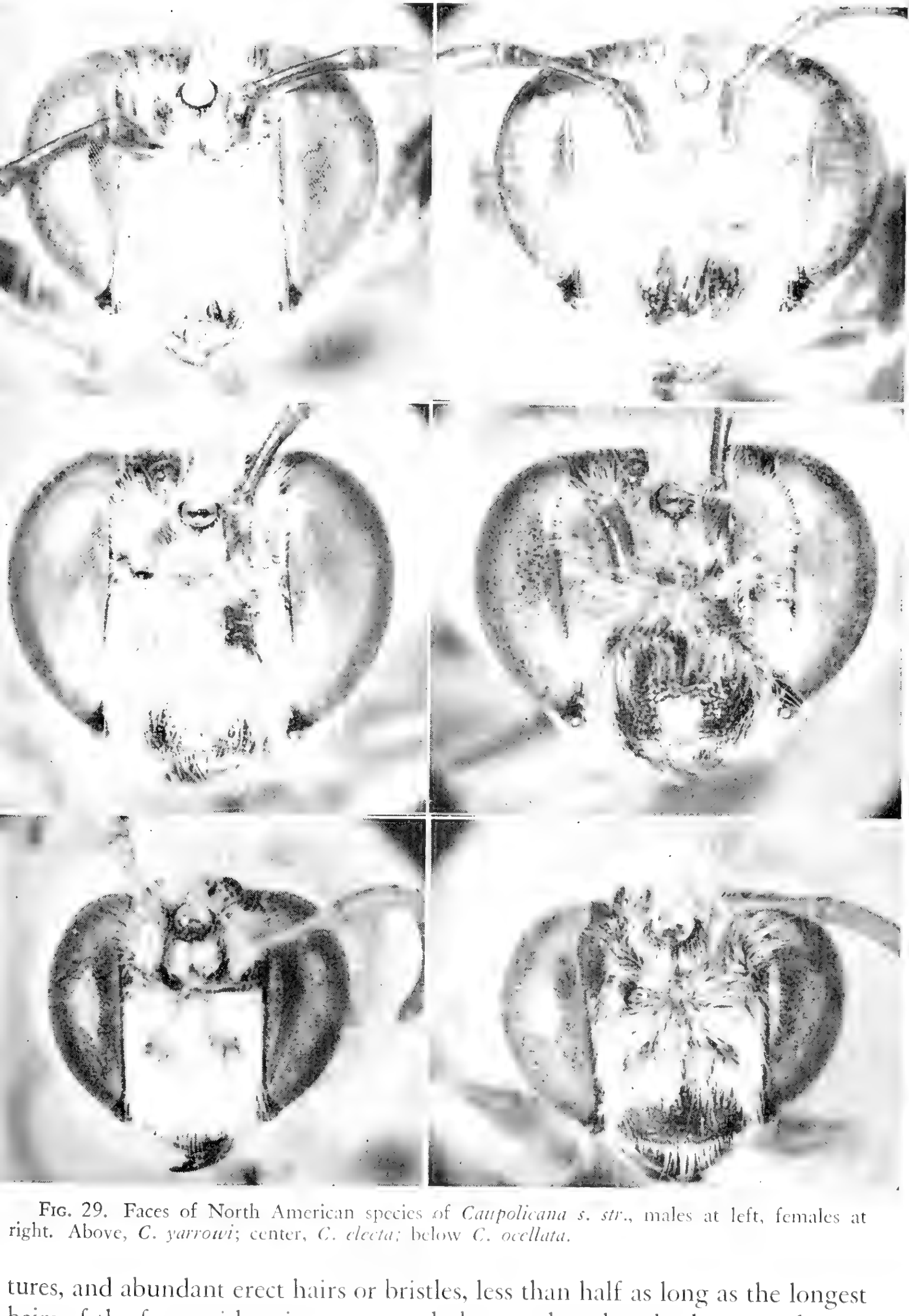


FIG. 29. Faces of North American species of *Caupolicana s. str.*, males at left, females at right. Above, *C. yarrowi*; center, *C. electa*; below *C. ocellata*.

tures, and abundant erect hairs or bristles, less than half as long as the longest hairs of the face, with apices commonly bent rather sharply downward.

The genitalia and hidden sterna of the two North American species are similar. They are illustrated for *clypeata;* those of *elegans* have been studied only in a dry state and differ from those of *clypeata* as follows: penis valves and gonoforceps somewhat less broad apically, the former with the preapical angle (basal to slender, downward directed apex) more rounded; apical process of eighth sternum not quite so broad medially, the apical part parallel sided.

Caupolicana (Zikanapis) clypeata (Smith)

(Figs. 12, 30-34, 47)

Megacilissa clypeata Smith, 1879, Descriptions of new species of Hymenoptera in the collection of the British Museum, p. 59.
Caupolicana clypeata; Cockerell, 1905, Trans. Amer. Ent. Soc., 31:343.
Zikanapis (Zikanapis) clypeata; Moure, 1964, Studia Ent., (n.s.) 7:439.

Male: Length 15-17 mm; wing length 12½-13 mm.

1. Eyes strongly converging above, upper interocular distance about as long as scape; interocellar distance about equal to maximum ocellar diameter; ocellocular distance clearly less than half an ocellar diameter. 2. Penis valves widest subapically. 3. Integument black, under side of flagellum, clypeus, tegula, anterior and middle legs, and hind tarsi variably light brown, sometimes considerably infuscated; posterior margins of metasomal segments broadly transparent brownish. 4. Pubescence ochraceous, sometimes slightly dusky on vertex; shorter hairs of dorsum of metasoma, especially on second and third terga, slightly dusky; no pale fasciae on metasoma; hairs of outer surface of middle tibia slightly dusky, those of outer surfaces of hind tibia and basitarsus dusky or blackish.

Female: Length 16-18 mm; wing length 11½-12 mm.

5. Interocellar distance slightly more than maximum ocellar diameter. 6. Integument black, under side of flagellum especially apically and tegula light brown; fore and middle legs with considerable brownish color. 7. Pubescence of head largely whitish except that of clypeus which is brown; fuscous hairs intermixed with white on rest of face and genal areas; hair of vertex fuscous. Hair of dorsum of thorax ochraceous with dusky tips; hair of sides and venter whitish, apices dusky on upper parts of sides. First metasomal tergum and first two sterna with hair pale ochraceous or whitish, remaining sterna with hair ochraceous and somewhat infuscated except for very long, plumose, pale ochraceous hairs laterally on sterna 3 and 4; second to fourth terga with hair except at extreme sides blackish, and with apical bands of appressed white hair, narrowed medially; fifth and sixth terga with strongly infuscated, deep ochre hairs. Hairs of legs ochraceous, those of outer sides of tibiae and tarsi infuscated (slightly so on foreleg), hind tibial hairs of basitibial region and extending to middle of tibia black, scopa including hairs of inner sides of hind tibiae white.

This species was described from Oaxaca, Mexico. It is not clear whether this means the city or elsewhere in the state. I have examined the type in the British Museum (Natural History).

A series was collected on a misty morning in complete darkness at Tuxpan, Michoacán, September 1, 1962, by D. H. Janzen. The vicinity consists of cultivated land. Seven males were taken at car lights between 5:10 and 5:20 a.m., two males between 5:20 and 5:35 a.m., two males between 5:35 and 5:45 a.m. One male was taken on flowers of *Salvia* at the side of the road at first light (still much too dark to see the bee) at 5:45 a.m., another at 6:00 a.m. Two females were taken at the car lights, both at 5:50 a.m.

A single female was taken, with no details as to collecting time, 2 miles east of Lake Patzcuaro, Michoacán, July 25, 1954 (J. W. MacSwain).

Moure (1964) records specimens from Amula (now Almolonga, 9.5 km northwest of Chilapa), Guerrero, at 6000 feet altitude and 11 miles southwest of Acambaro, Guanajuato, August 17, 1954.

Caupolicana (Zikanapis) elegans Timberlake

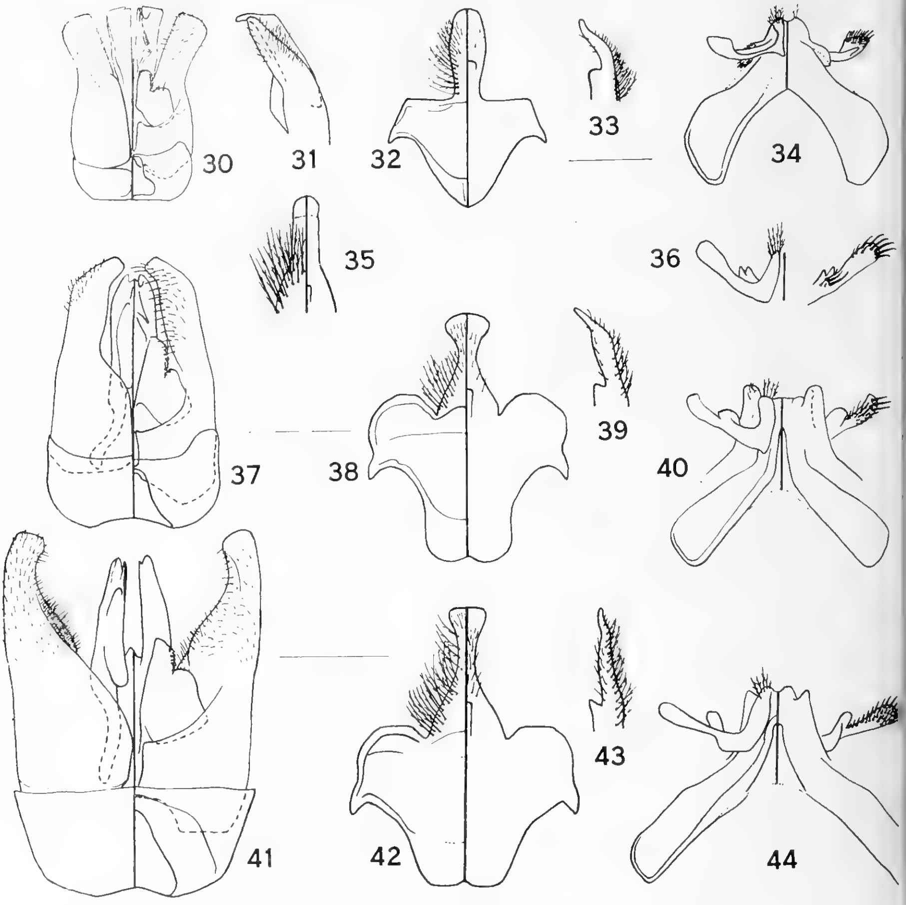
Caupolicana elegans Timberlake, 1965, Jour. New York Ent. Soc., 73:46.

Male: Length 14-16 mm; wing length 10½-13 mm.

1. Eyes moderately converging above, upper interocular distance about 1.6 times as long as scape; interocellar distance about 1.5 times maximum ocellar diameter; ocellocular distance slightly less than half an ocellar diameter. 2. Genitalia and hidden sterna similar to those of *clypeata*, the most conspicuous difference being that the penis valves are widest medially. 3. Integument black, underside of flagellum apically, tegula, and distal parts of tarsi light brown; fore and middle legs sometimes brownish; margins of metasomal segments broadly translucent. 4. Pubescence ochraceous, scattered dusky hairs on face along inner orbits (scarcely noticeable in type) and some fuscous hairs on vertex (not in type); hairs of dorsum of metasomal terga 2 to 4 black or fuscous, those of 5 and 6 reddish fuscous, posterior margins of terga 2 to 5 with bands of white appressed hair, these bands present only laterally on 2 and 3, broken medially on 4, and continuous on 5; hairs of outer surfaces of middle and hind tibiae and hind basitarsus blackish.

Female: Length 17 mm; wing length 11½ mm.

5. Interocellar distance over twice maximum ocellar diameter. 6. Integumental coloration as in male (character 3) but fore and middle legs black except for brownish small segments of tarsi. 7. Pubescence of head and thorax as described for *clypeata*. Pubescence of metasoma as described for *clypeata* but hairs of first tergum with dusky apices; sternal pubescence slightly paler, the very long hair at sides of sterna 3 and 4 whiter and more extensive; white fasciae on terga 2 to 4 broken medially, that on 4 narrowly so; hairs of terga



FIGS. 30-34, *Caupolicana (Zikanapis) clypeata,* male. 30, genitalia; 31, lateral view of apical part of same; 32, eighth sternum; 33, lateral view of apical process of same; 34, seventh sternum.

FIGS. 35-36, *Caupolicana (Alayoapis) notabilis*, male. 35, apical process of eighth sternum; 36, apical processes of seventh sternum. These drawings were sketched from dry preparations in the British Museum (Natural History).

FIGS. 37-40, *Caupolicana (Alayoapis) subaurata;* 41-44, *C. (A.) nigrescens*; males. For each species structures are genitalia (somewhat flattened artificially in *nigrescens*), eighth sternum, lateral view of apical process of same, and seventh sternum.

For further explanation see Figures 6-9. The scale lines do not apply to Figures 35 and 36.

5 and 6 largely reddish black. Hairs of legs as in *clypeata* but those of outer surfaces of middle and hind tibiae and tarsi black.

This species was described from one male taken near Portal, Cochise County, Arizona, at about 10:00 a.m. It is preserved in the American Museum of Natural History and was lent me for study by Dr. J. G. Rozen, Jr. It is smaller than the other specimens and with less dark hair on the head.

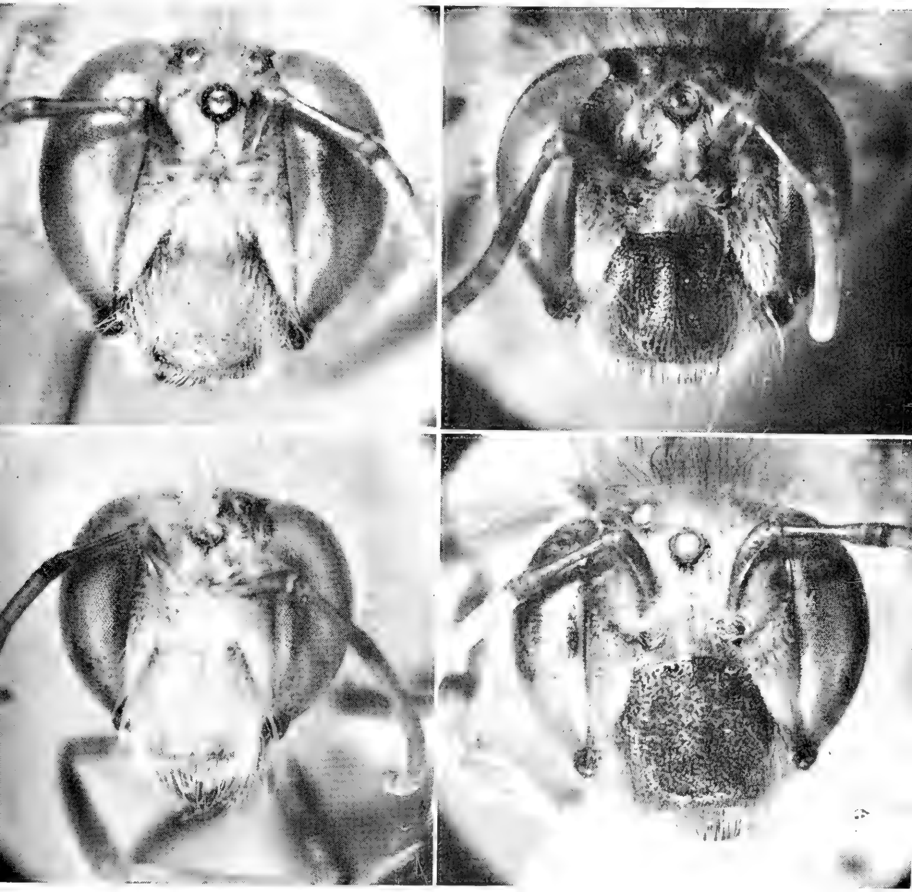


FIG. 47. Faces of North American species of the subgenus *Zikanapis*, females at right. Above, *C. (Z.) clypeata*; below, *C. (Z.) elegans*.

The only other known specimens are a pair taken on highway 150, 37 miles west of Tehuacán, Puebla, Mexico, August 31, 1962, on flowers of *Salvia*, the male at 6:00 p.m., the female at 6:40 p.m. (D. H. Janzen).

D4. THE SPECIES OF ALAYOAPIS

This subgenus is known from three species, the only Antillean representatives of the subfamily, which are characterized below:

Caupolicana (Alayoapis) nigrescens (Cresson)

Megacilissa? nigrescens Cresson, 1869, Trans. Amer. Ent. Soc., 2:295.

Male: Length 15-16 mm; wing length 13-14 mm.

1. Eyes very strongly converging above, upper interocular distance less

than length of scape, eyes closest at point over an ocellar diameter behind ocelli; interocellar distance about equal to ocellar diameter; ocellocular distance less than one sixth ocellar diameter. 2. Front coxa not spined; front femur about three times as long as wide. 3. Front tibia about 4.4 times as long as broad with some hairs as long as tibial diameter. 4. Middle femur with hair much shorter than that on other femora; femur not contorted. 5. Mediotarsal segments of middle leg nearly symmetrical. 6. Inner hind tibial spur gently curved medially. 7. First sternum with median apical spine; second and third sterna with margins recurved. 8. Hidden sterna and genitalia as shown in Figures 41 to 44. 9. Black, flagellum dark brown beneath, paler apically, apex of last segment reddish. Legs brown to reddish, more or less infuscated, coxae, trochanters, mediotarsi and distitarsi blackish. Tegula piceous to black. Wings brownish, slightly darker than in *yarrowi*. 10. Hair of face mixed black and white. Hair of vertex black, of occiput, genal areas, and under side of head white. Hair of prothorax white, blackish on posterior lobe of pronotum. Mesonotum with hair dark gray to blackish except for broad white band across front of scutum, narrower white band along scuto-scutellar suture, and white along posterior edge of scutellum and along lateral edge of scutum mesad from tegula. Pleural and ventral areas of thorax with dark gray to blackish hairs except for large dull white lateroventral mesepisternal area and dull white on metapleuron. Metanotum and posterior part of propodeum with white hairs, long dorsolateral hairs of propodeum partly black. Coxae and middle and hind trochanters with hairs dark gray to black; rest of legs with hairs pale yellowish in some lights, blackish in others, darkest on posterior femora, forelegs with the most yellowish. First tergum with hairs white anteriorly and laterally, black dorsally, with a small dorsolateral indication of apical white band. Remaining terga with hairs black, white at extreme sides of second, short on terga 2 to 4 with narrow, bright, white apical bands (narrower than in *yarrowi*). First sternum with hair white, others with hair dark gray.

Female: Length 16-18 mm; wing length 11 mm.

11. Basal part of labrum raised to form two strong longitudinal submedian carinae. 12. Maximum ocellar diameter less than ocellocular distance which is subequal to interocellar distance. 13. Apical spine of strigilis shorter than rest of strigilis. 14. Integumental coloration as described for male (character 9) but hind leg more consistently black. 15. Hair of face mixed black and white, sparse on shining (but punctured and minutely roughened) clypeal disc; median part of frons with hairs all white; hair of vertex black forward to and including transverse band of dense black hair between anterior and posterior ocelli, wholly black hair extending down in upper paraocular areas; subapical fringe of clypeus and lower fringe of mandible rufescent fuscous; genal and hypostomal areas with hair white. Thoracic pubescence (in poor condition in

available specimen) has a pattern similar to that of male. Hairs of legs black, reddish on fore legs and small segments of tarsi; femoral scopa white. Tergal pubescence as described for male but white band of tergum 2 present only laterally, of 3 broken medially. Sternal pubescence dusky reddish, whitish at extreme sides.

Caupolicana nigrescens is most similar to *subaurata.* Characters 1, 2, 4 (contorted femur), 5, 12, and the color differences are among the striking distinguishing features.

This species was described from Cuba without further data but the type, which is still in good condition in the Gundlach collection in Havana, bears the number 293; Dr. Pastor Alayo D. has looked this up in Gundlach's manuscript catalogue and found the notation "Yateras, Ote., XI." It is interesting that the type locality for this species and its relative, *subaurata,* should be the same place in Oriente Province.

Dr. Alayo writes of this species, "These bees are dwellers in the most dense forests of Cuba, specially in the mountains of Oriente Province, and I do not remember to have found any specimen in the lowlands."

Specimens have been studied by me or reported to me by Dr. Alayo (from his collection and that of Dr. F. de Zayas M.) from the following localities, all in Oriente Province, Cuba:

Sierra Cristal, Mayarí, May, 1955 (Zayas); Piloto, Moa, June, 1954 (Zayas and Alayo); Loma del Gato, Hongolosongo, Sierra del Cobre, June, July, September (Zayas and Alayo); same locality, September, 1935, October 1-2, 1935, 2600 to 3325 feet altitude (J. Acuña, S. C. Bruner, L. C. Scaramuzza, collectors); Pico (or Alto de) Cardero, Macizo del Turquino, June, 1963 (Alayo).

Caupolicana (Alayoapis) subaurata (Cresson)

(Figs. 37-40, 45, 48)

Megacilissa? subaurata Cresson, 1869, Trans. Amer. Ent. Soc., 2:296.

Male: Length 16 mm; wing length 13½ mm.

1. Eyes strongly converging above, upper interocular distance greater than length of scape, eyes closest at point less than ocellar diameter behind ocelli; interocellar distance greater than ocellar diameter; ocellocular distance over one fourth ocellar diameter. 2. Front coxa with short apical spine; front femur of male less than three times as long as wide. 3. Front tibia about four times as long as broad with some hairs nearly as long as tibial diameter. 4. Middle femur with hair much shorter than that on other femora; femur contorted (Fig. 45). 5. Mediotarsal segments of middle leg with posterior lobes much larger than anterior lobes. 6. Inner hind tibial spur strongly curved medially. 7. As in *nigrescens.* 8. Hidden sterna and genitalia as shown in Figures 37 to 40. 9. Black, flagellum as in *nigrescens.* Legs red, mediotarsi blackish, especially on mid and hind legs. Tegula reddish brown. Wings as in *nigrescens.*

10. Hair color pattern as in *nigrescens* but pale hair ochre instead of white, dark hairs dark only apically so that gray color is light and somewhat ochraceous, pale band on scuto-scutellar suture weak, pale ventrolateral mesepisternal area larger than in *nigrescens* so that midventral dark region is reduced and ventral and lateral pubescence of thorax may appear entirely ochraceous; hairs of legs ochreous. First metasomal tergum with ochraceous hairs anteriorly and laterally, gray or blackish dorsally except for complete narrow apical band of white. Remaining terga with black hairs, becoming reddish on 5 and 6 and extreme sides of 2, narrow apical white bands (narrower than in *nigrescens*) on 2-4 as well as 1. Sterna 1 and 2 with ochraceous hair, others with light ochreous gray hair.

Female: Length 17 mm; wing length 11 mm.

11. Basal part of labrum raised to form two strong longitudinal submedian carinae. 12. Maximum ocellar diameter about equal to ocellocular distance which is less than interocellar distance. 13. Apical spine of strigilis longer than rest of strigilis. 14. Integumental coloration as in male (character 9). 15. Pubescence of head as described for female *nigrescens* but pale hairs ochraceous, dark ones mostly dusky rather than black, at least basally; transverse band of dense hair between ocelli mixed dark and light, as are hairs of upper paraocular areas; subapical fringe of clypeus and lower fringe of mandible coppery. Thoracic hair coloration as in male, the striking pattern of *nigrescens* being only weakly evident. Hair of legs ochreous, even fulvous on tibiae and basitarsi. Tergal pubescence as described for male. Sternal pubescence dusky reddish, fulvous laterally.

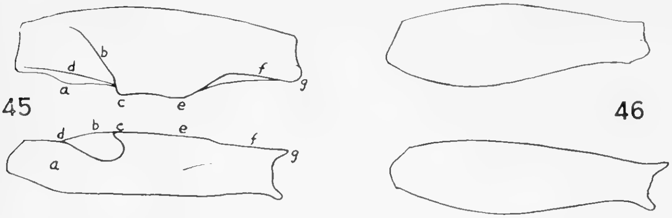
This species is closest to *C. nigrescens.* The most distinctive features are listed under that species.

This species was described from Cuba without further data. The type, which is in good condition in the Gundlach collection in Havana, bears the number 292. Dr. Pastor Alayo D. has found that this number in Gundlach's manuscript catalogue refers to the notation "Yateras, Ote., XI." This is also the type locality for *nigrescens* although other records are for localities different than those where *nigrescens* has been taken. *Caupolicana subaurata* may well be wider ranging both ecologically and geographically than *nigrescens.*

Specimens have been studied by me or reported to me by Dr. Alayo (from his collection and that of Dr. F. de Zayas M.) from the following localities:

Oriente Province: Puerto Boniato, Santiago de Cuba, October, 1943 (Alayo); Moa, Baracoa, June, 1954 (Alayo and Zayas); Capitolio, Río Yara, 1150 feet altitude, May 18, 1948 (Zayas).

Pinar del Río Province: Mogote de Xyla, Couret, carretera a Luis Lazo, November, 1956 (Jaume); San Vicente, Viñales, May, 1956 (Alayo and Zayas); Sierra Cajálbina, June, 1956 (Zayas); Rancho Mundito, Sierra Rangel, June, 1950 (Zayas).



FIGS. 45-46, Posterior and ventral views of middle femora of males of Cuban *Alayoapis*. Posterior views are above, with the dorsal surfaces uppermost; ventral views are below with the anterior surfaces uppermost. 45. *C. (A.) subaurata;* like letters indicate like localities. 46. *C. (A.) nigrescens.*

Caupolicana (Alayoapis) notabilis (Smith)

Megacilissa notabilis Smith, 1861, Jour. Ent., 1:149.

Male (the following is based on notes made from male type in the British Museum):

1. About as in *nigrescens.* 2. Front coxa not spined; front femur less than three times as long as wide. 3. Front tibia about six times as long as broad, with only very short hairs. 4. Middle femur with hair rather long and dense like that of hind femur; femur not contorted. 5. Not seen. 6. Inner hind tibial spur nearly straight. 7. First sternum not spined; second and third sterna with margins transverse. 8. Hidden sterna as in *subaurata* except as shown in Figures 35 and 36; genitalia as in *subaurata* but distal halves of parameres densely covered on dorsal and outer surfaces with black, plumose hairs (cleared preparation not made). 9. Black, legs and tegula dark brown, presumably faded from blackish. Wings light brownish, slightly darker apically than in *yarrowi.* Integument of metasoma red. 10. Hair of head white, light brownish on vertex, lower part of clypeus, and mandibles; intermixed long fuscus hairs on these areas and elsewhere below antennae; a tuft of fuscous or black hairs near eye margin at level of anterior ocelli. Hair of thorax gray, fuscous or darker gray on anterior lateral parts of scutum, anterior face of mesepisternum, scutellum, and posterior parts of sides of thorax; coxae and trochanters and much of anterior femora with gray hair, rest of hair of legs mostly fuscous. Metasomal hair fuscous, that of first segment gray ventrally and laterally.

Female: Length 17-19 mm; wing length 12-13½ mm.

11. Basal part of labrum with broad even median convexity. 12. Maximum ocellar diameter less than ocellocular distance which is slightly less than interocellar distance. 13. Apical spine of strigilis about as long as rest of strigilis. 14. Integumental coloration as in male (character 9) (tegula and legs blackish in more recently collected material). 15. Hair of head as described for female *nigrescens* but with some white hairs around ocelli and intermixed black hairs on genal and hypostomal areas. (Black hairs only dusky in female from Brit-

ish Museum approximately as old as male type.) Hair of thorax as in male, varying to all nearly black. Hair of legs black or nearly so, reddish on under sides of some tarsal segments, scopa grayish because axes of hairs are black but branches colorless. Metasomal hair as in male but fuscous hairs black in fresher material.

This species is known only from the Dominican Republic in the island of Hispaniola. The type which is a male, and one female, both from Santo Domingo, are in the British Museum. Six females in the United States National Museum were taken at Constanza, Dominican Republic, May 27, 1927 (A. Wetmore). Dr. Wetmore writes *(in litt.)* that his collecting was at about 4000 feet altitude in an area of pines mixed with patches of rain forest. The bees were collected near midday, on flowers growing in an opening among the pines.

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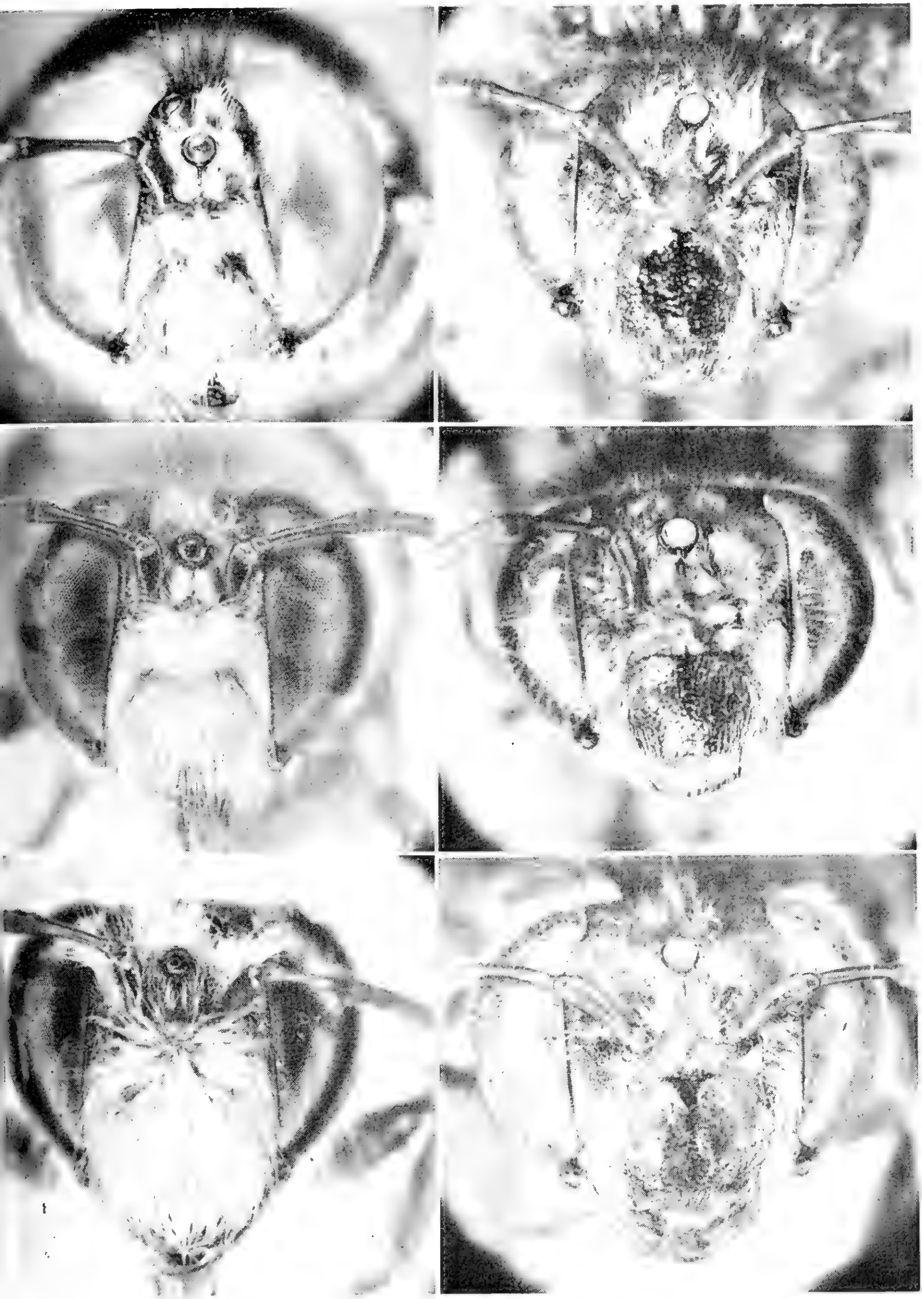

FIG. 48. Faces of the subgenera *Alayoapis* and *Caupolicanoides*, females at right. Above, *C. (A.) nigrescens*; center, *C. (A.) subaurata*; below left, *C. (C.) pubescens* male (from Concepción, Chile, labeled as "typus" of *herbsti* by Friese, USNM); below right, *C. (A.) notabilis*, female.

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A REVISION OF THE BEE GENUS *CALLIOPSIS* AND THE BIOLOGY AND ECOLOGY OF *C. ANDRENIFORMIS* (HYMENOPTERA, ANDRENIDAE)

By

Alvin F. Shinn

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A Revision of the Bee Genus *Calliopsis* and the Biology and Ecology of *C. andreniformis* (Hymenoptera, Andrenidae)[1]

ALVIN F. SHINN[2]

ABSTRACT

This is a taxonomic revision of the bee genus *Calliopsis;* information concerning distribution and biology is incorporated in the treatment of each species. *Calliopsis* occurs throughout North and Central America from southern Canada to southern Panama.

Four subgenera are recognized, including one new one: *Callopsima.* Thirty-eight species are included. One species is placed in synonymy; one is removed from synonymy; one is left as a *nomen nudum;* one is declared a *nomen dubium;* and two are transferred to other genera. About 7,000 specimens were examined.

Twenty-four new species are described: *C. granti, C. mourei, C. peninsularis, C. sonora, C. empelia, C. zora, C. helenae, C. rogeri, C. syphar, C. limbus, C. gilva, C. fulgida, C. yalea, C. rozeni, C. pectidis, C. timberlakei, C. unca, C. azteca, C. crypta, C. deserticola, C. hurdi, C. quadridentata, C. kucalumea,* and *C. micheneri.*

The biology and ecology of *Calliopsis andreniformis* were studied intensively at nesting sites in Lawrence, Kansas, and auxiliary observations were made on the species at Nacogdoches, Texas. It is primarily a summer bee which is active from May to September, and it forages mostly on legumes, especially alfalfa and clovers. It passes the winter underground as a prepupa. Emergence is in May about two weeks after the start of transformation to the pupa. Females typically make nest burrows in hard-packed clayey soil near or among clovers, and excavated soil is left as a closed mound on top of each burrow. The finished nest burrow of the female is a slanting, winding tunnel with one to ten short lateral burrows radiating around it at successively deeper levels. Each lateral burrow ends in a polished, waxed cell containing a spherical pollen ball within a thin, transparent membrane,

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and one frankfurter-shaped white egg atop it. The tunnel is four millimeters in diameter, and is up to 162 millimeters deep. In Kansas two generations per season are usual; in eastern Texas there are three generations.

A grid of squares each 30 centimeters on a side was fixed in place to cover two nesting areas of 41 square meters which included about 250 nests during one season. The succession of nesting phenomena, and physical and biotic factors were studied. Male and female burrows are aggregated in distinctly separate areas. Both sexes spend the night in their burrows, and marked individual males and females returned repeatedly to their same overnight burrows. The bees are active in winds up to 32 kilometers per hour, air temperatures of 27 to 40°C., and soil surface temperatures up to 54°C. The stimulus for daily emergence is a combination of soil temperature and soil moisture. Watered plots showed that rainfall increased burrowing activity.

Males patrol fairly well delineated areas. Each selects a resting place on the ground—a twig, stone, or leaf—and sets forth in a definite flight pattern, returning and alighting repeatedly at the same place. They often fly out of their flight pattern to make a sortie over nearby clover flowers. Mating takes place at the flowers or on the ground near the female burrows. An intruder in the male flyway is engaged in an aerial "dogfight," the two tumbling over each other, falling to the ground, kicking up dust, and biting one another. The intruder is repulsed. This is the first example of territorial behavior in the Andrenidae.

The female emits an odor of oil of lemongrass when slightly squeezed. The first mounds of female burrows contain this odor, but those of the males lack it. Experimentation suggests that its biological role is in aiding females to recognize their nest.

Parasites of *Calliopsis* are the bees, *Holcopasites calliopsidis, H. illinoiensis, H. arizonicus,* and *Sphecodes* spp.; the pyemotid mite *Trochometridium tribulatum;* and the molds *Penicillium cyclopium, Aspergillus flavipes,* and *A. sydowi.* An undetermined species of robber fly is a predator. *Bombylius ater* bombards with her eggs those open burrows where wind has blown away the tumulus, and bombyliid larvae were found in a few *Calliopsis* cells with no traces of the immature *Calliopsis.*

INTRODUCTION

The genus *Calliopsis* includes 38 described species of solitary, ground-nesting bees having white, cream or yellow areas on the head, legs, and mesosoma, and lacking such color on the metasoma. As the genus is currently interpreted, its species occur only, and are distributed widely, in North and Central America. Four subgenera are recognized and described. The state of the genus remained confused until Michener's decisive handling of it in Muesebeck, Krombein, and Townes (1951). In that publication numerous species of North America north of Mexico erroneously described as *Calliopsis* were transferred to their correct generic assignment. The only reliable published key to a circumscribed group of *Calliopsis* species is that of Mitchell (1960) which includes the three species known from the eastern United States. Other keys are totally useless because 24 of the present species were unrecognized by the authors of the keys. Most of the original descriptions are inadequate in the light of present knowledge, and therefore all species are redescribed herein. The types deposited in the British Museum are unavailable to me, but excellent notes on certain characteristics of them have been furnished, on my request, by Padre J. S. Moure.

The investigation of the biology and ecology of *Calliopsis andreniformis*, the type species of the genus, was undertaken to form a frame of reference for similar work on other species. An attempt was made to collect meaningful data on diverse phases of the bee's biology and ecology so that even meagre data on other species would have a basis for comparison. The results of the investigation reveal striking resemblances to the biology of *Andrena, Perdita,* and *Nomadopsis* as discussed in appropriate places. My field observations have convinced me that *C. andreniformis* is potentially a valuable pollinator of small-flowered clovers, e.g., alfalfa. Its wide distribution, intense activity, great range of flowers visited, and the larger numbers in the field than museum collections indicate, all spell an important role for this species in the maintenance of native vegetation, especially among the Leguminosae and Compositae.

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I am grateful also to the National Science Foundation for support of the behavioral parts of this study, through a grant (G11967) for Professor C. D. Michener to the University of Kansas, and to the Society of the Sigma Xi for a Sigma Xi-RESA Grant-in-Aid in the summer of 1958 which made possible comparative biological observations on *Calliopsis teucrii* and *Nomadopsis scitula* at Coaldale, Colorado.

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Museum, Albany; I. H. H. Yarrow, British Museum (Natural History), London, England; F. N. Young, Indiana University, Bloomington.

I thank particularly Dr. Karl V. Krombein for comparing specimens with types in his care; Professor T. B. Mitchell for his loan of homotypes of some species not available to me; Professor P. H. Timberlake for his magnanimous gesture in lending me his entire collection of *Calliopsis* including type specimens and specimens of species he recognized as new some years ago. Recognition should be accorded my son, Roger, for his assistance in the field and laboratory.

My cousin, Dr. Sylvia Earle Taylor, merits a special note of thanks for contributing the fine scratchboard drawings of *Calliopsis andreniformis* and *C. anomoptera*. To my sister, Mrs. Virginia S. Griggs, I am happy to extend thanks for aid in the exhaustive checking, ordering, and recording of collection data from the specimens used in the study.

Lastly, it gives me pleasure to acknowledge the moral and financial help of both my parents and my wife's parents in the last stages of the study, for without their aid the completion of the work would have been much delayed.

DISTRIBUTION

Ecologically, the distribution of the genus *Calliopsis* is virtually unknown. The bits of information available suggest a group which nests in hard-packed clayey soil less, usually much less, than 100 m from its pollen source. As exceptions to generalities, *C. (Verbenapis) nebraskensis* has been taken digging in sand dunes in Minnesota, and *Calliopsis andreniformis* was taken by my son, Roger, nesting in loam beside salt marshes at Hancocks Bridge, New Jersey, where it used the pollen of the Copper Mallow *(Malva neglecta)*.

Flower preferences are relatively pronounced for each subgenus, and differ among them. Although *Calliposis s.s.* is widely polylectic, it has been collected mostly on Leguminosae, especially the small-flowered clovers. *Perissander* occurs principally on Euphorbiaceae. *Calliopsima* is found primarily on the Compositae, particularly the Astereae and Heliantheae, with many records for *Heterotheca* and *Grindelia*. *Verbenapis,* as its name implies, is an oligolege of *Verbena*.

Perissander is apparently restricted to arid areas, but the other subgenera are amply represented in mountains, deserts, plains, and cultivated land, but not in heavily forested areas.

Seasonal distribution is somewhat different among the subgenera: *Calliopsis s.s.* has its peak activity soon after summer begins; *Verbenapis* shows maximum activity shortly afterwards, about midsummer; and *Perissander* and *Calliopsima* have their peaks in late summer. It should be borne in mind that these seasons, of course, occur at different calendar months depending upon latitude and altitude. Table 1 gives the seasonal distribution of the species of *Calliopsis*.

TABLE 1. Seasonal Distribution of Species of *Calliopsis*

	Species	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1.	*andreniformis*				----	----	----	----	----	----	----		
2.	*teucrii*						----	----	----				
3.	*granti*								----				
4.	*rhodophila*					----	----	----	----	----			
5.	*mourei*						----						
7.	*squamifera*							----	----	----	----		
6.	*hondurasica*	----	----	----	----	----	----	----	----	----	----	----	----
8.	*peninsularis*									----			
9.	*sonora*								----				
10.	*empelia*								----				
11.	*zora*								----				
12.	*helenae*							----	----				
13.	*anomoptera*							----	----	----	----		
14.	*rogeri*								----	----			
15.	*syphar*									----	----		
16.	*limbus*							----	----				
17.	*gilva*								----	----			
18.	*fulgida*									----			
19.	*yalea*								----				
20.	*rozeni*				----		----	----	----	----	----		
21.	*coloradensis*						----	----	----	----	----		
22.	*pectidis*								----	----	----		
23.	*timberlakei*								----	----	----		
24.	*bernardinensis*								----	----	----		
25.	*unca*									----			
26.	*crypta*								----	----	----		
27.	*azteca*									----			
28.	*chlorops*							----	----	----			
29.	*coloratipes*							----	----	----	----		
30.	*deserticola*				----								
31.	*pugionis*				----	----	----	----	----				
32.	*hurdi*			----									
33.	*quadridentata*								----				
34.	*kucalumea*							----	----				
35.	*verbenae*				----			----	----	----			
36.	*nebraskensis*					----	----	----	----	----			
37.	*hirsutifrons*					----	----	----	----				
38.	*micheneri*			----	----								

Geographically, the genus occurs from coast to coast in North America and from latitude 50° North in Canada to latitude 8° North in Panama. No specimens are known from the northwestern United States and adjacent Canada, viz., northern California, Oregon, Washington, and British Columbia. There is a similar lack of specimens from El Salvador, British Honduras, and Nicaragua, presumably because of lack of collecting.

Calliopsis s.s. and *Calliopsima* are represented throughout the range of the genus. The distribution of *Perissander* is limited to southeastern Arizona and the Sonoran Desert in México, Arizona, California, and Baja California. *Verbenapis* has been collected only about Mexico City northward to New Mexico and Texas and in the plains states east of the Rocky Mountains with an isolated population from northern New Jersey. I expect it will eventually be found in most of the eastern United States.

The richest concentration of species in each of the subgenera occurs in México or the arid southwestern United States. These regions are well known for their diverse habitats and abundant opportunities for geographic isolation.

PHYLOGENY AND SYSTEMATICS

There is no fossil record of these bees nor is there such a record for any panurgine bee. This situation forced an interpretation of phylogenetic relationships deduced from species at one level in time, and this interpretation is based primarily upon comparative morphology of the adults supplemented by the available distributional data. The resultant diagram of relationships is given in Fig. 1.

In Fig. 1 the species *syphar* and *yalea* are depicted with a relationship to

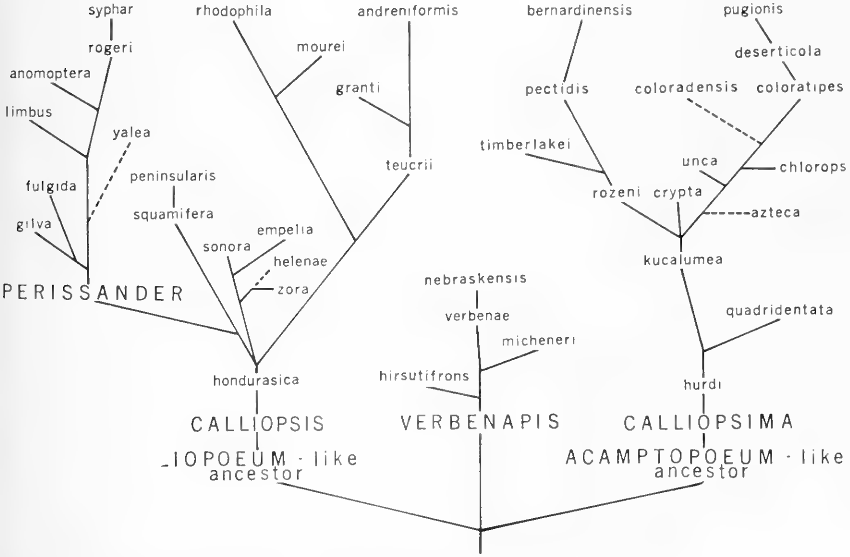


FIG. 1. Diagram of relationships of the genus *Calliopsis*.

Perissander. I believe they belong there, but this will only be determined upon discovery of the males. A dashed line indicates uncertainty.

Four genera of panurgine bees are closely related to *Calliopsis: Nomadopsis, Hypomacrotera, Acamptopeum,* and *Liopoeum.* Rozen (1951) has shown that the generic limits of these bees are questionable, and I agree with him. Various combinations of presumably important characters which appear in *Calliopsis* are found in these allied genera. The unsettled status of the genera makes it impossible to state which subgenera of *Calliopsis* have more primitive characters, and, moreover, it is not possible to make decisions upon which species within a subgenus are more primitive than others because particular specializations in each species are counterbalanced by other specializations in other species. This is the same predicament encountered by Rozen (1958) in his revision of *Nomadopsis.*

Three main types of male genitalia are represented among, and are characteristic of, the subgenera of *Calliopsis,* as explained below.

Type 1, *Calliopsis s.s.* and *Perissander:* penis short, thick; penis valve about twice penial length, in form of a thin, broad sheet which is usually wider medially, convex dorsally with intricate folds, lines, and thickenings, and hollowed ventrally; volsellae small, well-separated, knoblike or lobelike. See Figs. 8-57.

Type 2, *Calliopsima:* penis long, slender; penis valve narrow, tubular, slightly exceeding length of penis, having an expanded, flattened, dorsally directed terminal portion; volsellae large, well-separated, elongate. See Figs. 58-122.

Type 3, *Verbenapis:* penis long, thick; penis valve narrow, medio-ventrally concave, terminal portion directed dorsally, tip bent toward mesal line; volsellae small with projections so close as to give the impression of a single structure. See Figs. 123-143.

Primarily on the basis of a study of the genitalia and sterna of panurgine bees which are likely relatives of *Calliopsis,* I have concluded that the genera most closely related to it are the North American *Nomadopsis* and *Hypomacrotera,* and the South American *Acamptopoeum* and *Liopoeum.* The superficially somewhat similar South American genera *Spinoliella, Callonychium,* and *Arhysosage* (=*Ruiziella* Timberlake) do not belong in the same group. *Hypomacrotera* and *Micronomadopsis* parallel *Calliopsis s.s.* in male genitalia and sterna, yet are closer to *Verbenapis* on the basis of external characteristics.

The diagnosis excludes all panurgine genera except the South American *Acamptopoeum* Cockerell and some species of *Liopoeum* Friese. This is deliberately contrived because until a thorough review of the classification of the panurgine genera closely related to *Calliopsis* is completed, I am inclined to favor the possibility suggested by Michener (1944:246) that the "South

American genus *Parafriesea=Acamptopoeum* . . . is probably a mere subgenus of *Calliopsis*." I believe the species included by J. S. Moure (1956, personal communication) in *Liopoeum* represent more than one genus, but those considered by him to be *Acamptopoeum* are a clearcut group of closely related species. The differences and similarities among the subgenera of *Calliopsis* seem to be of the same order of magnitude as those between *Acamptopoeum* and any one of them. In any event, if my interpretation of the content of *Calliopsis* presented herein proves acceptable, then surely *Acamptopoeum* must fall as a subgenus of the older *Callopsis*. Padre Moure, however, would unhesitatingly accord generic rank to *Calliopsis s.s., Calliopsima, Perissander,* and *Verbenapis* (1957, personal communication). With such a classification, *Acamptopoeum* would also be of full generic rank. An investigator's position on a problem like this depends upon personal psychology, philosophy, and taste.

Species from South America which most closely resemble the genus *Calliopsis* as herein constituted are *Liopoeum hirsutulum* Friese, 1908 (not Spinola, 1851), and two apparently undescribed species of *?Liopoeum* (one may be *Camptopoeum laetum* Vachal) from Argentina. The latter two species may prove eventually to represent yet another group intermediate among *Calliopsis s.s., Calliopsima, Liopoeum,* and *Acamptopoeum*. Color patterns and head dimensions of *Calliopsima* are similar to those of *Acamptopoeum*. *Verbenapis* is most similar, among South American bees, to *Liopoeum trifasciatum* (Spinola, 1851); a number of important external characters are shared. These are, for example, placement of cream areas on face in the female; shape of face; presence of a few *curled hairs* on front tarsomeres 2-4; similar propodeum; and similarly shaped and sloped metasomal tergum 1. The genitalic pattern of *L. trifasciatum* is that of *Calliopsis s.s.,* however, although three or four metasomal terga bear yellow maculae. *Liopoeum* is a more likely progenitor of *Nomadopsis* than is *Spinoliella*. No counterparts of *Perissander* are known to me from South America.

The absence of closely related forms in the Palearctic region and the paucity of species in the northern and eastern United States, together with the numerous closely related forms from South America, argue for an origin of *Calliopsis* in South America with migrations northward through Central America and Mexico to the United States and Canada.

Taxonomically useful characters at the subgeneric level were relatively few with the females, but included hair color of the prepygidial and pygidial fimbriae; length of mouthparts; sculpture of the dorsal enclosure of the propodeum; extent of light color on the paraocular area; and relationships among the minimum interocular distance, clypeocellar distance, and flagellar length. The most reliable and hence the most useful bases for subgeneric groups, as well as for discrimination of species, were the male genitalia and sterna 5, 6, 7, and 8. Other useful ones for subgeneric grouping of the males were length of mouthparts, sculpture of the dorsal enclosure of the propodeum, extent of light color in the paraocular areas, color of subantennal plates, and presence or absence of scutellar and metanotal hair pads. No reliable differentiating character was found for the females of *Perissander;* the male must be known to make a positive subgeneric assignment.

Considerable difficulty was experienced in finding reliable characters to separate females of several closely related species. The most important criterion in every such case was the sculpture of the dorsal enclosure of the propodeum or the punctation and ground character of the integument of the scutum and metasomal terga 1 and 2.

The bases for the matching of the sexes, among sympatric species, are primarily the similarity of the punctation of the scutum and of metasomal terga 1 and 2 and the striking resemblance of the mouthparts other than the mandibles. Matching of the sexes proved troublesome in the case of the species *crypta* and *rozeni.* Most students of the wild bees assume that the capture of male and female bees *in copulo* is virtually proof that they are the same species. The following paragraph, however, shows that this may not be the case.

Initial analysis of the species in *Calliopsima* led me to group females of *chlorops, crypta,* and *rozeni* all under *chlorops.* This grouping was based on too few specimens for the recognition of *crypta* and *rozeni.* Specimens received recently have clarified the status of the three species involved. J. G. Rozen and G. I. Stage, both competent collectors, supplied mating pairs of *Calliopsis* including a male of *rozeni* in each case. Rozen's pair, however, included a female different from the one in Stage's pair. On the basis of the close similarity of both punctation and vestiture of Stage's male and female, I concluded that they were the same species and that Rozen's female represented *crypta.* Is it possible that females of these sympatric species resemble each other so closely that their respective males may make an error in identity and copulate with the wrong female?

Characters useful at the specific level included various quantitative dimensions and ratios among them, as well as qualitative characters, as noted in the keys and taxonomic treatments of the species. The black or dark brown integumental color is subject to fading, e.g., the female type of *teucrii* was described as "black . . . clypeus entirely black . . . tegulae shining piceous. . . ." The specimen is now brown to light brown. Fading is equally striking in older specimens of *chlorops, coloradensis, nebraskensis,* and *verbenae,* among others. The white, cream, or yellow maculations do not seem to change in quality. Because of fading, differences in darkness of ground color are described only in extreme cases, and the integument is to be taken as dark, nonmetallic, for all species unless otherwise described.

DESCRIPTIVE TERMINOLOGY AND METHODS

ABBREVIATIONS. These are held to a minimum and include the following:

2-5, 1-4, 9-wt, etc. Read as "2 to 5 inclusive, 1 to 4 inclusive," or "distance from position 2 to position 5, distance from position 9 to position wt," etc.

mio=minimum interocular distance.

mm=millimeter(s).

mow=middle ocellar width(s).

N.A.=not available, used where a structure cannot be examined or measured, usually because of its absence, the fragility of the specimen, or the unavailability of the specimen to me.

pwa=puncture width(s) apart.

S.W.R.S.=Southwestern Research Station of the American Museum of Natural History, 5 miles west of Portal, Chiricahua Mountains, Cochise County, Arizona.

wing, 12-13/13-14=forewing, the ratio of the distance between 12 and 13 to the distance between position 13 and 14 (cf. Fig. 5).

TERMINOLOGY. The terminology followed in the systematic portion of the paper is basically that of Michener (1944). An explanation or equivalent of certain terms which are used in this work or have been used in older works treating *Calliopsis* species is given below. The terms used here are italicized.

apicotarsus: collective term for the last four tarsomeres; used in apposition to basitarsus.

light coloration on the subantennal plates=dog-ear marks (Cockerell).

dorsal enclosure of the propodeum=disc of metathorax (Robertson)=horizontal (usually somewhat declivous) enclosure of the propodeum=basal, or upper, portion of the propodeal triangle. It differs markedly from the remainder of the propodeal triangle by its sculpturing.

eccentric punctures=punctures deviating from radial symmetry in being shallow at one end, becoming deeper with a vertical, or nearly vertical, wall at the other end.

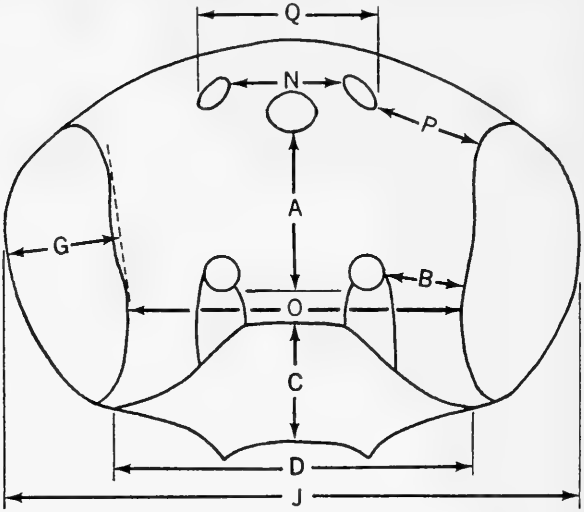
galeal gap=the distance between the tip of the galea in repose and the base of the prementum.

-mere=suffix used with tarsus and flagellum to designate real or apparent segments, e.g., tarsomere.

orbital convergence ratio=the ratio of the middle ocellar interocular distance (at the level of the lower border of the middle ocellus, Fig. 3,T) to the minimum interocular distance. It is used as a measure of the degree of ventral convergence of the inner orbits.

pebbled=a type of integumental sculpturing which resembles the surface of pebble-grained leather.

pronotal lobes=tubercles=the lobelike, dorsolateral projections of the pronotum.



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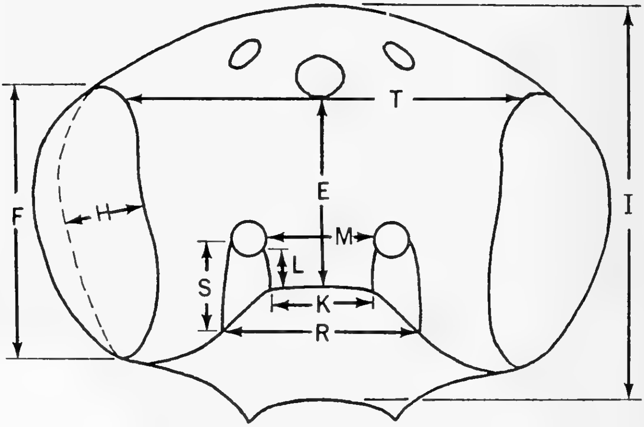

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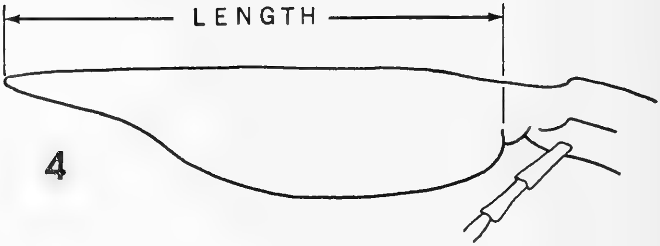

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propodeal flats=the posterolateral faces of the propodeum, immediately adjacent to the propodeal triangle, where such faces are relatively plane, sometimes medially convex, areas.

scutellar and *metanotal hair pads*=calluslike areas of mesoscutellum and metanotum of certain *Calliopsis* males (Timberlake)=well-defined patches of dense, extremely short, profusely branched—hence mosslike—pubescence, which occupy, respectively, the depression between the disc of the scutellum and the base of the hind wing, and the lateral portions of the metanotum.

scutellum=mesoscutellum.

scutum=mesoscutum=thoracic dorsulum (Cockerell).

sternum=metasomal sternum, where unqualified.

tergum=metasomal tergum.

MEASUREMENTS. Head and galeal measurements are shown in Figs. 2-4.

All measurements are given in millimeters and were made at 30× magnification with a Bausch & Lomb StereoZoom(R) Microscope and an ocular micrometer with each micrometer unit equal to 17 microns or 0.017 mm. The precision of the decimal ratios can be inferred from the number of digits given, the last digit being the doubtful one.

Lengths of scutum, scutellum, metanotum, and propodeum are measured along the median longitudinal line. The intertegular distance is the minimum distance measured transversely across the scutum between the edges of the concavities of the thorax which receive the tegulae. Forewing length is length including tegula. Hindwing length is from the junction of the wing with the thorax to the wing tip. It is as good an indicator of general body size as the forewing.

The forewing of a male *Calliopsis andreniformis* is illustrated in Fig. 5. An arbitrary numbering system was used in the analysis of similarities and differences of the wings within and among species. Lengths of wing veins were measured from the midpoints of the vein intersections shown. The length of the marginal cell was taken as the maximum length measured between the *inside* edges of the bordering veins. Distance from the tip of the marginal cell to the wing tip was measured at 9-wt (Fig. 5).

Abdominal width is the maximum width and invariably occurs on metasomal tergum 3.

FIGS. 2-4. Measurements of head and galea. 2-3: A, frontal line; B, antennocular distance, minimum; C, clypeal length, median; D, clypeal width, the lateral limit usually mesal to the lowest point on the orbit; E, clypeocellar distance; F, eye length; G, eye width, facial view; H, eye width, basal, the straight line distance between anterior and posterior orbital margins; I, head length; J, head width, maximum; K, inner subantennal sutural distance, minimum; L, inner subantennal suture, vertical length; M, interantennal distance; N, interocellar distance; O, interocular distance, minimum; P, ocellocular distance, minimum (=ocellocular line); C + E, ocellolabral distance; Q, outer ocellar distance; R, outer subantennal sutural distance; S, outer subantennal suture, vertical length; T, interocular distance at level of median ocellus. 4: Galea, lateral view, showing measurement of length.

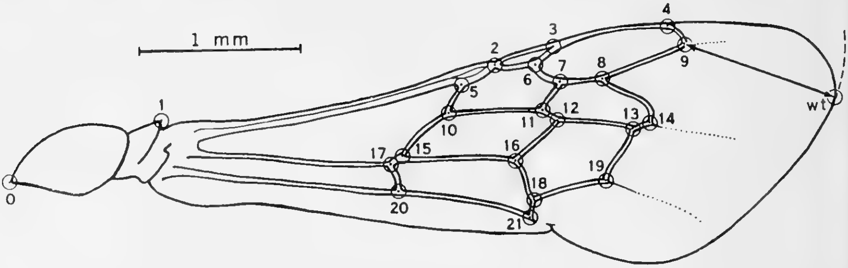


FIG. 5. Forewing of male *Calliopsis andreniformis*. Wing dimensions are obtained by measuring point to point, 0-wt, wing length including tegula; 1-2, length of vein C; 2-3, length of stigma; 2-5, length of prestigma; 2-6, length of stigma from base to vein r; 3-4, length of marginal cell (=2nd R_1) along costal margin of wing; 3-4-9, length of vein R_1; 5-10, basal side of 1st submarginal cell (=1st abscissa of R_s); 6-7, length of crossvein r; 6-9, length of marginal cell; 7-8, length of costal side of 2nd submarginal cell (=2nd abscissa of R_s); 8-9, length of free part of marginal cell (=3rd abscissa of R_s); 10-11, length of posterior side of 1st submarginal cell (=R_s+M); 10-15, length of basal vein (=1st abscissa of M); 11-12, distance from 1st transverse cubital or intercubital to 1st recurrent vein (=2nd abscissa of M); 11-14, length of posterior side of 2nd submarginal cell (=2nd to 4th abcissae of M); 12-13, distance between anterior ends of recurrent veins (=3rd abscissa of M); 12-16, length of first recurrent vein (=1st m-cu); 13-14, distance between transverse cubital and 2nd recurrent veins (=4th abscissa of M); 13-19, length of 2nd recurrent vein (=2nd m-cu); 15-16, length of 1st abscissa of Cu; 15-17, distance from cu-v to basal vein; 15-18, length of Cu; 16-18, length of 2nd abscissa of Cu; 17-20, length of transverse medial crossvein (=cu-v); 18-19, length of Cu_1; 18-21, length of Cu_2; 20-21, length of 2nd abscissa of V.

The word "distance" as well as the dimensional units are usually omitted from various facial and body measurements to save needless repetition, and where units are not specified they are millimeters, e.g., "clypeocellar 0.85" means that the clypeocellar *distance* is 0.85 mm.

Basitarsal length in *Verbenapis* is measured along the lateral median line and hence excludes the ventral apical prolongation present in this subgenus; basitarsal length in the other subgenera is measured from extreme base to apex which includes any apical prolongation present.

NOTES ON TECHNIQUES. In various places a magnification is specified for an observation by placing it in parentheses following the observation. For example, "facial fovea shiny, unsculptured (15×)." This is done because terms such as shiny, impunctuate, polished, unsculptured, etc., are sometimes applicable only within a certain range of magnification, and the above statement, while true, might also read "facial fovea dull, roughened (120×)."

Optimum lighting is diffused daylight, and the Bausch & Lomb Fluorescent Illuminator used in this study yielded 500 foot candles of illumination at the specimen. Integumental punctation and propodeal sculpture will be obscured or distorted for some species with undiffused light.

Accurate measurements of mouthparts may occasionally be necessary. Where relaxation in a moist chamber followed by manual manipulation failed to extend the mouthparts as desired, I used the following method: relaxed specimen in a moist chamber; dissected away mouthparts and placed them in cold lactophenol solution; brought to boiling point and held there until structures extended; rinced in hot glycerin; allowed to cool; transferred to fresh glycerin for measurements. This method has worked on specimens 80 years old.

The same technique produces cleared genital and sternal preparations which retain their deposited melanins and fine hairs. I find this superior to the caustic potash treatment except that occasionally the genital capsule has entrapped air which, on expansion and escape, tears the capsule.

DESCRIPTIONS. The description of a new species is based upon the holotype and allotype with parenthetical notes referring to paratypes which differ significantly from the type. Variation of other specimens is discussed under Remarks or Geographic Variation.

Redescription of a previously described species is treated in a similar manner when the type(s) is available. Otherwise the redescription is based on metatypes, homotypes, notes made on types by a reliable hymenopterist, topotypes, or the most representative specimen among all available, with parenthetical notes referring to specimens which differ significantly from the described specimen.

The initial part of the description of each sex of a species gives measurements which are general indicators of the size of the bee. Least reliable is the length of the bee, because it is dependent upon the degree of extension of both head and metasomal terga. Clypeal length is the measurement showing the highest correlation with the length of the bee.

A number is given to each character or group of characters described for each subgenus and each species. This numbering is used to facilitate comparisons among the taxa. Where a particular number is absent for a given species, the character is not of comparative importance for the subgeneric or species group in which the species occurs.

Descriptions of the species ordinarily omit verbal treatment of the genitalia and sterna because the illustrations are adequate in themselves. Details of those which are of particular significance in separation of closely allied species are designated by an arrow on the illustration which points to the diagnostic feature.

Detailed collection data are given for new species, but such data are given only for the uncommon redescribed species.

Distributional maps depict the known range of each species. Collections and biological data are too few to attempt prediction of the total range of most species. Each symbol for a species represents one or more specimens collected at that locality, and in some cases represents several collections made at nearby localities. This procedure is justified on a small scale map provided that the collections so plotted are from similar localities. Of course, every locality is listed in the written treatment.

TAXONOMIC TREATMENT

Genus CALLIOPSIS Smith

Type species. Calliopsis andreniformis Smith, 1853, by designation of Ashmead, 1889, Trans. Amer. Ent. Soc. 26:85.

DIAGNOSIS: (a) American panurgine bees with white, cream or yellow integumental markings on head, mesosoma, and their appendages, on a black ground, metasoma without such light markings; (b) marginal cell truncate apically, its length along costal margin of wing beyond apex of stigma subequal to or less than distance from its tip to tip of wing, except in *anomoptera;* (c) two submarginal cells, lengths along posterior margins subequal; (d) second submarginal cells along longitudinal axis of wing much longer than broad; (e) middle tarsus of male longer than hind tarsus; (f) horizontal portion of propodeum impunctate with various sculptural patterns or smooth and shiny with depressions; (g) metasomal terga with conspicuous, although not necessarily complete, bands of light hair along posterior margins (1×).

FEMALE. Length 5-10 mm. Integument sculptured or smooth, unsculptured (120×).

Head. Integumental background color black, occasionally metallic. Light colored areas: (1) paraocular area; (2) clypeus; (3) labrum, sometimes absent; (4) supraclypeal area, except usually absent in *Verbenapis;* (5) subantennal plate, often absent, and variable intraspecifically; (6) mandible, basal position, or absent, tip reddish or reddish brown. (7) Scape, pedicel, and dorsal surface of flagellomeres 1-4 brown to black, ventral surface usually much lighter with darker color of flagellomeres 1-3 (sometimes 4) encircling part way ventrad, flagellomeres 5-10 of uniform color ventrally. (8) Hair of head variable from black to white, but hair of gena always white. (9) Punctures usually finer than in corresponding male. (10) Puncture size and density variable. (11) Frontal line with lower portion moderately elevated, narrowly sulcate, rarely weakly carinate. (12) Clypeus evenly convex or with lower half of disc flattened or medially concave, slightly to strongly protuberant beyond anterior edge of eye in profile. (13) Inner orbits convergent below: orbital convergence ratio 1.05-1.30. Facial fovea shallow, indistinct to deep, distinct; narrow, linear to broad, ovoid. (14) Galea variable in length, shape, and sculpture; galeal gap absent to about 3.8 mow. Glossa cylindrical, flabellate (flat, truncate, flabellum absent in *squamifera, peninsularis,* and *anomoptera* group of subgenus *Perissander.* (15) Head width/head length, 1.2-1.5. (16) Median apical border of clypeus below orbit by 0.5-1.3 mow. (17) Ratios of eye length, mio, and flagellar length variable. (18) Interocellar, ocellocular, antennocular, interantennal variable with respect to each other. (19) Ocellolabral subequal to or greater than clypeal width. (20) Clypeocellar greater than outer subantennal sutural. Outer subantennal sutural 2 times or more length of inner subantennal sutural. (21) Basal labial palpomere from 1.5-6.0 times length of others combined. (22) Flagellomere 1 longer than 2, 2 shorter than 3, 3 shorter than 4. Flagellum with maximum width subequal to mow. Flagellar length 1.8-2.8 times length of scape, relatively uniform within a subgenus.

Mesosoma. (23) Integumental background color black, occasionally metallic. Light colored areas: medially interrupted stripe along posterior dorsal border of pronotum except in *Verbenapis;* pronotal lobe, often; scutellar crest, often. (24) Scutal and scutellar hair variable in length, density, and color. Mesepisternal hair white, usually longest of mesosoma, flowing, with numerous minute branches. Posterior half of scutellum with many long, erect hairs. Metanotal hair white to fulvous, with long, medial hairs directed posteriorly but curving upward apicad. A narrow strip of white to fulvous, densely branched, minute hairs clustered along scutellar crest. Metanotum with similar strip along posterolateral border, of greater extent, hair sparser, longer. Scutellar and metanotal hair pads absent or obsolete. Propodeal hair white. (25) Scutal disc with punctures and character of interspaces variable. (26) Dorsal enclosure of propodeum completely smooth to variously sculptured, only rarely with a few punctures. (27) Legs with light color usually the same as on face. Foreleg with light coloration. (28) Middle leg with light coloration. Spur no more than 0.8 times basitarsal length, pectination variable (absent in *squamifera*). (29) Hind leg dark except in the closely related species *pectidis, timberlakei,* and *bernardinensis*. (30) Tegula usually transparent, at least posteriad, often with anteroapical patch of light color. Humeral plate white to brown. (31) Wing iridescent, colorless or faintly smoky to brown in the apical region beyond cells. Costal vein progressively darker apicad. Subcostal vein brown, darkest in the wing. Stigma slightly wider, or narrower, than prestigma, width including costal vein in both cases. (32) Marginal cell 6-9 and 3-4 variable with respect to 9-wt, see Fig. 5.

Metasoma. (33) Integumental background color of terga black (except orange to reddish on some terga of *anomoptera*), occasionally with metallic tints, of sterna black to brown. (34) Tergal hair bands white or fulvous, denser laterad. Band of tergum 1 usually sparse or interrupted medially. Suberect hair of discs of terga 4-5 black to white. Prepygidial and pygidial fimbriae smoky to white. (35) Tergum 1 with punctures variable. (36) Tergum 2 with punctures of median area finer, denser than tergum 1. Pygidial plate present, distinct, narrowly rounded apically. (37) Sternal color testaceous to black, light coloration absent. Sternum 6 usually with a median, clear (rarely extremely dark) circular or subcircular area in the apical sclerotized portion (indistinct in some specimens).

MALE. Length, 4-9 mm. Integument as in female.

Head. Integumental background color as in female. Light colored areas:

(1) paraocular area; (2) clypeus, except for narrow, testaceous to black apical border and two tiny, testaceous to black wedge-shaped marks always present near dorsolateral corners of median portion; (3) labrum, rarely absent; (4) supraclypeal area (sometimes absent in *Verbenapis*); (5) subantennal plate (absent in *Verbenapis*); (6) as in female. (7) As in female but of lighter hue than corresponding female. (8,9,10) As in female. (11) Frontal line with lower portion moderately to strongly elevated, either narrowly sulco-carinate or sharply carinate. (12) As in female. (13) Inner orbits more strongly convergent below than in female: orbital convergence ratio about 1.15-1.45. Facial fovea obsolete to distinct; smaller than that of female; shape similar to that of female. (14) As in female. (15) Head width/head length about 1.10-1.50. (16, 17) As in female. (18) Interocellar variable with respect to ocellocular, both greater than either antennocular or interantennal; antennocular greater than interantennal. (19,20,21) As in female. (22) As in female but flagellomere 1 sometimes subequal to or shorter than 2. Flagellum with maximum width subequal to mow. Flagellar length 2.8-4.2 times length of scape.

Mesosoma. (23) As in female except all subgenera exclusive of *Verbenapis* have some species with more or less extensive light color on sterna. (24) Scutal, scutellar, mesepisternal and metanotal hair similar to that of female. Scutellar and metanotal hair pads present in *Calliopsis s.s.,* absent in other subgenera. (25,26) As in female. (27) Legs with light color usually the same as on face. Foreleg with more extensive light coloration than in female. (28) Middle leg with more extensive light coloration than in female. (29) Hind leg with much more extensive light coloration than in female except in *Verbenapis* where leg may be completely brown or have only basitibial plate with light coloration. (30,31,32) As in female.

Metasoma. (33,34) As in female. (35) Tergum 1 with punctures of median area as in female but rarely sparse. (36) As in female but often less distinct. (37) As in female but rarely with some yellow. (38) Genitalia without gonostyli, penis not fused with penis valves. Sterna and genitalia distinctive for the subgenera as described.

DISCUSSION. The diagnosis excludes the distantly related genus *Perdita* by the combination of characters (b,c,d), and usually (a); the closely related *Nomadopsis* by the combination of (a,b,g); and the equally closely related *Hypomacrotera* by the combination of (b,e,g).

KEYS TO THE SPECIES OF *Calliopsis*

The following keys are separated by sexes because of dimorphism in all species. Every attempt was made to avoid characters requiring dissection, but this was not always possible. The section on Descriptive Terminology and Methods should be consulted before use of the keys, with special attention being given to the part on measurements. It has been possible for the most part to place related species together, and this should help in the final determination which might have to be based upon the description of the species.

The male terminalia are illustrated by drawings which portray their average condition, but minor variations are to be expected. In some instances, an arrow points to a particularly significant condition which is mentioned in the keys or in the descriptive treatment of the species.

MALES

1\. Dorsal area of propodeum unsculptured, highly polished, with median depression with longitudinal, low ridge giving impression of twin pits; subantennal plates black (subgenus *Verbenapis*) 2

Dorsal area of propodeum sculptured, or, if polished, lacking kind of depression described above; subantennal plates variable in color 5

2(1). Tegula with opaque white patch on outer anterior portion; pygidial plate with sides at angle of less than 35°, length of margined portion of plate about 2.0 times width at base; depth of incision between lobes of sternum 6 twice width of a lobe .... *micheneri*

Tegula without white coloration; pygidial plate with sides at angle of 40° or more, length of margined portion of plate less than 1.5 times width at base; depth of incision between lobes of sternum 6 equal to or less than width of a lobe 3

3(2). Hind basitarsus light brown to dark brown; elevation bordering anterior edge of posterior depressed margin of metasomal tergum 1 absent medially (use 20× or less); punctures of medial area of dorsum of tergum 1 finer than mesoscutal punctures, mostly 2 or more pwa .... *nebraskensis*

Hind basitarsus whitish or cream colored; elevation bordering anterior edge of posterior depressed margin of metasomal tergum 1 entire; punctures of medial area of dorsum of tergum 1 as large or larger than mesoscutal punctures, mostly 1-2 pwa .. 4

4(3). Clypeus entirely cream colored with two small brownish triangular clypeal dots; supraclypeal area usually with a cream dot; eye length exceeding minimum interocular distance; hindwing length 2.7-3.3 mm. .... *hirsutifrons*

Clypeus cream colored except for triangular brown dorsolateral corners; supraclypeal dot absent; eye length less than minimum interocular distance; hindwing length 3.5 mm. or more .... *verbenae*

5(1). Without velvety patches of dense, short, moss-like hairs on the lateral portions of the scutellum and metanotum *(Perissander* and *Calliopsima)* 6

With velvety patches of dense, short, moss-like hairs on the lateral portions of the scutellum and metanotum (*Calliopsis* s.s.) 10

6(5). Sternum 6 with a pair of long, mesolateral, posteriorly directed, directed, subacicular processes; ratio of length of middle tibia to length of middle basitarsus less than 0.95; mesopleural punctures very fine, some indistinct, mostly more than 2 pwa; galea usually not exposed beyond closed mandibles, but may extend as much as 1 mow in *gilva;* penis valve broad, width one-third or more of length; penis short, scarcely reaching to midlength of penis valve *(Perissander)* 7

Sternum 6 with a pair of short, mesolateral, variously directed, variously shaped (but never subacicular) processes; ratio of length of middle tibia to length of middle basitarsus greater than 1.00; mesopleural punctures large, deep, distinct, mostly less than 2 pwa; galea always exposed beyond closed mandibles, length exposed usually more than 2 mow; penis valve narrow, width about one-eighth of length; penis long, almost reaching apex of penis valve *(Calliopsima)* 18

7(6). At least terga 1-3 reddish orange; forewing with tip bent abruptly posteriad and drawn out into a rounded apex (Fig. 5) .... *anomoptera*

Terga 1-3 black, or black with metallic tints; forewing with tip normal (Fig. 4) 8

8(7). Thoracic dorsum and terga 1-4 with brassy tints (30×); wing tip distinctly brown to the naked eye; sternum 8 in ventral view with apical portion paddle-shaped, the paddle portion about as long as broad .... *rogeri*

Thoracic dorsum and terga 1-4 without metallic tints (30×); wing tip clear to smoky to the naked eye; sternum 8 in ventral view with apical portion distinctly longer than broad 9

9(8). Scutal punctures with smooth, shiny interspaces (30×); hind tarsomere 2 cylindrical to club-shaped in dorsal view; eye length about one-sixth greater than mio .... *gilva*

Scutal punctures with interspaces roughened; hind tarsomere 2 equilaterally triangular in dorsal view; eye length subequal to mio .... *limbus*

10(5). Scape with ventral surface largely yellow 11

Scape with ventral surface entirely dark 15

11(10). Scape entirely yellow, except sometimes with a small triangle of light brown with base at mesolateral apex of scape, apex of triangle attenuate ventrally and not reaching middle of scape; metanotal hair pads dark brown to black (pale brown in Baton Rouge, La., specimen), small, separated by 3 mow; hind femur often with a brown patch posteriorly .. *andreniformis*

Scape partly yellow on ventral surface and sometimes on dorsal surface, too, with at least a large area of the mesolateral apical corner brown or black (if brown area is apparently small, then flagellum much longer than head); metanotal hair pads tan or gray, or if brown then separated by less than 1 mow; hind femur yellow 12

12(11). Tegula with a yellow patch; tiny species with hindwing length (or forewing 1-9) from 1.90 to 2.30 mm .... *squamifera*

Tegula brown; larger species with hindwing length (or forewing 1-9) 2.63 mm, or larger 13

13(12). Metanotal hair pads tan to pale brown, separated by more than 3 mow .... *hondurasica*

Metanotal hair pads brown or gray, separated by less than 1 mow 14

14(13). Flagellar length subequal to head length, about one-fifth longer than head width, about 3.5 times scape length; metanotal hair pads brown; Sonora, Mexico .... *sonora*

Flagellar length about one-fourth longer than head length, subequal to head width, about 4.0 times scape length; metanotal hair pads gray; southeastern Arizona .... *empelia*

15(10). Integument with metallic cobalt blue tints on dark frons, vertex, and thoracic dorsum, and metallic green tints on metasomal terga; light markings of face, pronotal lobe, and interrupted posterior pronotal stripe, white or cream color; light markings of legs yellow; state of México .... *mourei*

Integument either non-metallic or with brassy tints especially on lower frons, vertex and thoracic dorsum, and with or without brassy tints on metasomal terga; light markings of face, pronotal lobe, interrupted posterior pronotal stripe, and legs concolorous, yellow 16

16(15). Metanotal hair pads ligulate, confined to metanotum, separated by two-thirds or more mow .... *teucrii*

Metanotal hair pads large, subquadrate or oval, covering dorsal propodeum, contiguous, at least posterioly 17

17(16). Integument black; scutellar hair pads separated by less than 2 mow; metanotal hair pads subquadrate; galea aciculate, smooth, shiny, length exposed beyond closed mandibles about three times galeal gap; punctures of disc of scutum fine, about 2 pwa, interspaces smooth .... *rhodophila*

Integument black with brassy tints, especially on head and thoracic dorsum; scutellar hair pads separated by more than 2 mow; metanotal hair pads oval; galea narrowly rounded but not aciculate, uniformly pebbled, length exposed beyond closed mandibles subequal to galeal gap; punctures of disc of scutum larger, about 1 pwa, interspaces shiny but finely roughened, more so anteriad .... *granti*

18(16). Pedicel with anterolateral surface yellow; scape entirely yellow or at most with brown apical rim or brown line on posterior surface; all coxae with at least a spot of yellow about half the area of median ocellus 19

Pedicel brown (1 specimen of *bernardinensis* with anterolateral surface yellow); scape, posteriorly and at least mesoapical corner anteriorly, brown; all coxae brown, or at most a tiny patch of yellow on the fore coxae 20

19(18). Scape entirely yellow or at most with light brown apical rim; ratio of maximum length of middle tibia to maximum length of middle basitarsus 1.00-1.08; scutal punctures not visible from directly above because of profuse branching of dense, short (about 1 mow), hairs (30×); punctures of scutal disc mostly less than 1 pwa .... *pectidis*

Scape yellow except for brown apical rim and narrow brown triangle with apex attenuated toward base of scape on posterior surface; ratio of maximum length of middle tibia to maximum length of middle basitarsus 1.11-1.29; scutal punctures visible from directly above, hairs with very short branches, longer (mostly 2 mow) (30×); punctures of scutal disc mostly 1-2 pwa .... *timberlakei*

20(18). Scape entirely brown to black 21

Scape with yellow on anterior surface 25

21(20). Front apicotarsus yellow; marginal cell 6-9 about one-sixth to one-fifth longer than 9-wt. 22

Front apicotarsus brown; marginal cell 6-9 about one-fourth to one-third longer than 9-wt. 23

22(21). Expanded midlateral portion of metasomal sternum 8 bearing sharp points at posterior corners; posteroventral projections of base of genital capsule small, short, rounded .... *chlorops*

Expanded midlateral portion of metasomal sternum 8 smoothly rounded at posterior corners; posteroventral projections of base of genital capsule large, long, sharply pointed .... *crypta*

23(21). Tegula with yellow macula; tip of humeral plate yellow; expanded midlateral portion of metasomal sternum 8 smoothly rounded at posterior corners; anterior surfaces of front and hind tibiae entirely yellow; genital capsule with four posteroventral projections from base .... *quadridentata*

Tegula without yellow macula; humeral plate entirely brown; expanded midlateral portion of metasomal sternum 8 bearing sharp (sometimes tiny!) points at posterior corners; anterior surfaces of front and hind tibiae with large areas of brown; genital capsule with two posteroventral projections from base 24

24(23). Outer surface of hind basitarsus brown; basal labial palpomere with length 3 or more times combined length of remaining palpomeres (1.14:0.36); length of galea exposed beyond closed mandibles about 4 times galeal gap .... *hurdi*

Outer surface of hind basitarsus yellow with brown border; basal labial palpomere less than 2.6 times combined length of remaining palpomeres (0.78:0.34); length of galea exposed beyond closed mandibles less than 2 times galeal gap .... *kucalumea*

25(20). Twin mesolateral posterior projections of metasomal sternum 6 flat (readily observable on intact specimens) 26

Twin mesolateral posterior projections of metasomal sternum 6 bent distinctly ventrad thus forming a pair of short to rather long prongs 28

26(25). Front and middle apicotarsi bright yellow; anterior surface of hind tibia yellow; anterior surface of hind basitarsus yellow, often with partial or complete brown border .... *rozeni*

Front and middle apicotarsi testaceous to brown; anterior surface of hind tibia half or more brown; anterior surface of hind basitarsus brown 27

27(26). Length of galea exposed beyond closed mandibles 3.0-4.5 times galeal gap; interantennal more than 1.8 times galeal gap; mow less than maximum flagellar diameter; tegula and tip of humeral plate with yellow maculation; Colorado Desert .... *deserticola*

Length of galea exposed beyond closed mandibles less than 2.5 times galeal gap; mow greater than maximum flagellar diameter; tegula and humeral plate brown; southwestern California .... *pugionis*

28(25). Hair bands of metasomal terga 1-4 complete, dense, snow-white, hairs erect with somewhat decumbent apices, profusely branched, integument below bands not or barely visible from above; punctures of entire middle third of metasomal tergum 1 uniformly crowded, about one-third pwa; metasomal sternum 7 with median portion broad apically (Fig. 78); southwestern California .... *bernardinensis*

Hair bands of metasomal terga 1-4 never all complete, hairs sparse, whitish, appressed, branches virtually nonevident (30×), integument below readily visible from above; punctures of entire middle third of metasomal tergum 1 not uniformly crowded, more than one-half pwa; metasomal sternum 7 with median portion narrowed apically (Fig. 59); not known from California 29

29(28). Fore tibia with posterior surface yellow or yellow at apex and base with a patch of brown medially; hind tibia with posterior surface yellow or yellow with a median patch of brown, rarely brown patch at tibial apex 30

Fore tibia with posterior surface brown or brown except for basal area subequal to 2 times area of median ocellus; hind tibia with posterior surface brown or brown with yellow outer margin widening into a yellow basal area 32

30(29). Dorsal surface of metasomal tergum 1 with a wide, impunctate, shiny area 0.5-1 mow in length adjacent to upper rim of anterior declivity .... *azteca*

Dorsal surface of metasomal tergum 1 punctate all the way to upper rim of anterior declivity 31

31(30). Medial half of dorsal enclosure of propodeum with ridges strongly vermiform; punctures of dorsal median fifth of metasomal tergum 1 large, deep, distinct, contiguous; volsella with posterolateral corner bent sharply dorsad, hence called "hooked"; metasomal sternum 6 with lateral margin at base of each posterorior projection slightly swollen (Fig. 84) .... *unca*

Medial half of dorsal enclosure of propodeum with ridges straight or slightly bowed; punctures of dorsal median fifth of metasomal tergum 1 small, usually shallow, often eccentric 0.5 or more pwa; volsella with posterolateral corner not "hooked"; metasomal sternum 6 with lateral margin at base of each posterior projection not swollen (Fig. 64) .... *coloradensis*

32(29). Hind tibia with posterior surface all brown; metasomal sternum 6 with lateral margin at base of each posterior projection slightly swollen (Fig. 88) .... *crypta*

Hind tibia with posterior surface brown with a yellow border along outer margin usually widening into a yellow area basad;

metasomal sternum 6 with lateral margin at base of each posterior projection not swollen 33

33(32). Dorsal surface of metasomal tergum 1 with a wide, impunctate, shiny area 0.5-1 mow in length adjacent to upper rim of anterior declivity .... *azteca*

Dorsal surface of metasomal tergum 1 punctate all the way to upper rim of anterior declivity 34

34(33). Metasomal tergum 1 with large, coarse punctures less than 1 pwa laterad; about 8 punctures per 0.01 mm^2 in middle of tergum; dorsal enclosure of propodeum with a carinate posterior border, median portion of about 1 mow with quite vermiform ridges, remaining ridges longitudinal, relatively straight .. *chlorops*

Metasomal tergum 1 with small, fine punctures mostly more than 1 pwa, about 10 punctures per 0.01 mm^2 in middle of tergum; dorsal enclosure of propodeum with at most a weak carina only along median portion of posterior border, median portion of about 1 mow with longitudinal ridges relatively straight and similar to remaining ridges .... *coloratipes*

FEMALES

1. Dorsal area of propodeum unsculptured, highly polished, with median depression with longitudinal, rounded ridge giving the impression of twin pits; subantennal plate black or dark brown (subgenus *Verbenapis*) 2

Dorsal area of propodeum sculptured, without such a depression; subantennal plate variable in color 5

2(1). First metasomal tergum with a shallow concavity in median dorsal area, sharply sloped anteroventrally; punctures of median dorsal area of tergum 1 very few, 3 or more pwa on a very shiny ground; metasomal tergum 2 with a distinct median convex bump; fore basitarsus, ratio length/width, 3.5-4.5 .... *nebraskensis*

First metasomal tergum without such a concavity, the dorsal area a smooth, continuous curve from side to side; punctures of median dorsal area abundant, 2 or less pwa on a moderately shiny ground; metasomal tergum 2 without a distinct median convex bump; fore basitarsus, ratio length/width, 5.5 or more 3

3(2). Mandible with basal half brown or black, or with a tiny, indistinct yellowish spot at extreme outer base; dorsal median margin of clypeal cream coloration straight or shallowly concave .... *verbenae*

Mandible with basal fourth to half cream colored; dorsal median margin of clypeal cream coloration strongly convex upward 4

4(3). Tegula transparent dark brown; hindwing length less than 3.6 mm; fore basitarsus, ratio length/width, 8.0-9.5 .... *hirsutifrons*

Tegula transparent smoky straw color with opaque cream maculation anteriorly; hindwing length equal to or more than 4.0 mm; fore basitarsus, ratio length/width, 4.5-5.5 .... *micheneri*

5(1). Prepygidial and pygidial fimbriae smoky, reddish-brown, or black; disc of metasomal terga 3-5 bearing numerous short, black hairs 6

Prepygidial and pygidial fimbriae fulvous or white; disc of metasomal terga 3-5 bearing fulvous or white hairs 23

6(5). Galea in repose extending beyond closed mandibles 1.25 mow or more 7

Galea in repose extending beyond closed mandibles 1 mow or less (*Perissander,* and *Calliopsis s.s.* in part) 15

7(6). Medium sized species, hindwing length 3.80 mm or less, mio less than 1.36 mm; maxillary palpomere 2 shorter than, or at most equal to maxillary palpomere 3 (30×); lateral portion of clypeus brown to black *(Calliopsis s.s.)* 8

Large sized species, hindwing length 3.90 mm or more, mio more than 1.50 mm; maxillary palpomere 2 distinctly longer than maxillary palpomere 3 (30×); lateral portion of clypeus yellow (*Calliopsima,* in part) 32

8(7). Tegula with at least a dot of yellow 9

Tegula without yellow, straw color to black 10

9(8). Disc of scutum with fine punctures more than 1 pwa, interspaces shiny, becoming only faintly roughened anteriorly; flagellar length subequal to mio; yellow area of tegula larger than median ocellus; Texas, Coahuila .... *helenae*

Disc of scutum with coarse punctures 1 pwa, interspaces shagreened, becoming strongly roughened anteriorly; flagellar length one-sixth shorter than mio; yellow area of tegula smaller than median ocellus; southeastern Arizona .... *empelia*

10(8). Galea highly polished, tapered to a sharp point (20×), length exposed beyond closed mandibles about 3 mow; metasomal tergum 1 highly polished with very fine, sparsely distributed punctures about 3 pwa on the disc, posterior area impunctate (20×) .... *rhodophila*

Galea lightly pebbled, at least on apical fourth, and tapered to a blunt, rounded tip, length exposed beyond closed mandibles 1.5-2.5 mow; metasomal tergum 1 dull, or if polished, then punctures fairly evenly distributed, usually 2 or less pwa on disc, posterior area punctate (20×) 11

11(10). Scutum and metasomal tergum 1 with ground dulled by abundant fine roughening; basal labial palpomere with stout setae ventrally; frons without brassy, metallic tints (*hondurasica* group, in part) 12

Scutum and metasomal tergum 1 with ground smooth, sometimes shiny, or if roughened, then roughening confined to anterior portion of scutum; frons with weak, brassy, metallic tints 14

12(11). Hairs of stipes straight or slightly curved from bases to apices; punctures of scutum coarse; less than 0.5 pwa on disc with punctures becoming much more crowded anteriorly .... *zora*

Hairs of stipes, at least many of them, more or less abruptly bent over at the tip, frequently curled at the tip; punctures of scutum fine, mostly more than 1 pwa with punctures becoming somewhat more crowded anteriorly 13

13(12). Flagellar length about one-tenth longer than mio; larger species, hindwing length about 3.5 mm, head length 1.62 mm or more, intertegular 1.39 mm or more .... *hondurasica*

Flagellar length subequal (one-twentieth more or less) to mio; smaller species, hindwing length about 2.9 mm, head length 1.53 mm or less, intertegular 1.33 mm or less .... *sonora*

14(11). Declivity of metasomal tergum 1 with a dull, satiny surface; punctures of disc of metasomal tergum 1 fine, shallow, with moderately shiny interspaces, actual diameter about 8 μ or less, 2 pwa on anterior portion of dorsum; Rocky Mountain states, southeastern Canada, central and eastern United States .... *andreniformis*

Declivity of tergum 1 finely lineolate with a high polish; punctures of disc of metasomal tergum 1 fine, deep, with highly polished interspaces, actual diameter about 12 μ, 1 pwa on anterior portion of dorsum; central Mexico, Arizona, New Mexico, Colorado .... *teucrii*

15(6). Mesotibial spur, untoothed (60×) 16

Mesotibial spur with at least 2 apical teeth 17

16(15). Mesotibial spur three-fourths or more of length of middle basitarsus; middle tibial length subequal to middle basitarsal length; Arizona .... *squamifera*

Mesotibial spur less than 0.6 times length of middle basitarsus; middle tibial length 0.3 times longer than middle basitarsus; Baja California .... *peninsularis*

17(15). Mesotibial spur with 2-4 coarse teeth on apical 0.4, the basal 0.6 perfectly bare .... *gilva*

Mesotibial spur with 7 or more fine teeth 18

18(17). Metasomal terga 1-4 largely orange or reddish-orange .. *anomoptera*

Metasomal terga 1-4 black or metallic brassy 19

19(18). Scutum with all interspaces between punctures finely, distinctly roughened; marginal cell 6-9 less than 9-wt; ratio of length of flagellum to length of scape, 2.6-2.8 .... *limbus*

Scutum either with all interspaces between punctures smooth, or only roughened anteriorly; marginal cell 6-9 more than 9-wt; ratio of length of flagellum to length of scape, 2.0-2.4 20

20(19). Smaller species, hindwing length (forewing 1-9 gives same measurement) 2.0-2.7 mm; median portion of dorsal enclosure of propodeum with fine lines originating posteriorly, fanning out anterolaterally toward base of propodeum 21

Larger species, hindwing length (forewing 1-9 gives same measurement) 3.0 mm or larger; dorsal enclosure of propodeum not as above 22

21(20). Brassy, metallic colored integument on frons, scutum, scutellum, and metasomal terga .... *rogeri*

Black or dark brown integument on frons, scutum, scutellum, and metasomal terga .... *syphar*

22(20). Mesotibial spur with 6-8 teeth; facial fovea long, linear, 4-5 times longer than wide, deeply impressed with distinct lateral margin; posterior portion of metasomal tergum 1 with mirror-like polish, virtually impunctate; southeastern Arizona and southwestern New Mexico .... *fulgida*

Mesotibial spur with about 15 teeth; facial fovea moderately long, broader at midlength, 3-4 times longer than wide, shallowly impressed with relatively indistinct lateral margin; posterior portion of metasomal tergum 1 shiny, completely punctate; Michoacan .... *yalea*

23(5). Tibiae with dorsal or anterior surfaces mostly yellow 24

Tibiae with dorsal surfaces bearing yellow color only at extreme bases 25

24(23). Scutal hair dense, appearing nap-like (10×) and obscuring punctation because of its profuse, relatively long, branches; scutal length one-tenth or more greater than eye length; front basitarsal length equal to or greater than front apicotarsus .... *pectidis*

Scutal hair thin (10×) with punctures readily visible; scutal length subequal to eye length; front basitarsal length about one-tenth shorter than front apicotarsus .... *timberlakei*

25(23). At least basal fifth of mandible brown or black 26

At least basal fifth of mandible yellow or cream color 28

26(25). Both long and short scutal hairs fulvous 27

Long scutal hairs brown, short ones fulvous .... *crypta*

27(26). Metasomal tergum 1 with large, deep, punctures, sparser medially .... *rozeni*

Metasomal tergum 1 with very fine punctures, not sparser medially, often denser medially .... *coloradensis*

28(25). Metasomal tergum 1 with punctures very dense, crowded medially, less than 0.5 pwa, about 11 punctures per 0.01 mm^2 of median area .... *bernardinensis*

Metasomal tergum 1 with very sparse punctures, from 0-3 punctures per 0.01 mm^2 of median area 29

29(28). Labrum brown; the two lateral brown bars of median disc of clypeus joined by a strip of brown at least along dorsal side of preapical groove of clypeus; facial light color a deep, rich lemon yellow .... *pugionis*

Labrum cream color, pale yellow, or rarely, mostly brown; the two lateral brown bars of median disc of clypeus not joined; facial light color cream or very pale yellow 30

30(29). Punctures of metasomal tergum 1 moderately large, usually sparse medially, but may be rather regularly spaced medially becoming sparser laterally; horizontal enclosure of propodeum distinctly longer medially than laterally, bearing longitudinally vermiform ridges which are fairly readily distinguishable from each other (30×) .... *chlorops*

Punctures of metasomal tergum 1 very fine, always sparser medially than laterally, interspaces highly polished; horizontal enclosure of propodeum with median third of about equal length throughout, bearing either straight, longitudinal ridges well separated from each other, or densely packed, very fine, longitudinally vermiform ridges difficult to distinguish from each other (30×) 31

31(30). Disc of clypeus with tiny, twin, wedge-shaped, light brown spots or very light brown, narrow bars; basal labial palpomere one-tenth to one-fifth shorter than clypeocellar .... *coloratipes*

Disc of clypeus with large, twin, dark brown bars; basal labial palpomere one-tenth to one-fifth longer than clypeocellar .... *deserticola*

32(7). Largest species of the genus, hindwing length 4.9 mm; basal labial palpomere one-sixth longer than clypeocellar; forewing 3-4 about one-tenth less than 9-wt; disc of metasomal tergum 1 finely roughened .... *hurdi*

Moderately large species, hindwing length 3.8-4.4 mm; basal labial palpomere subequal to clypeocellar to one-tenth less; forewing 3-4 subequal to or less than 9-wt; disc of metasomal tergum 1 smooth, shiny .... *kucalumea*

Subgenus CALLIOPSIS Smith

Calliopsis Smith, 1853, Catalogue of Hymenoptera in the British Museum 1:128; Michener, 1951, *in* Muesebeck *et al.*, U.S. Dept. Agric., Monogr., No. 2:1103; Mitchell, 1960, North Carolina Agric. Exp. Sta. Tech. Bull. No. 141:288-294.

Type species. Calliopsis andreniformis Smith, 1853, by designation of Ashmead, 1899, Trans. Amer. Ent. Soc., 26:85.

This subgenus is closer to *Perissander* than to the other subgenera. Its closest South American relatives seem to be apparently unnamed Argentinian species of *Liopoeum*. Two groups of species fall together rather naturally: the *andreniformis* group, including *teucrii, mourei, rhodophila, wilda,* and *helenae;* and the *hondurasica* group, including *sonora, empelia, squamifera, peninsularis,* and probably *zora.*

This is the most widespread subgenus. It occurs from Panamá to Canada, and from the eastern United States west to Utah and southwest to Nevada, California, and the tip of Baja California Sur. The species favor Leguminosae, especially *Trifolium, Melilotus, Medicago,* and *Psoralea,* with next choices being Verbenaceae and Compositae.

Calliopsis differs from the other subgenera in the male by the prominent scutellar and metanotal hair pads, and in the female by the combination of the length of galea exposed beyond closed mandibles being greater than 1 mow (except in *squamifera*), the prepygidial and pygidial fimbriae being smoky to dark reddish brown, and in both sexes by the tumid paraocular area.

Female. Length, 5.0-7.5 mm.

Head. Yellow areas: (1) paraocular area below a line originating between middle of outer subantennal suture and near upper end of suture and extending diagonally upward ending on orbit approximately at level of upper rim of antennal socket, usually below level of facial fovea (above in *helenae*), or yellow area reduced to small patch along orbit; lower inner paraocular area adjoining junction of frontoclypeal suture and outer subantennal suture tumid, most strongly in *andreniformis,* least in *hondurasica;* (2) clypeus with a median longitudinal band originating at frontoclypeal suture, ending at or slightly above clypeal apex; lateral areas brown except in *helenae* and some *rhodophila* which have several blotches of yellow; (3) absent on labrum except on apex of labral plate in *zora* and *helenae;* (4) supraclypeal area pentagonal or semilunar with apex approximately at midlevel of antennal socket; (5) subantennal plate highly variable from totally dark to totally light (6) absent on mandible. (7) Scape and pedicel black, ventral surfaces of flagellomeres 1-2 black, of 3-4 black with median portions tan, of remaining ones tan; dorsal surface of basal flagellomeres dark brown, flagellomeres becoming progressively lighter brown apicad. (8) Hair of vertex mixed colorless and light brown, or mixed fulvous and dark brown, of frons white or fulvous, of clypeus pale brown to black and coarser than on other areas, of gena white. (10) Punctures along ocellocular line fine, interspaces variable; impunctate area lateral to posterior ocellus shiny to exceedingly dulled by roughening; punctures of frons with interspaces sometimes metallic, shiny to very dull (30×). (11) Frontal line with lower portion a narrow sulcus rising gradually to a summit on frontal prominence between antennal sockets slightly above their midline. (12) Clypeus with punctures of disc somewhat eccentric, or at least with sloping sides like a volcano cone. Clypeus with disc convex medially. Projections beside median apical emergination of clypeus pointed. (13) Inner orbits slightly convergent below. Facial fovea shallow to deep, linear to broadened medially and narrowed at both ends. (14) Galeal length variable, length of galea exposed beyond closed mandibles variable from absent to within 1 mow of base of prementum. (15) Head width/head length 1.25-1.60. (17) Eye length variable with respect to mio, but equal to or less than flagellar length (except much greater in *empelia*), and subequal to outer subantennal sutural. (18) Interantennal to antennocular variable, interantennal less than 2 mow. (19) Ocellolabral equal to or greater than mio. (21) Basal labial palpomere 1.5-3.8 times length of others combined. (22) Flagellomere 1 with length variable with respect to flagellomere 9. Flagellar length 1.8-2.5 times length of scape.

Mesosoma. (23) Light colored areas: medial interruption of pronotal stripe 1-4 mow; apex of pronotal lobe; scutellar crest. (24) Scutal and scutellar hairs of two kinds, longer ones fulvous to brown, shorter ones fulvous. (25) Scutal disc with punctures usually distinct, interspaces highly polished to extremely dulled by minute roughening. (26) Dorsal enclosure of propodeum variously sculptured, always with some longitudinal ridges. (27) Legs with light color the same as on face. Foreleg with basal spot of yellow on tibia, and sometimes on extreme apex of femur. (28) Middle leg with basal spot of yellow on tibia, sometimes on extreme apex of femur; spur with many fine teeth (bare in *squamifera*). (29) Hind leg brown. (30) Tegula brown, with anterior yellow spot in some species. Humeral plate brown. (31) Wing smoky apically beyond cells. Stigma brown. (32) Marginal cell 6-9 subequal to, or longer than, and 3-4 shorter than 9-wt.

Metasoma. (34) Tergal hair bands white to fulvous (orange fulvous in some *andreniformis*), dense, appressed. Band of tergum 1 broadly interrupted, of tergum 2 narrowly interrupted; other tergal bands entire (all at 10×). Suberect hair of discs of terga 4-5 dark brown to black. Prepygidial and pygidial fimbriae smoky to dark brown. (35) Tergum 1 with punctures of median area variable, uniformly to irregularly distributed to partially impunctate; interspaces exceedingly dull to highly polished; punctures smaller than on scutum. Declivity of tergum 1 usually finely lineolate, somewhat dull (shiny in *rhodophila* and most specimens of *teucrii*).

MALE. Length, 4.0-6.5 mm.

Head. Yellow areas (white in *mourei* and *squamifera*): (1) paraocular area below a relatively straight, or a dorsally convex line, from upper outer edge of antennal rim tangent to or slightly indented by lower end of facial fovea, ending on orbit at or slightly above lower end of facial fovea; lower half of paraocular area tumid, most strongly so near junction of outer subantennal suture and frontoclypeal suture; (2) clypeus except a clear to black border on lateral portion of apex; frontoclypeal suture yellow to black; (3) labrum, except for 3 small circular or subcircular clear to black spots, one in each laterobasal corner and a median one approximately in center of labral plate; (4) supraclypeal area apex from slightly below midlevel of antennal socket to about 0.5 mow above upper edge of socket; (5) subantennal plate except sometimes black near junction of outer subantennal suture and frontoclypeal suture; (6) mandible basal fourth or more, some species with anterior and posterior border brown to black. (7) Scape and pedicel all yellow, yellow and brown, or all black; flagellomeres as in female, except some species with yellow on ventral surface of first two or three flagellomeres, remainder having successively more tan toward apex of flagellum. (8) Hair of vertex variable, of frons white or fulvous, of clypeus colorless, fulvous, brown, or black. (10) Punctures of face variable. (11) Frontal line with lower portion a sharp high carina or a relatively low, extremely finely sulcate carina. (12) Clypeus with punctures of disc as in female except finer; median portion strongly protuberant, usually protruding 0.17 mm or more in front of eye in lateral view. (13) Inner orbits strongly convergent below. Facial fovea usually with ill-defined mesal border. (14) Galeal length and length of galea exposed beyond closed mandibles as in female, galeal gap greater than inner subantennal sutural, but less in *rhodophila*. (15) Head width/head length 1.15-1.38. (17) Eye length greater than mio, considerably less than flagellar length. (18) Interantennal greater than antennocular, and less than 2 mow. (21) As in female. (22) As in female except flagellar length about 3.0-4.1 times length of scape.

Mesosoma. (23) As in female. (24) Scutal and scutellar hair all light, or in some species with longer hair brown, other hair as in female. Scutellar hair pads well developed, never contiguous, composed of densely packed, short, profusely branched hairs occupying lateral portion of scutellum, sometimes part of median portion also. Metanotal hair pad much greater in extent than on scutellum, contiguous medially in *granti* and *rhodophila*. (25) Scutal disc with punctures as in female. (26) Dorsal enclosure of propodeum variously sculptured, with at least some longitudinal ridges which may be somewhat vermiform or reticulate. (27) Legs with light color the same as on face except in *mourei* and *squamifera*. Foreleg color pattern variable. (28) Middle leg color pattern variable. (29) Hind leg color pattern variable. (30) Tegula brown, with anterior yellow spot in *squamifera* and rarely in *andreniformis*. Humeral plate brown. (31) Wing as in female but tip much darker, pale brown. Stigma as in female. (32) Marginal cell 6-9 subequal to or greater than, and 3-4 equal to or less than 9-wt; 11-12 shorter than 13-14.

Metasoma. (34) As in female but hair bands much less dense. (35) As in female but size of punctures variable with respect to scutal punctures. Declivity of tergum 1 variable. (36) Pygidial plate ill-defined, disc irregularly concave, usually with median apical emargination. (37) Sterna brown to black (rarely, with median preapical yellow spot in *andreniformis*). Sternum

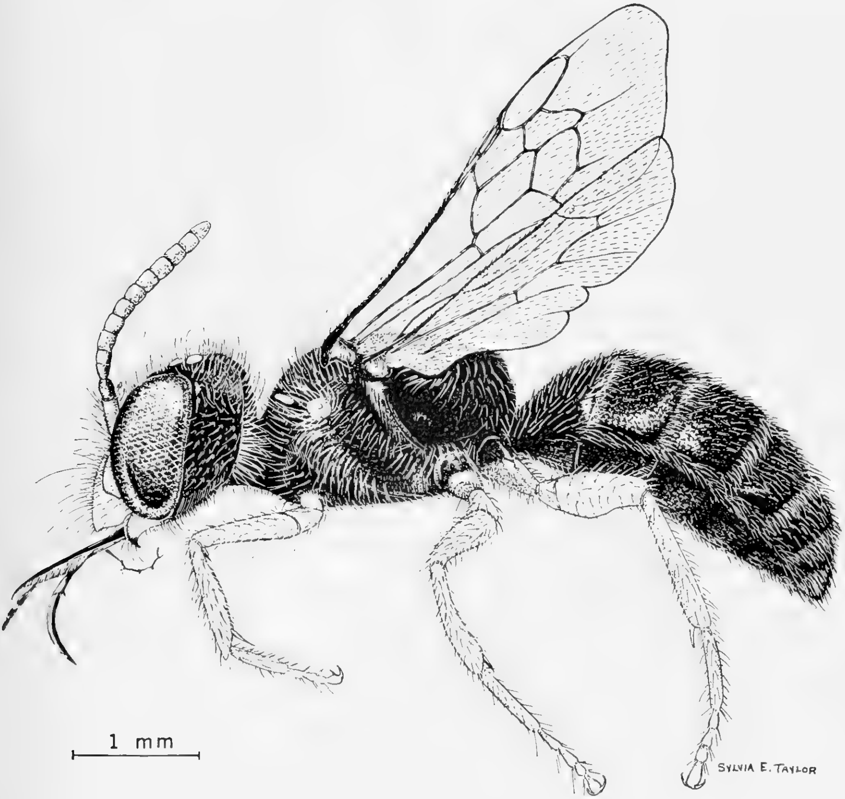


Fig. 6. Lateral view of male *Calliopsis (C.) andreniformis* Smith.

5 produced posteriorly into a long, tapered point. Sternum 6 with apical margin produced into a pair of long, aciculate, spine-like processes. Sternum 8 with a relatively broad, apical paddle-like portion. (38) Sterna and genitalia as illustrated (Figs. 8-45).

CALLIOPSIS (CALLIOPSIS) ANDRENIFORMIS Smith

(Figs. 5,6,8-13; Map 1)

Calliopsis andreniformis Smith, 1853, Catalogue of Hymenoptera in the British Museum, 1:128, female; Cockerell, 1897, Canad. Ent., 29:290; Cockerell, 1898, Trans. Amer. Ent. Soc., 25:196; Robertson, 1898, Trans. Acad. Sci. St. Louis, 8:48; Ashmead, 1899, Trans. Amer. Ent. Soc., 26:85 (type species of *Calliopsis*); Bridwell, 1899, Trans. Kansas Acad. Sci., 16:210; Cockerell, 1899, Ent. News, 10:3; Graenicher, 1905, Bull. Wisconsin Nat. Hist. Soc., 3:159; Lovell and Cockerell, 1906, Psyche, 13:113; Swenk and Cockerell, 1907, Ent. News, 18:178; Cockerell, 1909, Ann. Mag. Nat. Hist., (8)4:28; Tucker, 1909, Trans. Kansas Acad. Sci., 22:282; Smith, 1910, Ann. Rep. New Jersey State Mus. 1909: 691; Graenicher, 1911, Pub. Mus. City Milwaukee Bull., 1:238; Crawford, 1913, Canad. Ent., 45:271; Gibson, 1913, 44th Ann. Rep. Ent. Soc. Ontario: 20; Viereck, 1916, *in* Britton, Connecticut Nat. Hist. Surv. Bull., 22:722; Washburn, 1919, Minnesota Agric. Exp. Sta., Jour. series, No. 156:229; Stevens, 1919, Canad. Ent., 51:210; Britton, 1920, Connecticut Geol. Nat. Hist. Surv. Bull. 31:345; Rau, 1922, Trans. Acad. Sci. St. Louis, 24(7):33; Robertson, 1922, Psyche, 29:168; Reinhard, 1924, Ann. Rep. Smithsonian Inst., 1922, Publ. Number 2738:371-373 (biol.); Lovell, 1925, Maine Naturalist, 5:7; Leonard, 1926, Cornell Univ. Agric. Exp. Sta. Mem., 101:1021; Robertson, 1926, Psyche, 33:118 (biol.); Robertson, 1928, Flowers and Insects, p. 10+(biol.); Hendrickson, 1930, Iowa State Coll. Jour. Sci., 4(2): 163 (biol.); Pearson, 1933, Ecol. Monogr., 3:387, 409-11, 418 (biol.); Graenicher, 1935, Ann. Ent. Soc. Amer., 28:303; Cockerell, 1936, Amer. Mus. Novitates, 831:3; Ainslie, 1937, Canad. Ent., 69(5): 97-100 (biol.); Brimley, 1938, Insects of North Carolina, p. 453; Procter, 1938, Biological Survey of the Mount Desert Region [Maine], 6:442 and 1946, 7:504 (biol.); Lovell and Lovell, 1939, Rhodora, 41:185 (biol.); Timberlake, 1947, Pan-Pac. Ent. 23:29; Crandall and Tate, 1947, Jour. Amer. Soc. Agronomy, 39:161-163 (biol.); Michener, 1947, Amer. Midl. Nat., 38:477; Stevens, 1950, North Dakota Agric. Exp. Sta. Bimonthly Bull., 12:93-94; Michener, 1951, *in* Muesebeck *et al.,* U.S. Dept. Agric. Monogr. No. 2:1103; Rozen, 1951, Jour. Kansas Ent. Soc., 24:142; Mitchell, 1956, Jour. Elisha Mitchell Sci. Soc., 72(2)207 (biol.); Montgomery, 1957, Proc. Indiana Acad. Sci., 66:129 (biol.); Wille, 1958, Ann. Ent. Soc. Amer., 51(6):544 (anat.); Mitchell, 1960, North Carolina Agric. Exp. Sta. Tech. Bull. No. 141:288-289, 291-294; Byers, 1962, Jour. Kansas Ent. Soc., 35:320 (biol.).

Calliopsis flavipes Smith, 1853, Catalogue of Hymenoptera in the British Museum, 1:128, male.

Calliopsis lepidus Cresson, 1878, Trans. Amer. Ent. Soc., 7:68, female; Cockerell, 1898, Trans. Amer. Ent. Soc., 25:196; Cresson, 1916, Mem. Amer. Ent. Soc., 1:122.

Panurgus vernalis Provancher, 1882, Nat. Canad., 13:204; 1883, Faune entomologique du Canada, Hyménoptères, 704.

Calliopsis flavifrons; Banks, 1912, Ent. News, 23:107 (misidentification).

Calliopsis rhodophila; Stevens, 1919, Canad. Ent., 51:210 (misidentification).

The female of *andreniformis* was considered to resemble females of the genus *Andrena,* hence its name. Its closest relative is *C. teucrii.* The male of *andreniformis* is distinguished readily from that of *teucrii* by its entirely yellow scape, whereas that of *teucrii* is brown. The female of *andreniformis* is distinguished from *teucrii* only with difficulty. The anterior slope of metasomal tergum 1 has a satiny sheen on the surface in *andreniformis* but has a finely lineolate polish in *teucrii;* the integument of the anterior portion of the dorsum of the scutum is brassy colored in *andreniformis,* non-metallic in *teucrii.*

FEMALE. Length, 7.0 mm (type 7.4 mm); forewing length, 4.8 mm (type 5.0 mm); hindwing length, 3.4 mm; clypeal length, 0.54 mm (type 0.51 mm); scutal length, 1.31 mm.

Head. Yellow areas: (1) paraocular area, except lowermost corner, below a line originating about midlevel of antennal socket and extending diagonally upward to a point on the orbit slightly below or slightly above level of upper rim of antennal socket and below lower margin of facial fovea (to almost all black); area below level of middle portion of frontoclypeal suture tumid; (2) clypeus with narrow, longitudinal stripe medially (to all black, rarely); (4) supraclypeal area in a semilunar shape (absent, rarely); (5) absent on subantennal plate (to completely yellow). (8) Hair of vertex mixed colorless and brown, of frons fulvous, both longer than long hairs of scutum; of clypeus black. (10) Punctures along ocellocular line 2-3 pwa with smooth interspaces; impunctate area laterally adjacent to posterior ocellus finely roughened; punctures of frons adjacent to upper portion of frontal line deep, distinct, less than 1 pwa, interspaces brassy, faintly roughened (30×). (12) Clypeus with punctures of disc approximately equal in size to the average frontal puncture, deep, 3-4 pwa, interspaces finely roughened (to barely discernibly roughened in part) (30×). (13) Orbital convergence ratio as 1.31:1.21, 1.08 (type 1.33:1.26, 1.05). Facial fovea with indistinct mesal border, broader medially, narrowed above and below. (14) Galea shiny despite minute pebbling; length intermediate between antennocellar and clypeocellar; galeal gap exceeds length of galea exposed beyond closed mandibles. (15) Head width/head length 2.16:1.75, 1.23 (type 2.21:1.84, 1.20). (17) Eye length, mio, and flagellar length as 1.28:1.21:1.26 (type 1.28:1.26:N.A.). (18) Interocellar, ocellocular, antennocular, and interantennal as 0.31:0.39:0.31:0.32 (type 0.29:0.39:0.32:0.31). (19) Ocellolabral greater than clypeal width 1.45:1.36, 1.07. (20) Clypeocellar to outer subantennal sutural as 0.90:0.71, 1.27 (type 0.90: N.A.). (21) Basal labial palpomere 3.6 (type 3.0) times length of others combined, 40:11 (type 36:12). (22) Flagellar length about 2.3 times length of scape, 1.26:0.54 (type 1.29:0.57).

Mesosoma. (23) Light areas yellow; medial interruption of pronotal stripe about 2.5 times mow. (24) Scutal and scutellar hairs of two kinds, longer ones brown (to fulvous). Hair of metanotum fulvous. (25) Scutal disc with punctures fine, about 2 pwa, interspaces shiny, becoming exceedingly fine and crowded to less than 1 pwa anteriad, interspaces finely roughened and faintly (to strongly) brassy colored. (26) Dorsal enclosure of propodeum relatively dull with fine, irregularly longitudinal ridges, median portion not distinctly bordered posteriorly, length not much exceeding length of lateral area. (27) Legs with light color the same as on face. (28) Spur with about 25 fine, short teeth; spur length half length of middle basitarsus, 0.51:0.80 (type 0.51:0.75). (30)Tegula dark brown. Humeral plate dark brown.

(32) Marginal cell 6-9 subequal to and 3-4 less than 9-wt, 1:00:0.80:1.04 (type 1.05:N.A.:1.02).

Metasoma. (35) Tergum 1 with punctures of median area extremely fine, about 2 pwa, interspaces shiny (or with a silken sheen). Declivity of tergum 1 with a fine, silken sheen.

MALE. Length, 6.0 mm (type 6.2 mm); forewing length, 5.0 mm (type 4.6 mm); hindwing length, 2.86 mm; clypeal length, 0.44 mm (type 0.53 mm); scutal length, 0.95 mm.

Head. Yellow areas: (1) paraocular area below an ascending diagonal line from upper outer edge of antennal rim tangent to (or indented by) lower end of facial fovea, ending on orbit slightly above level of end of facial fovea; (2) clypeus; (4) supraclypeal area extending well above level of upper antennal rims (0.2-0.5 mow); (5) subantennal plate and adjacent antennal rim; (6) mandible, basal two-thirds; (7) scape (sometimes with small, brown, trianguliform area on inner upper corner). (8) Hair of vertex, frons, and clypeus fulvous (clypeus sometimes with a few apically light brown hairs to many completely light brown hairs), of gena white. (10) Punctures along ocellocular line minute, about 3 pwa (to 1 pwa), interspaces shiny; impunctate area adjacent to lateral border of posterior ocellus finely roughened; lower, dark portion of frons heavily roughened. (11) Frontal line with lower, yellow, carinate portion ending at midlevel of antennal sockets. (12) Clypeus strongly protuberant with medial portion between clear clypeal dots raised somewhat conically (sometimes raised as an indistinct, short longitudinal ridge). (13) Orbital convergence ratio 1.12:0.87, 1.29. (14) Galea dull, completely pebbled, length as in female; galeal gap subequal to length of galea exposed beyond closed mandibles. (15) Head width/head length as 1.85:1.53, 1.21 (type 2.16:N.A.). (17) Eye length, mio, and flagellar length as 1.11:0.87: 1.38 (type 1.21:1.04:N.A.). (18) Interocellar, ocellocular, antennocular, and interantennal as 0.26:0.34:0.17:0.26 (type 0.29:0.39:0.24:0.24). (19) Ocellolabral greater than clypeal width, 1:22:1.14, 1.07 (type 1.43:N.A.). (20) Clypeocellar to outer subantennal sutural as 0.77:0.58, 1.33 (type 0.90:N.A.). (21) Basal labial palpomere 1.5-1.8 times length of others combined. (22) Flagellar length 3.0-3.4 times length of scape, 1.38:0.43.

Mesosoma. (23) Yellow areas: large patch between middle coxal cavities truncate anteriorly 1 mow or more posterior to front coxae; smaller area between hind coxal cavities contiguous anteriorly with mesosternal patch; medial interruption of pronotal stripe about 2 mow. (24) Scutal and scutellar long and short hairs fulvous (white in faded specimens). Scutellar hair pad dark brown, barely extending to mesal end of yellow of scutellar crest. Metanotal hair pad dark brown, mesal margins separated by about 3 mow. (25) Scutal disc with punctures fine, 1 pwa or less, interspaces finely roughened but relatively shiny (30×), becoming very fine and crowded anteriorly. (26)

Dorsal enclosure of propodeum with fine, reticulate ridges medially, and distinct, fine roughening laterally. (27) Foreleg yellow (sometimes with base of coxa brown, apicotarsus testaceous); mediotarsomeres somewhat dorsoventrally flattened, widths about 0.75 times lengths. (28) Middle leg yellow (often with base of coxa brown, femur with basal brown spot, apicotarsus testaceous); mediotarsomeres cylindrical, widths about half of length. (29) Hind leg yellow (often with variable amounts of brown on base of coxa, inner surface of trochanter, base of femur especially inner or posterior surface; posteroventral surface of basitarsus and entire apicotarsus testaceous), mediotarsi similar to front mediotarsi but larger. (30) Tegula brown with anterior yellow spot (to all brown). Humeral plate brown (to testaceous). (32) Marginal cell 6-9 greater than, and 3-4 considerably less than 9-wt, 0.80:0.66: 0.77.

Metasoma. (35) Tergum 1 with punctures of median area very minute, smaller than on scutum, 1-2 pwa, interspaces shiny.

TYPE MATERIAL. Holotype female of *andreniformis*, No. 17.a.1798, and holotype male of *flavipes*, No. 17.a.1799, both from East Florida and both collected by E. Doubleday in 1838, are in the British Museum (Natural History). The type of *C. lepidus*, from Georgia, collected by Morrison, is in the Academy of Natural Sciences of Philadelphia, Pennsylvania. The type of *vernalis* is presumably in the Provincial Museum, Quebec, Canada. The above descriptions are primarily based upon specimens from northern Georgia with comparative measurements for the female type of *andreniformis* and the male type of *flavipes*.

DISTRIBUTION. This is the most widespread species in the United States. It occurs in the entire eastern United States and southeastern Canada and the Maritime Provinces. With the exception of a mating pair of specimens from the southwestern corner of Utah, all records are from east of the Rocky Mountains and its western boundary is the Rocky Mountain Front Range from Montana to Colorado, southeast to central Oklahoma, south to East Texas and the Texas Gulf coast.

It has been collected from early April to late September in the southern states, but mostly in June and July. In the northern states it has been taken from early June to early October, but mostly in July. Doubtless, further collecting will find it with an extreme as late in the southern states as in the northern ones.

The highest altitude at which it is recorded is about 5700 feet at the foot of the Front Range of the Rocky Mountains at Boulder, Colorado.

Ecologically, it occurs in bare, clayey soil (loam, clay loam, silt loam) where small-flowered leguminous plants, especially of the clover group, thrive during its active season. It is likely to be found on almost any school campus, playground, or sports field within its range. For this reason I suggest the common name, the Campus Bee.

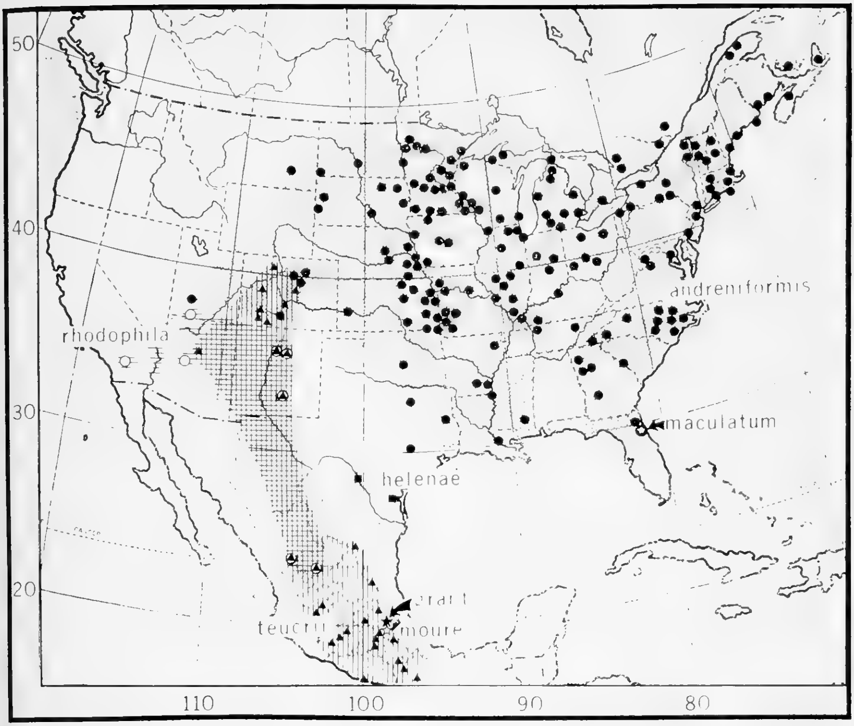
I have not examined the type material in the British Museum but I have examined the type of *C. lepidus* as well as Prof. T. B. Mitchell's homotypes of *andreniformis* and *flavipes*. In addition, I have examined approximately 5,000 specimens from the localities shown in Map 1.

The following western localities seem worth indicating in detail: COLORADO: Alamosa; Boulder; Golden, South Table Mountain; Longmont; White Rocks, near Valmont. MONTANA: Forsyth. UTAH: Parowan Canyon. The other localities are cited in a thesis on deposit in the library of The University of Kansas.

GEOGRAPHIC VARIATION. The most striking variation in the males is in the coloration of middle and hind trochanters and femora. Males from east of the Mississippi exhibit a higher incidence and greater amount of dark color on these parts. The amount of yellow increases to a maximum with a specimen from near Parowan, Utah. The most obviously variable feature in the females is the amount of yellow on the face. It parallels the situation in the male legs. No males exhibit all brown middle or hind femora, and no females exhibit all black faces. Some females from North Carolina and Vermont, however, have the yellow reduced to a mere spot on the paraocular area and a line or dot on the disc of the clypeus. Clypeal hairs of both male and female show a similar trend although they are subject to considerable fading after preservation.

BIONOMICS. This is fully discussed in the section on biology and ecology of *C. andreniformis*.

FLOWER RECORDS. *Achillea, Ailanthus altissima, Ammania coccinea, Amorpha canescens, Anaphalis margaritacea, Asclepias, Aster ericoides villosus, Bidens aristosa, Boltonia asteroides, Brassica, Castanea pumila, Ceanothus americanus, Chrysanthemum leucanthemum, Chrysopsis, Cleome, Convolvulus arvensis, C. sepium, Coreopsis palmata, C. tripteris, Cryptotaenia canadensis, Cucumis, Desmodium marilandicum, D. paniculatum, Dianthera americana, Epilobium, Erigeron, Eryngium yuccifolium, Gerardia tenuifolia, Geum album, Gillenia stipulacea, Hedeoma pulegioides, Hedyotis nigricans, H. purpurea, Helenium, Hypericum perforatum, Lindernia dubia riparia* (Raf.) (=*Ilsyanthes riparia*), *Lespedeza capitata, L. procumbens, L. repens, L. reticulata, Ligustrum, Lippia lanceolata, Lycopus sinuatus, Lythrum alatum, Medicago sativa, Malva neglecta, M. rotundifolia, Melilotus alba, M. officinalis, Nepeta cataria, Oenothera laciniata, Oxalis dillenii, O. stricta, Penstemon, Petalostemon candidum, Polygala sanguinea, Polygonum buxiforme, P. convolvulus, P. pennsylvanicum, Portulaca, Potentilla monspeliensis, P. recta, Prunella vulgaris, Prunus, Psoralea onobrychis, P. tenuiflora, P. tenuiflora floribunda, Pycnanthemum flexuosum, P. pilosum, P. virginianum, P. lanceolatum, Raphanus sativus, Rhus glabra, Rosa* (wild), *Rubus, Rudbeckia triloba, Serinea oppositifolia, Sisymbrium repardum, Solanum carolinense, Solidago canadensis, Spiranthes gracilis, Stachys palustris, Stellaria,*



Map 1. Map showing the known distributions of *Calliopsis (Calliopsis) andreniformis* Smith, *C. (C.) rhodophila* Cockerell, *C. (C.) helenae* Shinn, *C. (C.) teucrii* Cockerell, *C. (C.) mourei* Shinn, and *C. (C.) granti* Shinn. The presumptive collection locality for *Acamptopoeum maculatum* (Smith) is also shown.

Strophostyles pauciflora, Stylosanthes biflora, Symphoricarpos, Tamarisk, Trifolium hybridum, T. pratense, T. repens, Verbena bracteata, V. bracteosa, V. hastata, V. stricta, V. urticifolia, Verbesina helianthoides, Veronica spicata, Vicia.

CALLIOPSIS (CALLIOPSIS) TEUCRII Cockerell

(Figs. 14-17; Map 1)

Calliopsis teucrii Cockerell, 1899, *in* Cockerell and Porter, Ann. Mag. Nat. Hist. (7) 4:412, female; Cockerell, 1906, Trans. Amer. Ent. Soc., 32:299; Michener, 1951, *in* Muesebeck *et al.*, U.S. Dept. Agric., Monogr. No. 2:1103.

Calliopsis lepida var. *a* Cockerell, 1901, Ann. Mag. Nat. Hist., (7) 7:128, male, female.

Calliopsis lepida Cockerell, 1906 (not Cresson, 1878), Trans. Amer. Ent. Soc., 32:299. (misidentification)

Calliopsis sp., Wille, 1956, Univ. Kansas Sci. Bull., 38:453, 474-475, female (thoracic musculature).

Closest to *andreniformis,* the females of which are virtually identical with *teucrii,* and are best separated by the key characters. The male of *teucrii* has a brown scape, but that of *andreniformis* is yellow.

FEMALE. Length, 6.7 mm; forewing length, 4.6 mm; hindwing length, 3.2 mm, clypeal length, 0.46 mm, scutal length, 1.02 mm.

Head. Yellow areas: (1) paraocular area with a small patch bordering orbit below midlevel of antennal socket (to yellow, except lowermost corner, below a line originating at middle of, or slightly above, outer subantennal suture and extending diagonally upward ending on orbit at or below midlevel of antennal socket, well below lower rim of facial fovea, and lower than *andreniformis* in most cases); (2) absent on clypeus (to broad longitudinal median stripe from frontoclypeal suture to about 0.5 mow above preapical groove); (4) supraclypeal area with 2 minute dots (to full semilunar area reaching to slightly below midlevel of antennal socket); (5) absent on subantennal plate (to completely yellow). (8) Hair of type faded. Hair of fresh specimens: on vertex mixed brown and fulvous, on frons fulvous, on clypeus blacker, coarser, thicker than in *andreniformis.* (10) Punctures along ocellocular line 2-3 pwa, interspaces smooth; impunctate area adjacent to lateral border of posterior ocellus almost imperceptibly roughened (30×) and quite shiny; punctures of frons adjacent to upper portion of frontal line as in *andreniformis* except larger and more distinctly roughened (30×). (11) Frontal line with lower portion as in *andreniformis* except more distinct. (12) Clypeus with punctures of disc larger than frontal punctures, deep, 2-3 pwa, interspaces shinier than in *andreniformis* with extremely fine roughening. (13) Orbital convergence ratio as 1.19:1.11, 1.08. Facial fovea with distinct mesal border, linear but slightly wider below, narrower than in *andreniformis.* (14) Galea somewhat shiny but finely pebbled; length as in *andreniformis* (except in Flagstaff, Arizona, specimens where length exceeds clypeocellar 1.19:0.94); galeal gap to length of galea exposed beyond closed mandibles, variable. (15) Head width to head length as 1.96:1.55, 1.26 (1.20-1.28). (17) Eye length, mio, and flagellar length as 1.11:1.11:1.21(1.24:1.19:1.29). (18) Interocellar, ocellocular, antennocular, and interantennal as 0.29:0.36:0.28:0.28 (0.31:0.39:0.31:0.31). (19) Ocellolabral greater than clypeal width, 1.29:1.19, 1.08. (20) Clypeocellar to outer subantennal sutural as 0.83:0.63,1.32. (21) Basal labial palpomere about 4.0(3.9-4.8) times length of others combined. (22) Flagellar length about 2.4 times length of scape, 1.21:0.49.

Mesosoma. (23) Light areas yellow; medial interruption of pronotal stripe about 2 mow. (24) As in *andreniformis* except long scutal and scutellar hairs always brown. (25) Scutal disc with punctures slightly larger than in *andreniformis,* 1 pwa, interspaces shiny, becoming finer and crowded anteriorly, but less so than in *andreniformis,* less than 1 pwa, no discernible roughening (30×) (to very slight), faintly to strongly greenish metallic colored. (26) Dorsal enclosure of propodeum relatively dull, with finer, more regularly longitudinal ridges than in *andreniformis;* median portion more distinctly bordered posteriorly, and proportionately longer in relation to lateral areas than in *andreniformis*. (27) Legs with light color the same as on face. Foreleg with yellow like that of *andreniformis*. (28) Middle leg and spur as in *andreniformis* except spur length about 0.6 (to 0.7) of length of middle basitarsus, 0.47:0.73. (30) Tegula brown. (32) Marginal cell 6-9 longer than, and 3-4 shorter than 9-wt, 0.99:0.83:0.94.

Metasoma. (34) Tergal hair bands white. Bands of terga 1-2 as in *andreniformis*. (35) Tergum 1 with punctures of median area fine, mostly 1 pwa, interspaces highly polished. Declivity of tergum 1 with a high polish.

Male. Length, 5.5 mm; forewing length, 4.3 mm; hindwing length, 3.13 mm; clypeal length, 0.48 mm; scutal length, 0.78 mm.

Head. Yellow areas: (1) paraocular area as in *andreniformis* but more horizontally truncate above; (2) clypeus as in *andreniformis* except apical border black; (4) supraclypeal area as in *andreniformis* except height of area lowered with decreasing latitude, upper limit of area below middle of antennal socket near southern limit of range; (5) subantennal plate as in *andreniformis*. (7) Scape and pedicel brown. (8) Hair on vertex and frons fulvous, on clypeus brown (to black), on gena white. (10) As in *andreniformis* except impunctate area usually very shiny despite minute roughening, and punctures of lower, dark portion of frons larger than in *andreniformis*. (11) Frontal line with lower, carinate portion ending slightly above midlevel of antennal socket. (12) Clypeus as in *andreniformis*. (13) Orbital convergence ratio as 1.09:0.85,1.28. (14) Galea dull, completely pebbled, somewhat ligulate in repose; galeal gap subequal to (to less than) length of galea exposed beyond closed mandibles. (15) Head width to head length as 1.77:1.56,1.13. (17) Eye length, mio, and flagellar length as 1.02:0.85:1.53. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.27:0.34:0.17:0.26, close to *andreniformis*. (19) Ocellolabral greater than clypeal width, 1.24:1.11,1.12. (20) Clypeocellar to outer subantennal sutural as 0.77:0.61,1.25. (21) Basal labial palpomere 1.4-2.0 times length of others combined. (22) Flagellar length about 3.6 times length of scape, 1.53:0.43.

Mesosoma. (23) Light areas yellow; medial interruption of pronotal stripe about 1.5 mow. (24) Scutal and scutellar hair of two kinds, one short, fulvous, the other long, brown. Metanotal hair fulvous (to dirty white). Scutellar and metanotal hair pads as in *andreniformis* except metanotal hair pads much closer, 1.5 mow between mesal margins. (25) Scutal disc with punctures larger than *andreniformis*, 1 pwa or less, interspaces smooth (to finely roughened), becoming crowded anteriad. (26) Dorsal enclosure of propodeum with larger, thicker, reticulate ridges medially, with shorter longitudinal ridges laterally partly hidden by metanotal hair pad. Median portion of enclosure distinctly larger and longer than in *andreniformis*. (27) Legs with light color the same as on face. Foreleg with yellow on coxal apex, ventral trochanteral surface, basal half, more or less, of femur, tibia entirely except for posterior brown patch, tarsus entirely; mediotarsus as in *andreniformis.* (28) Middle leg colored like foreleg except apicotarsus testaceous; mediotarsomeres as in *andreniformis.* (29) Hind leg colored like middle leg except yellow greatly reduced on trochanter, and brown patch present on posterior tibial surface; apicotarsus testaceous; mediotarsomeres as in *andreniformis.* (30) Tegula brown. (31) Wing tip more distinctly brown apically beyond cells than in *andreniformis.* (32) Marginal cell 6-9 greater than, and 3-4 subequal to 9-wt, 0.97:0.85:0.85.

Metasoma. (34) Tergal hair bands white. Bands of terga 1-2 more broadly interrupted than in *andreniformis.* (35) As in *andreniformis.* (37) Sterna brown.

Type Material. Holotype female from Las Vegas, New Mexico, July 11 (T. D. A. Cockerell), on *Teucrium laciniatum,* is at the University of California, Riverside, California. It has the yellow markings of the face greatly reduced compared to usual specimens, and is smaller than the average as well.

The above description of the male is based primarily on a specimen from Coaldale, Colorado, 7800 ft., Aug. 4, 1957 (C. D. Michener).

Distribution. Colorado to Oaxaca. The species is widespread in central México but no specimens bridge the gap from Fresnillo, Zacatecas to San Jose, New Mexico. This seems likely to be a collecting bias rather than a real gap in distribution.

Seasonal distribution is June to Aug. 31 with one late record of Sept. 24, 1938, at Agua Fría, Hidalgo (L. J. Lipovsky).

The numerous records of the bee at altitudes of 5,000 to 8,000 ft. may indicate it is a mountain form that may, indeed, be absent from the desert parts of Durango and Chihuahua.

In addition to the type material approximately 305 specimens have been studied from the following localities: Arizona: Flagstaff (4 mi. N.; 6 mi. W.). Colorado: Animas, 6600 ft.; Coaldale, 7800 ft., Fremont Co.; Eleven-Mile Canyon, 8000 ft., Park Co.; Estes Park; Florissant; Ouray, 8500 ft.; Pagosa Springs, 7500 ft.; Ridgway, 7000 ft. New Mexico: Las Vegas; Ruidoso; Santa Fe; San Jose; Sapello. Distrito Federal: Contreras. Durango: Nombre de Dios, 5900 ft. Guerrero: Acapulco. Hidalgo: Agua Fría; Epazoyucan; Jacala (21 mi. S.W.; 7, 24 mi. N.E.), 5000 ft.; Lagunilla; Pachuca (14 mi. S.W.), 7500 ft.; Tepeapulco (3 mi. N.); Tizayuca (13.5 mi N.E.), 7700 ft. Jalisco: San Juan de los Lagos; Tepatitlán. Mexico: Chapingo; Tepexpán, 6900 ft. Michoacan: Morelia (22 mi. W.), 6800 ft.; Pátzcuaro; Tzitzio (3 mi. N.), 5500 ft. Morelos: Cuernavaca. Nuevo Leon: El Cercado (4 mi. W.). Oaxaca: Oaxaca (14 mi. E.), 5000 ft.; Tamazulapan (2 mi. N.W.), 6000 ft. Puebla: Chila (5 mi. S.), 5700 ft.; Huachinango (4 mi. S.W.), 5700 ft.; Teziutlán (5 mi. N.E.), 5100 ft. Queretaro: San Juan del Rio (10 mi. E.), 6500 ft. San Luis Potosi: Ciudad del Maíz (5 mi. E., 4700 ft.; 20 mi. N.E., 3000 feet). Tlaxcala: Apizaco (8 mi. W.; 8 mi. W.N.W.), 8200 ft. Zacatecas: Fresnillo (9 mi. S.).

Flower Records. *Asclepias, Convolvulus incanus, Heterotheca chrysopsidis, Melilotus officinalis, Oxalis, Potentilla, Stylosanthes, Taraxacum, Teucrium laciniatum.*

CALLIOPSIS (CALLIOPSIS) GRANTI, new species

(Figs. 18-21; Map 1)

The species is named in honor of the late Dr. Harold J. Grant, Jr., my long time friend and companion in the field. The species is intermediate between *teucrii* and *rhodophila,* but is closer to the latter. It is easily separated from both species by the key characters.

Male. Length, 5.2 mm; forewing length, 4.2 mm; hindwing length, 3.02 mm; clypeal length, 0.39 mm; scutal length, 0.80 mm. Integument of head, mesosoma, and first metasomal tergum with faint brassy, metallic tints.

Head. Yellow areas: (1) paraocular area as described for subgenus, upper boundary somewhat convex dorsally; (2) clypeus, dots black; border of lateral portion of apex black; frontoclypeal suture black. (4) Supraclypeal area, summit below midlevel of antennal socket; (5) subantennal plate, except lowermost outer corner triangularly black; (6) mandible with anterior and posterior borders black. (7) Scape, pedicel, flagellomeres 1 and 2, black. (8) Hair of vertex and frons fulvous, of clypeus black. (10) Punctures of upper frons larger than in *teucrii,* interspaces shiny. (11) Frontal line with lower portion a low, finely sulcate, carina. (13) Orbital convergence ratio as 1.05: 0.83,1.26. (14) Galea strongly pebbled, but little shiny, shinier than *teucrii,* with rounded, blunt tip; galeal gap estimated to be shorter than length of galea exposed beyond closed mandibles, 0.36:0.37. (15) Head width to head length as 1.67:1.43,1.17. (17) Eye length, mio, and flagellar length as 0.95: 0.83:1.19. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.27:0.32:0.17:0.27. (19) Ocellolabral equal to clypeal width, 1.12:1.12,1.00. (20) Clypeocellar to outer subantennal sutural as 0.73:0.54,1.34. (21) Basal labial palpomere 1.4 times length of others combined. (22) Flagellar length about 3.2 times length of scape, 1.19:0.37.

Mesosoma. (23) Light areas yellow. (24) Scutal and scutellar hairs short, white and long, brown. Scutellar hair pads black, separated by 0.37 mm, slightly more than 2 mow, somewhat farther than in *rhodophila.* Metanotal hair pads black, subquadrate, contiguous posteriorly, separated anteriorly leaving a triangular area from which arises a tuft of long white hairs. (25) Scutal disc with punctures slightly larger than in *teucrii,* much larger than in *rhodophila,* 1 pwa or less, interspaces shiny. (26) Dorsal enclosure of propodeum covered by metanotal hair pad except for small median area which is abruptly elevated. (27) Legs with light color the same as on face. Foreleg yellow except dark brown on basal half of coxa, dorsal half of trochanter; anterior half, passing dorsally to posterior three-fourths, of femur, and most of posteroventral surface of tibia; mediotarsus testaceous, distitarsus brown. (28) Middle leg colored like foreleg. (29) Hind leg colored like middle leg except brown patch on posterior surface of tibia reduced and located medially.

(30) Tegula brown. (32) Marginal cell 6-9 greater than, and 3-4 subequal to 9-wt, 0.94:0.80:0.82.

Metasoma. (34) Tergal hair bands very sparse on all terga. Band of tergum 1 represented by only a small lateral group of sparse hairs. (35) Tergum 1 with punctures of median area scarce, larger than on scutum, irregularly distributed, of area immediately laterad larger than on scutum, about 1 pwa, interspaces highly polished; punctures shallow, some eccentric, giving pockmarked appearance suggesting deformity but bilaterally symmetrical. Declivity of tergum 1 finely lineolate, very shiny.

TYPE MATERIAL. Holotype male from Apizaco (8 miles W.N.W.), Tlaxcala, 8200 feet, June 18, 1961 (University of Kansas Mexican Expedition), on *Stylosanthes,* is in the Snow Entomological Museum of The University of Kansas, Lawrence.

CALLIOPSIS (CALLIOPSIS) RHODOPHILA Cockerell

(Figs. 22-25; Map 1)

Calliopsis andreniformis rhodophila Cockerell, 1897, Proc. Acad. Nat. Sci. Philadelphia, 49:350, male, not female; *idem,* Bull. Univ. New Mexico, 24:19; *idem,* 1898, Trans. Amer. Ent. Soc. 25:196.

Calliopsis rhodophila; Cockerell, 1898, Bull. Denison Univ., 11:52: Birkman, 1899, Ent. News, 10:244 (rec., Fedor, Lee Co., Texas, det. Friese); Cockerell, 1902, Amer. Naturalist, 36:810; *idem,* 1906, Trans. Amer. Ent. Soc., 32:299; *idem,* Bull Amer. Mus. Nat. Hist., 22:440; *idem,* 1921, Amer. Mus. Novitates, 24:14; *idem,* 1922, 40:4; Timberlake, 1947, Pan-Pac. Ent., 23:29; Michener, 1951, *in* Muesebeck *et al.,* U.S. Dept. Agric., Monogr. No. 2:1103.

Closest to *teucrii* and *granti* but fairly easily separated from them by the long, sharply pointed galeae which are slim and tapering towards their apices, and the galeae appear to be somewhat converging towards each other. The few specimens of this bee I have examined have come from widely separated geographic areas, and the species appears to be rare.

FEMALE. Length, 6.8 mm; forewing length, 4.8 mm; hindwing length, 3.43 mm; clypeal length, 0.51 mm; scutal length, 1.12 mm.

Head. Yellow areas: (1) paraocular area, except lowermost corner, below a sinuous line originating at middle of, or slightly above outer subantennal suture and extending upward ending on orbit at or above midlevel of antennal socket, usually not touching lower border of facial fovea, but if touching lower border of fovea then ending on orbit above lower border of fovea, usually below upper rim of antennal socket; (2) clypeus, a median, longitudinal stripe about as wide as width of yellow supraclypeal area, upper portion somewhat constricted just below base; lower margin about 0.5 mow above clypeal apex; (4) supraclypeal area broadly semilunar to broadly pentagonal, extending to midlevel, or above, of antennal socket; (5) usually absent on subantennal plate, but sometimes on lower half. (8) Hair like *andreniformis,* except clypeal hairs finer. (10) Punctures along ocellocular line sparse, very fine, with shiny interspaces, impunctate area adjacent to lateral border of posterior ocellus shiny (30×); punctures of frons adjacent to upper portion of frontal line deep, distinct, 1-2 pwa, interspaces smooth, moderately shiny (30×). (12) Clypeus with punctures of disc larger than frontal punctures, deep 2-3 pwa, interspaces shiny, highly polished, except faintly roughened beside subantennal plate. (13) Orbital convergence ratio as 1.28:1.17, 1.09. Facial fovea linear, distinctly bordered medially. (14) Galea smooth, shiny; apex pointed (30×) in contrast to varying degrees of broadness in other species of *Calliopsis s.s.;* length only slightly less than antennocellar; galeal gap less than length of galea exposed beyond closed mandibles. (15) Head width to head length as 2.11:1.58,1.33. (17) Eye length, mio, and flagellar length as 1.19:1.19:1.22. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.34:0.34:0.29:0.32. (19) Ocellolabral subequal to clypeal width, 1.34:1.36. (20) Clypeocellar to outer subantennal sutural as 0.83:0.70, 1.19. (21) Basal labial palpomere about 2.0 times length of others combined; ventral hairs fine, straight. (22) Flagellar length about 2.3 times length of scape, 1.22:0.54.

Mesosoma. (23) Light areas yellow; medial interruption of pronotal stripe about 2 mow. (24) As in *andreniformis.* (25) Scutal disc with punctures fine, deep, distinct, about 3 pwa, interspaces shiny, becoming crowded anteriorly to 1 pwa with shiny interspaces. (26) Dorsal enclosure of propodeum shiny, with obliquely longitudinal ridges laterally, straight medially; posterior border carinate, a small medial portion of border raised distinctly upward; median portion longer than lateral portion. (27) Foreleg without (or with) yellow spot on extreme apex of femur. (28) Middle leg colored like foreleg; spur length about 0.6 length of middle basitarsus, 0.49:0.82. (30) Tegula brown. (32) Marginal cell 6-9 greater than, and 3-4 less than 9-wt, 1.07:0.88:1.02.

Metasoma. (34) Tergal hair bands white. (35) Tergum 1 with punctures of median area exceedingly fine, 2-3 pwa anteriorly to impunctate posteriorly, interspaces highly polished.

MALE. Length, 5.9 mm; forewing length, 4.3 mm; hindwing length, 3.10 mm; clypeal length, 0.46 mm, scutal length, 0.75 mm.

Head. Yellow areas: (1) paraocular area as in *teucrii;* (2) clypeus, dots pale brown; lateral border of apex black; frontoclypeal suture black; (4) supraclypeal area, summit between midlevel and upper border of antennal socket; (5) subantennal plate; (6) mandible with anterior and posterior borders black. (7) Scape and pedicel black; flagellomeres 1-2 partly black. (8) Hair on vertex and frons white, on clypeus black. (10) Punctures of upper frons largest of the *andreniformis* group, contiguous, shallow, indistinct, interspaces dulled by fine roughening. (11) Frontal line with lower portion a high, sharp, non-sulcate carina, distinctly higher than other species of subgenus. (13) Orbital convergence ratio as 1.17:0.88,1.33. (14) Galea highly polished, smooth, rather slim, galeal gap slightly more than half (to a third) of length of galea exposed beyond closed mandibles. (15) Head width to head length as (1.77:1.51,1.17). (17) Eye length, mio, and flagellar length as 1.09:0.88:1.48. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.31:0.32:0.19:0.27. (19) Ocellolabral subequal to clypeal width (1.21: 1.19), 1.02. (20) Clypeocellar to outer subantennal sutural as 0.78:0.58,1.35. (21) Basal labial palpomere 1.3 times length of others combined. (22) Flagellar length about 3.5 times length of scape, 1.48:0.43.

Mesosoma. (23) Light areas yellow. (24) Scutal and scutellar short hairs white, long hairs white (sometimes a few fulvous to brown on scutum posteriorly, and on scutellum). Scutellar hair pads black, apart by 0.31 mm, about 2 mow, somewhat closer than in *granti*. Metanotal hair pads as in *granti* except triangular area with apex more acute, pads larger, more extensive. (25) Scutal disc with punctures finer than in *teucrii,* mostly 2 pwa, interspaces shiny, smooth (sometimes faintly roughened). (26) Dorsal enclosure of propodeum as in *granti*. (27) Legs with light color the same as on face. Foreleg colored as in *granti*. (28) Middle leg like *granti*. (29) Hind leg colored like *granti,* except tibial patch black, located medially (or apically). (32) Marginal cell 6-9 greater than, and 3-4 subequal to 9-wt, 0.94:0.83:0.85.

Metasoma. (34) Tergal hair pads as in *granti*. (35) Tergum 1 with punctures of median area regularly distributed, finer than on scutum, extremely fine, about equal in size to those in *andreniformis,* but much more distinct, further apart at 3 pwa, interspaces highly polished. Declivity of tergum 1 highly polished.

Type Material. Holotype male from Santa Fe, New Mexico, July (T. D. A. Cockerell, Cockerell No. 3844), on *Sphaeralcea,* is in the U.S. National Museum, U. S. N. M. Type No. 3701. The female allotype, same label data except Cockerell No. 3842, U. S. N. M. Type No. 3702, is actually *teucrii.*

The above description of the female is based primarily on a specimen from Santa Fe, New Mexico, July (T. D. A. Cockerell, Ckll. No. 3843), on *Sphaeralcea!*

Distribution. The southwestern United States south to slightly north of central Mexico. Seasonal occurrence is from May to August. The highest altitudinal collection record is 5900 ft., and other records suggest a bee adaptable to low mountains.

In addition to the type material, 7 males and 18 females have been studied from the following localities: Arizona: Chino Valley. California: Kelso (7 mi. S.), Providence Mts., San Bernardino Co.; Mt. Laguna, San Diego Co.; Piñon Flat, San Jacinto Mountains, Riverside Co. New Mexico: Las Vegas; Ruidoso, Lincoln Co.; Santa Fe. Utah: Orderville, Kane Co. Durango: Nombre de Dios, 5900 ft. Zacatecas: Fresnillo (9 mi. S.E.; 1.5, 5, and 9 mi. S.).

Discussion. Too few specimens are available for positive conclusions, but the Arizona specimen, a female, is considerably duller than the others. The galeal gap in males is proportionately greater in specimens from New Mexico (half of length of galea exposed beyond closed mandibles) than in those from Utah, California, and Mexico (a third of length of galea exposed beyond closed mandibles). Males from New Mexico are shorter than those from other states. The hair pads show very little variation.

FLOWER RECORDS. *C. rhodophila* has been collected on *Sphaeralcea* in California in May, in New Mexico in July, Aug., Sept., and in Zacatecas in Aug. One record for *Solidago* is from Zacatecas in Aug.

CALLIOPSIS (CALLIOPSIS) MOUREI, new species

(Figs. 26-29; Map 1)

I take great pleasure in naming this distinctive species in honor of Padre Jesus S. Moure, C. M. F., of the University of Paraná, Curitiba, Brazil, who gave me a solid foundation for understanding the panurgine bees of South America most closely related to *Calliopsis.*

This species may be closest to *rhodophila,* but is easily distinguished from all other species of *Calliopsis s.s.* by the white facial color in combination with the cobalt blue color of the head and mesosoma.

MALE. Length, 5.2 mm; forewing length, 4.1 mm; hindwing length, 3.01 mm; clypeal length, 0.44 mm; scutal length, 0.87 mm. Integumental background color of head and mesosoma metallic cobalt blue, of metasoma metallic greenish.

Head. White areas: (1) paraocular area as described for subgenus, upper boundary dorsally convex; (2) clypeus, dots testaceous; border of lateral portion of apex black; frontoclypeal suture light; (4) supraclypeal area, summit 0.5 mow above upper edge of antennal socket; (5) subantennal plate; (6) mandible with anterior and posterior border black. (7) Scape, pedicel, and flagellomere 1 black; flagellomere 2 partly black. (8) Hair on vertex, frons, clypeus, and gena white. (10) Punctures of upper frons fine, 2-3 pwa, interspaces shiny, cobalt blue, minutely roughened (30×). (11) Frontal line with lower portion a medium-height, non-sulcate carina. (13) Orbital convergence ratio as 1.11:0.82,1.35. (14) Galea finely pebbled, dull, width somewhat slim as in *rhodophila,* tip very narrowly rounded, intermediate between *rhodophila* and *granti;* galeal gap slightly shorter than length of galea exposed beyond closed mandibles, 0.36:0.37. (15) Head width to head length as 1.73:1.50,1.16. (17) Eye length, mio, and flagellar length as 1.02:0.82:1.39. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.32:0.31:0.17:0.26. (19) Ocellolabral greater than clypeal width, 1.22:1.11,1.11. (20) Clypeocellar to outer subantennal sutural as 0.78:0.56,1.39. (21) Basal labial palpomere 1.8 times length of others combined. (22) Flagellar length about 3.6 times length of scape, 1.39:0.39.

Mesosoma. (23) Light colored areas: of pronotal stripe, pronotal lobe, meso- and metasternum, white; of scutellar crest, yellow. (24) Scutal and scutellar hair white. Scutellar hair pads black, widely separated, confined to lateral scutellar areas, separated by 0.49 mm. Metanotal hair pads black, large, broadly oval, separated by 0.14 mm, less than 1 mow. (25) Scutal disc with punctures finer than in *rhodophila,* distinct, mostly 2 pwa, interspaces shiny, smooth. (26) Dorsal enclosure of propodeum with median portion exposed, lateral portion only covered anteriorly by metanotal hair pad; seven slightly irregularly longitudinal ridges on median portion, interspaces shiny; less distinct, lower ridges on lateral portion, interspaces shiny posteriorly, roughened anteriorly. (27) Legs with light color the same as on face except yellow on front and middle coxae. Foreleg colored as in *granti* except dark tibial patch much smaller. (28) Middle leg colored as in *granti* except dark tibial patch much smaller. (29) Hind leg colored as in *granti* except dark tibial patch much smaller. (32) Marginal cell 6-9 greater than, and 3-4 slightly less than 9-wt 0.87:0.75:0.80.

Metasoma. (34) Tergal hair bands as in *granti.* (35) Tergum 1 with punctures of median area regularly distributed, finer than on scutum, slightly larger than in *rhodophila,* 2-3 pwa, interspaces smooth shiny. Declivity of tergum 1 roughened, somewhat shiny.

TYPE MATERIAL. Holotype male from Tepexpán, state of México, Aug. 12, 1954 (University of Kansas Mexican Expedition), is in the Snow Entomological Museum of The University of Kansas, Lawrence.

DISCUSSION. This striking species is the only one of the genus to display a metallic cobalt blue integument. Nothing is known of its biology.

CALLIOPSIS (CALLIOPSIS) HONDURASICA Cockerell

(Figs. 30-33; Map 2)

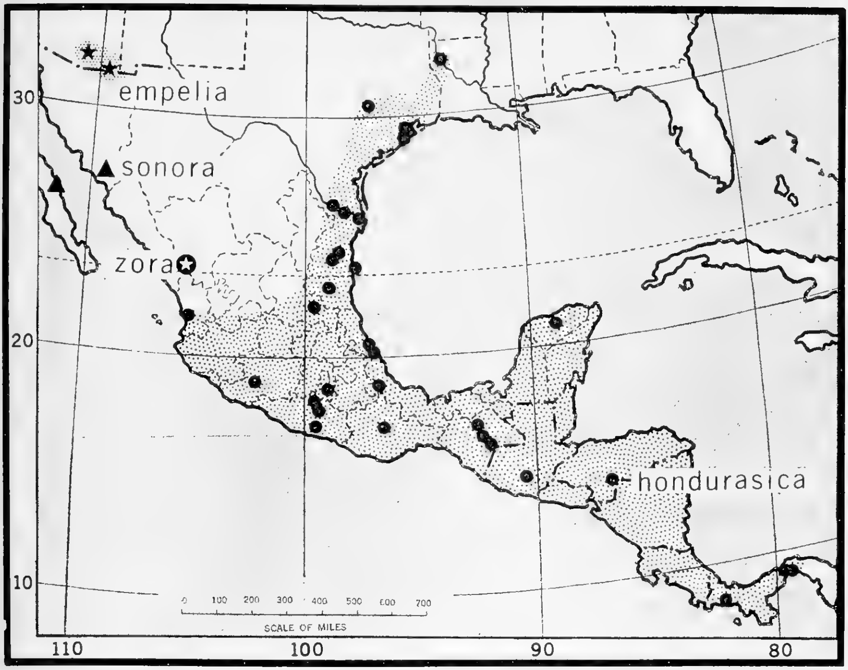
Calliopsis hondurasica Cockerell, 1949, Proc. U.S. Nat. Mus., 98 (3233): 437; Michener, 1951, *in* Muesebeck et al., U.S. Dept. Agric., Monogr. No. 2:1103; Michener, 1954, Bull. Amer. Mus. Nat. Hist., 104(1):36-38.

Calliopsis andreniformis; Cockerell, 1932, Bull. Brooklyn Ent. Soc., 27:11 (misidentification).

The closest relative of this species is *sonora* from which it is differentiated in the male by the small tan scutellar and metanotal hair pads, and in the female by the key characters of couplet 14. In Louisiana and Texas it may be mistaken for *andreniformis,* from which it is readily distinguished in the male by the much longer flagellum, and in the female by the distinctive fine puncturing on a finely roughened ground.

FEMALE. Length, 7mm; forewing length, 4.9 mm; hindwing length 3.45 mm; clypeal length, 0.49 mm; scutal length, 1.29 mm.

Head. Yellow areas: (1) paraocular area as in *rhodophila* but yellow not



MAP 2. Map showing the known distributions of *Calliopsis (Calliopsis) empelia* Shinn, *C. (C.) sonora* Shinn, *C. (C.) zora* Shinn, and *C. (C.) hondurasica* Cockerell.

touching lower border of facial fovea; (2) as in *rhodophila;* (4) supraclypeal area, broadly semilunar, extending to below midlevel of antennal socket; (5) absent on subantennal plate (to all yellow). (8) Hair like *andreniformis,* except clypeal hairs fulvous (to brown). (10) Punctures along ocellocular line 3 pwa, very fine, with dull roughened interspaces; impunctate area laterally adjacent to posterior ocellus dull (30×); frontal punctures adjacent to upper portion of frontal line finer than in *rhodophila,* distinct, somewhat shallower, 1-2 pwa, interspaces dull, roughened (30×). (12) Clypeus with punctures of disc much larger than upper frontal ones, 2-3 pwa, interspaces roughened except shiny in median apical portion. (13) Orbital convergence ratio as 1.38: 1.31,1.05. Facial fovea shallow, broadened medially (to almost borderless in some Panamanian specimens). (14) Galea smooth, shiny; length slightly less than, to subequal to, antennocellar; galeal gap more than twice length of galea exposed beyond closed mandibles, 0.61:0.26. Some hairs of stipes bent abruptly at tip and often curled in a plane perpendicular to the shaft. (15) Head width to head length as 2.30:1.72,1.34. (17) Eye length, mio, and flagellar length as 1.24:1.31:1.41. (18) Interocellar, antennocular, and interantennal as 0.37:0.41:0.36:0.34. (19) Ocellolabral greater than clypeal width, 1.45:1.38, 1.05. (20) Clypeocellar to outer subantennal sutural as 0.94:0.75,1.25. (21)

Basal labial palpomere 1.5 times length of others combined; many ventral hairs, thickened to stout setae. (22) Flagellar length about 2.3 times length of scape, 1.41:0.61.

Mesosoma. (23) Light area yellow; medial interruption of pronotal stripe about 2.5 mow. (24) Longer scutal and scutellar hairs only slightly darker than shorter hairs. Hair of metanotum white. (25) Scutal disc with punctures very fine, deep, distinct, about 2 pwa, interspaces extremely dulled by very fine roughening. (26) Dorsal enclosure of propodeum shiny, with numerous vermiform ridges, posterior border carinate; median portion about same length as lateral portion. (27) Foreleg without yellow spot on femur. (28) Middle leg colored like foreleg; spur length about 0.6 times length of middle basitarsus. (30) Tegula brown. (32) Marginal cell 6-9 greater than, and 3-4 less than 9-wt, 1.11:0.85:1.00.

Metasoma. (34) Tergal hair bands white. (35) Tergum 1 with punctures of median area exceedingly fine, 3 pwa, interspaces dull, finely roughened.

MALE. Length, 6.0 mm; forewing length, 4.5 mm; hindwing length, 3.40 mm, clypeal length, 0.44 mm, scutal length, 1.05 mm.

Head. Yellow areas: (1) paraocular area as described for subgenus, upper boundary a relatively straight line; (2) clypeus, dots testaceous; lateral border of apex pale; frontoclypeal suture pale; (4) supraclypeal area, truncate dorsally (to somewhat emarginate) at midlevel of antennal socket; (5) subantennal plate; (7) scape, except a roughly triangular area of brown, base of triangle along apex of scape anteriorly and posteriorly, apex of triangle near middle of scape; pedicel, on lateral half; flagellomeres 1 and 3 partly brown. Scape unusually long. (8) Hair on vertex, frons, and clypeus fulvous. (10) Punctures of upper frons finest in subgenus, 2 pwa, interspaces smooth. (11) Frontal line with lower portion a relatively high (lower than in *rhodophila,* higher than in *mourei*), sharp carina. (13) Orbital convergence ratio as 1.33: 1.04,1.28. (14) Galea shiny, smooth at tip, lightly pebbled, dulled basad, slim, tip narrowly rounded; galeal gap greater than (to subequal to) length of galea exposed beyond closed mandibles, 0.46:0.26. (15) Head width to head length as 2.13:1.63,1.30. (17) Eye length, mio, and flagellar length as 1.17: 1.04:2.16. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.32:0.41:0.26:0.31. (19) Ocellolabral slightly less than clypeal width, 1.29:1.34, 0.96. (20) Clypeocellar to outer subantennal sutural as 0.85:0.70,1.22. (21) Basal labial palpomere 1.4 times length of others combined. (22) Flagellar length about 4.1 times length of scape, 2.16:0.53.

Mesosoma. (23) Light areas yellow. (24) Scutal and scutellar hair white to pale fulvous. Scutellar hair pads tan, small, confined to outer half of lateral portion of scutellum; often hidden by base of wing. Metanotal hair pads tan, oval, separated by 0.39 mm or about 2 mow. (25) Scutal disc with punctures fine, mostly 1.0-1.5 pwa, interspaces finely roughened, somewhat shiny. (26)

Dorsal enclosure of propodeum with indistinct reticulated ridges, interspaces strongly roughened, somewhat shiny. (27) Legs with light color the same as on face. Foreleg yellow except basal half of coxa dark brown, distitarsus testaceous. (28) Middle leg yellow except dorsal half of coxa dark brown, apicotarsus testaceous. (29) Hind leg yellow except base of coxa, dorsal apex of femur, and basal rim (often entire base) of basitibial plate brown, apicotarsus testaceous. (32) Marginal cell 6-9 greater than, and 3-4 slightly less than 9-wt, 1.02:0.75:0.88.

Metasoma. (34) Tergal hair bands as in *granti*. (35) Tergum 1 with punctures of median area exceedingly fine, distinct, 2-3 pwa, interspaces finely roughened, dull. (37) Sterna brown.

Type Material. The female holotype taken at Zamorano, Honduras, in December, is in the U.S. National Museum (U.S.N.M. No. 58444). Zamorano is S.S.E. of Tegucigalpa, in the mountains, at latitude 14.01° N., longitude 87.01° W. The above description of the male is principally based on a specimen from Amatitlán, Guatemala, 4000 ft., July 6, 1947 (C. and P. Vaurie).

Distribution. This is the most widespread species in the genus. It occurs from Central Panamá to northwestern Louisiana. It is remarkable that despite the huge area covered by this bee, it is instantly recognizable and varies relatively little geographically. Specimens from Chiapas are darker than others, with the male pronotal lobes almost entirely dark; they also show considerable pebbling which dulls the galea, whereas others are smooth and very shiny.

This bee is the only species of *Calliopsis* which has been collected in every month of the year, owing to its occurrence in tropical latitudes. Likely enough its activity span in any one area is little more than in its relatives: a few months. Collections in Panamá tend to confirm this opinion: they date only from November to February. Michener (1954) suggests the limitation of *hondurasica* activity by rainfall rather than temperature. *C. hondurasica* flies during the early part of the dry season when moist conditions with clear, sunny days bring numerous flowering plants into bloom.

In addition to the type, specimens have been studied from the following localities: Louisiana: Robson, U.S.D.A. Pecan Field Station. Texas: Brownsville; Cameron Co.; Giddings, Lee Co.; Hidalgo; Mission (State Park on Rio Grande nearby), Hidalgo Co.; Progreso; Richmond, Fort Bend Co.; Riogrande (5 mi. E.); San Manuel (10 mi. S.); Santa Maria; Southmost, Cameron Co.; Sweeny. Chiapas: Comitán (15 mi. N.W.); San Cristóbal de las Casas (39 mi. E.); Simojovel (4 mi. S.). Guerrero: Amula, 6000 ft.; Chilpancingo, 3700 ft.; Iguala (13 mi. N.), 3900 ft.; Taxco (19.5 mi. N.E.), 4800 ft.; Tepetlapa, 3000 ft. Michoacan: Apátzingan (4, 11 mi. E.). Morelos: Yautepec (4 mi. S.W.), 3800 ft. Nayarit: San Blas (5 mi. E.), 25 ft. Oaxaca: Oaxaca. San Luis Potosi: Ciudad del Maíz (5 mi. E.), 4700 ft.; El Naranjo (3.4 mi. N.E.), 800 ft.; El Salto, 1800 ft. Tamaulipas: El Limón; Jiménez (22 mi. S.); Padilla; Tampico. Veracruz: Córdoba; Gutiérrez Zamora (4 mi. E.), 100 ft.; Nautla; Puente Nacional (4 mi. W.), 900 ft. Yucatan: Temax. Guatemala: Amatitlán, 4000 ft.; Guatemala City, 5000 ft. Honduras: Agua Azul; Zamorano. Costa Rica: Playa del Coco. Panama: Chillibre, Panamá Province; Davíd; Old Panamá; Panamá City; Pueblo Nuevo, Panamá Province; Salanas. Canal Zone: Ancon Hill; Chiva Chiva; Corozal; Fort Clayton; Summit.

BIONOMICS. Professor Alvaro Wille of the University of Costa Rica at San Jose has kindly furnished, through Professor Charles D. Michener, fragmentary notes on nesting sites, nest density, and the form of the burrow. These are discussed in comparison with *andreniformis* in connection with biology and ecology of the latter.

FLOWER RECORDS. *Cassia, Kallostroemia hirsutissima, Lippia, Nama undulatum, Phyla strigosa, Teucrium, Trifolium repens, Verbena.*

CALLIOPSIS (CALLIOPSIS) SQUAMIFERA Timberlake

(Figs. 42-45; Map 3)

Calliopsis squamifera Timberlake, 1947, Pan-Pacific Ent., 23:28, male; Michener, 1951, *in* Muesebeck *et al.*, U.S. Dept. Agric., Monogr. No. 2: 1103.

Timberlake considered this one of the species of *Calliopsis s.s.* and I concur, but it has characters which link it as an intermediate between *Calliopsis s.s.* and *Perissander.*

It is closest to *C. peninsularis,* which will doubtless be proven a *Calliopsis s.s.* when the male becomes known, but is readily distinguished by the mesotibial spur being bare and 0.75 times or more the length of the middle basitarsus (less than 0.60 in *peninsularis*).

FEMALE. Length, 5.0 mm; forewing length, 3.3 mm; hindwing length, 2.40 mm; clypeal length, 0.34 mm; scutal length, 0.85 mm.

Head. White areas: (1) paraocular area, except for lowermost corner, below a sinuous line originating at about middle of outer subantennal suture and extending to a point on orbit about 0.4 eye length below summit of eye; (2) clypeus with a broad, inverted T, the base bordering the supraclypeal area, the crossbar bordering the narrow, testaceous apical margin to the extent of the total width of clypeal emargination (reduced in some specimens to a narrowed, vertical part of the T); (4) supraclypeal area to about level of middle of antennal socket, dorsal margin evenly convex; (5) subantennal plate (to all black). (8) Hair on vertex fulvous, longer than long scutal hairs, on frons and clypeus fulvous. (10) Punctures of vertex and along ocellocular line with interspaces roughened (30×). Median punctures of frons deep, subconfluent, interspaces shiny (30×). (11) Frontal line with lower portion narrowly sulcate, becoming obsolete, ending in a slightly raised prominence at level of upper rim of antennal socket. (13) Orbital convergence ratio as 1.05:0.94,1.13. (14) Galea finely pebbled, hidden with mandibles closed. (15) Head width to head length as 1.73:1.22,1.42. (17) Eye length, mio, and flagellar length as 1.00:0.94:1.02. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.31:0.29:0.27:0.22. (19) Ocellolabral greater than clypeal width, 1.05:0.94, 1.13. (20) Clypeocellar to outer subantennal sutural as 0.71:0.51,1.40. (21)

Basal labial palpomere 0.8 times length of others combined. (22) Flagellar length about 2.2 times length of scape, 1.02:0.46.

Mesosoma. (23) Light areas yellowish; medial interruption of pronotal stripe about 3 mow. (24) Scutal and scutellar hair fulvous apicad, light brown basad, darker than hairs of vertex. Hair of metanotum fulvous. (25) Scutal disc with punctures finer and deeper than on vertex, 1-2 pwa, interspaces shiny (60×). (26) Dorsal enclosure of propodeum generally dull, slightly declivous, median portion with fine, close, vermiform, interrupted ridges, interspaces roughened, ridges becoming longitudinal and several ridge widths apart laterad, interspaces roughened. Proposed triangle adjacent to enclosure dull, roughened. (27) Legs with light color more yellowish than on face. Foreleg with cream (to yellow) on dorsal apex of femur and knee of tibia. (28) Middle leg colored like foreleg; spur entirely smooth, dark brown, length very long, about 0.8 length middle basitarsus, 0.53:0.60. (30) Tegula transparent, testaceous, with small anterior patch of cream (to yellow) color. Humeral plate testaceous. (32) Marginal cell (6-9) subequal to, and 3-4 shorter than 9-wt, 0.70:0.61:0.71.

Metasoma. (34) Tergal hair bands white. Band of tergum 1 narrowly (to broadly) interrupted medially, others entire. Suberect hair of disc of tergum 4 fulvous (to brownish), of disc of tergum 5 white (to fulvous). (35) Tergum 1 with punctures of median area exceedingly fine, dense, regularly spaced, 1-1.5 pwa, interspaces shiny though minutely roughened (60×), the tergum with a silky sheen (15×). Declivity of tergum 1 moderately shiny (to very shiny) though finely roughened.

MALE. Length, 4.0 mm (type 4 mm); forewing length, 2.9 mm (type 2.8 mm); hindwing length, 2.2 mm; clypeal length, 0.32 mm; scutal length, 1.33 mm.

Head. White areas: (1) paraocular area below a line originating at dorsolateral rim of antennal socket and extending diagonally upward, passing below the facial fovea, to a point on orbit about 0.4 eye length below summit of eye; (2) clypeus, except for apical pale testaceous margin; (4) supraclypeal area, pentagonal shape, to level of upper rim of antennal socket; (5) subantennal plate. (7) Scape broadly yellow (to yellowish white) in front, the mesoapical portion brown; pedicel brown with a lateral yellow spot; dorsal surface of flagellum dusky, darker basad, with brown extending part way round flagellomeres 1, 2, and 3; ventral surface of flagellum tan, flagellomere 1 with a lateral yellow spot. (8) As in female. (10) Punctures of vertex and along ocellocular line with interspaces shiny but faintly roughened (60×). Median punctures of frons shallow, contiguous, dull. (11) Frontal line with lower portion carinate. (13) Orbital convergence ratio as 0.92:0.68,1.36. (14) Galea as in female. (15) Head width to head length as 1.39:1.12,1.24. (16) As in female. (17) Eye length, mio, and flagellar length as 0.83:0.68:1.41.

(18) Interocellar, ocellocular, antennocular, and interantennal as 0.26:0:26: 0.15:0.19. (19) Ocellolabral greater than clypeal width, 0:92:0.82,1.13. (20) Clypeocellar to outer subantennal sutural as 0.60:0.43,1.42. (21) Basal labial palpomere 0.7 times length of others combined. (22) Flagellar length about 4.0 times length of scape, 1.41:0.36.

Mesosoma. (23) Light areas yellow; medial interruption of pronotal stripe about 2 mow. (24) Scutal and scutellar hairs whitish. Scutellar hair pads pale grayish-brown (to tan), their combined width slightly less than width of median portion of scutellum. Metanotal hair pads same color, broadly oval, failing to meet medially by less than mow, covering metanotum except for a median triangular area with base at anterior border of metanotum. Hair of metanotum white. (25) Scutal disc with punctures finer, deeper than on vertex, 2 or more pwa, interspaces shiny (60×). (26) Dorsal enclosure of propodeum with fine ridges originating anteriorly at the median line, each curving laterally along the width of the enclosure, giving the impression of tightly stretched, wrinkled skin. Remainder of propodeal triangle shiny. (27) Legs with light color bright yellow. Foreleg entirely yellow. (28) Middle leg with basal half of coxa dark, remainder of leg yellow with distitarsus pale testaceous. Lengths of tibia, basitarsus, and apicotarsus as 0.80: 0.85:1.00. (29) Hind leg colored like middle leg except distitarsus brown. Mediotarsomeres triangular in shape. (30) As in female. (32) Marginal cell lengths similar to female, 0.66:0.58:0.65.

Metasoma. (33, 34) As in female. (35) As in female except punctures 2 pwa.

TYPE MATERIAL. Holotype male from Picacho Pass (5 mi. S.E. of Picacho) [summit is at 1800 ft. altitude], Pinal Co., Arizona, Aug. 7, 1940 (P. H. Timberlake), on *Euphorbia,* is in the Timberlake collection at the University of California, Riverside, California. The above description of the male is based primarily on a topotypical specimen collected by C. D. Michener in company with Prof. Timberlake at the time of collection of the holotype.

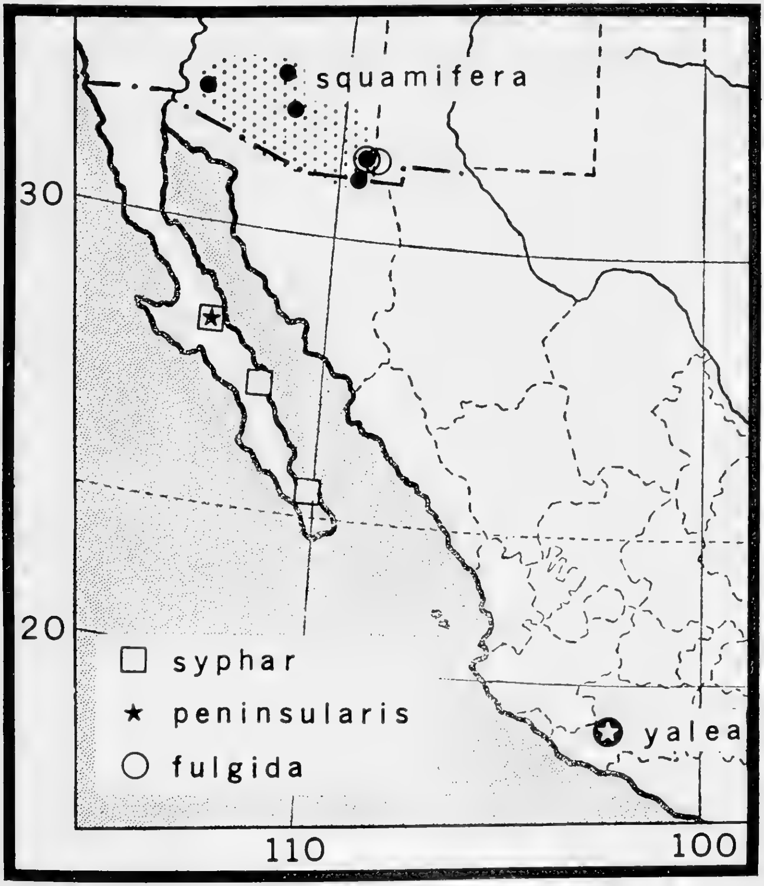
DISTRIBUTION. Known only from southern Arizona but to be expected from southwestern New Mexico and northern Sonora, southeastern California, and Baja California.

Specimens have been studied from the following localities: ARIZONA: Apache (5 mi. S.E.; 14 mi. S.W.), Cochise Co., Aug. 7-11, on *Euphorbia,* (13 mi. S.W.), Aug. 19-26, on *Euphorbia,* (5 mi. S.W.), Aug. 17, on *Baccharis glutinosa;* Douglas, Aug. 26 (3 mi. N.; 17 miles E.), Cochise Co., Aug. 8, on *Euphorbia;* Picacho Pass (5 mi. S.E. of Picacho), Pinal Co., Aug. 7, on *Euphorbia;* Portal (2 mi. N.E.), Cochise Co., Sept. 14; Roll, Yuma Co., July 11-Aug. 11, Oct. 20, on *Euphorbia* and Alfalfa; Tempe, Aug. 1.

GEOGRAPHIC VARIATION. Specimens from Roll in southwestern Arizona differ from those in middle southern and southeastern Arizona by having denser, shorter, more plumose hair on the face, thorax, and abdominal hair bands. Females from Apache and Douglas have greatly reduced areas of cream color on the head. Other minor differences in certain head and thoracic dimensions occur, but without males I must consider these within the range of variation of the species.

DISCUSSION. Most of the flower records are from *Euphorbia,* a biological datum bolstering the morphological data which indicate a relationship with *Perissander.*

BIONOMICS AND FLOWER RECORDS. Nothing is known of the bionomics of *squamifera,* but it has been taken on each one of the favorite plant families for the genus: Compositae, *Baccharis glutinosa;* Euphorbiaceae, *Euphorbia;* and Leguminosae, Alfalfa, *Medicago sativa.*



MAP 3. Map showing the known distribution of *Calliopsis (Calliopsis) peninsularis* Shinn, *C. (C.) squamifera* Timberlake, *C. (Perissander) syphar* Shinn, *C. (P.) fulgida* Shinn, and *C. (P.) yalea* Shinn.

CALLIOPSIS (CALLIOPSIS) PENINSULARIS, new species

(Map 3)

The specific name is from the Latin, *peninsula,* because of occurrence on the peninsula of Baja California.

The species resembles *C. squamifera* and *C. syphar.* It is distinguished from the former by the much shorter, pectinate mesotibial spur, and from the latter by the distinctly reticulated ridges on the dorsal enclosure of the propodeum.

Female. Length, 5.5 mm; forewing length, 3.6 mm; hindwing length, 2.50 mm; clypeal length, 0.37 mm; scutal length, 0.90 mm.

Head. Cream colored areas: (1) paraocular area below a line originating at about middle of outer subantennal suture and extending dorsally, inclining slightly laterad, to about 1 mow above antennal socket then convexly curved upward passing just below facial fovea and ending on orbit about 0.4 times eye length below summit of eye; (2) clypeus with a broad, inverted T, the base bordering the supraclypeal area, the crossbar bordering the narrow, testaceous apical margin for almost full width of clypeus, thus isolating two subtriangular brown areas with bases along subantennal plates, and two tiny patches of brown in the extreme lower corners of clypeus; (4) as in *squamifera*; (5) subantennal plate. (8) As in *squamifera.* (10) As in *squamifera* except roughening confined to vertex and virtually undetectable (30×). (11) As in *squamifera.* (13) Orbital convergence ratio as 1.05:1.00,1.05. Facial fovea ellipsoidal, distinct, width a fourth to third of length. (14) As in *squamifera* except glossa less broad medially. (15) Head width to head length as 1.80:1.28,1.41. (17) Eye length, mio, and flagellar length as 1.04: 1.00:1.05. (18) Interocellar, ocellocular, antennocular and interantennal as 0.31:0.31:0.26:0.24. (19) Ocellolabral greater than clypeal width, 1.09:1.05,1.02. (20) Clypeocellar to outer subantennal sutural as 0.71:0.54,1.31. (21) Basal labial palpomere 0.8 times length of others combined. (22) Flagellar length about 2.3 times length of scape, 1.05:0.46.

Mesosoma. (23) Light areas cream colored; medial interruption of pronotal stripe about 1.5 mow. (24) Scutal, scutellar, and metanotal hair fulvous (may be faded!). (25) As in *squamifera* except punctures apicad from anterior end of parapsidal line becoming crowded to subconfluent with interspaces roughened. (26) Dorsal enclosure of propodeum with medial portion dull, bearing a distinct reticulum of ridges, lateral portion having about 7 longitudinal ridges with interspaces shiny (30×). Area of propodeal triangle adjacent to lateral areas of enclosure roughened but relatively shiny. (27) Legs with light color the same as on face. Foreleg with cream color on dorsal apex of femur and a slanting patch to slightly less than midpoint of tibia.

(28) Middle leg colored like foreleg except tibial patch extends only slightly beyond knee; spur finely, evenly pectinate, testaceous, its length to length of basitarsus as 0.34:0.61,0.55. (30) Tegula transparent, almost colorless, with small anterior patch of cream color. (32) Marginal cell 6-9 and 3-4 greater than 9-wt, 0.77:0.71:0.70.

Metasoma. (34) Tergal hair bands white, hairs longer, less dense, and less plumose than in *squamifera* or in *syphar*. Prepygidial and pygidial fimbriae smoky, denser and longer than *squamifera*. (35) Tergum 1 with punctures of median area fine, larger than *squamifera*, dense, regularly spaced, 1.0-1.5 pwa, interspaces shiny (30×), the tergum without a silken sheen (15×). Declivity of tergum 1 shiny, finely lineolate.

TYPE MATERIAL. Holotype female from San Ignacio (15 mi. N.), Baja California Sur, Sept. 29, 1941 (E. S. Ross and R. M. Bohart), is in the California Academy of Sciences, San Francisco.

CALLIOPSIS (CALLIOPSIS) SONORA, new species

(Figs. 34-37; Map 2)

The specific name is from the state of Mexico in which it occurs. It is closest to *hondurasica*. The female is distinguished from *hondurasica* by the smaller size and proportionately shorter flagellum relative to the minimum interocular distance. The male is distinguished by the smaller size and by the brown or gray metanotal hair pads which are separated by less than 1 mow.

FEMALE. Length, 6.0 mm; forewing length, 4.2 mm; hindwing length, 2.90 mm; clypeal length, 0.46 mm, scutal length, 1.16 mm.

Head. Yellow areas: (1) paraocular area below a sinuous line originating at about middle of outer subantennal suture and passing below facial fovea ending on orbit slightly below facial fovea, well above antennal socket; (2) as in *hondurasica* except median stripe only 0.25 mow from clypeal apex; (4) as in *hondurasica;* (5) subantennal plate except uppermost portion. (8) Hair as in *hondurasica*. (10) Punctures along ocellocular line 1-2 pwa, fine but larger than *hondurasica,* interspaces dull but less so than in *hondurasica;* impunctate area laterally adjacent to posterior ocellus dull, roughened, but less so than in *hondurasica;* frontal punctures adjacent to upper frontal line as in *hondurasica* except interspaces very faintly metallic (30×). (12) Clypeus with punctures of disc larger than upper frontal ones, 2-3 pwa, interspaces roughened, except shiny in median apical portion. (13) Orbital convergence ratio, as 1.22:1.19,1.03. Facial fovea distinct, shorter than *hondurasica,* linear. (14) Galea smooth, shiny except faintly roughened basad; length shorter than antennocellar; galeal gap greater than length of galea exposed beyond closed mandibles. Hair of stipes as in *hondurasica*. (15) Head width to head length as 2.04:1.50,1.36. (17) Eye length, mio, and flagellar length as 1.12:1.19:1.21.

(18) Interocellar, ocellocular, antennocular, and interantennal as 0.37:0.37:0.29:0.32. (19) Ocellolabral greater than clypeal width, 1.29:1.24,1.04. (20) Clypeocellar to outer subantennal sutural as 0.83:0.65,1.29. (21) Basal labial palpomere about 1.4 times length of others combined; ventral hairs as in *hondurasica* except smaller in diameter and fewer present. (22) Flagellar length about 2.2 times length of scape, 1.21:0.54.

Mesosoma. (23) Light areas yellow; medial interruption of pronotal stripe about 2 mow. (24) As in *hondurasica.* (25) Scutal disc with punctures finer, shallower than in *hondurasica,* about 2 pwa, interspaces as in *hondurasica* except finer roughening. (26) Dorsal enclosure of propodeum as in *hondurasica.* (27) Foreleg as in *hondurasica.* (28) Middle leg colored like foreleg; spur length about 0.6 times length middle basitarsus, 0.44:0.73. (30) Tegula brown. (32) Marginal cell 6-9 greater than, and 3-4 less than 9-wt, 0.90:0.70:0.85.

Metasoma. (34) Tergal hair bands white. (35) Tergum 1 with punctures of median area exceedingly fine, 2-3 pwa, interspaces dull, finely roughened.

MALE. Length, 5.9 mm; forewing length, 4.0 mm; hindwing length, 2.81 mm; clypeal length, 0.43 mm; scutal length, 0.85 mm.

Head. Yellow areas (dull, not shiny like *hondurasica*): (1) paraocular area as described for subgenus, upper boundary relatively straight; (2) clypeus, dots colorless; frontoclypeal suture pale; (4) supraclypeal area, extending higher than in *hondurasica,* onto lower edge of frontal carina, summit slightly below level of upper border of antennal socket; (5) subantennal plate. (7) Scape, as in *hondurasica* except apex of triangular brown area only about 0.4 distance towards base of scape. Scape with length proportionately shorter than in *hondurasica.* (8) Hair as in *hondurasica.* (10) Punctures of upper frons fine, less so than *hondurasica,* less distinct than in *hondurasica,* 1 pwa, interspaces smooth, rather dull. (11) Frontal line with lower portion as in *hondurasica.* (13) Orbital convergence ratio as 1.17:0.99,1.19. (14) As in *hondurasica.* (15) Head width to head length as 1.87:1.53,1.22. (17) Eye length, mio, and flagellar length as 1.05:0.99:1.56. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.31:0.36:0.22:0.26. (19) Ocellolabral less than clypeal width, 1.22:1.26,0.97. (20) Clypeocellar to outer subantennal sutural as 0.80:0.61,1.30. (21) Basal labial palpomere 1.3 times length of others combined. (22) Flagellar length about 3.5 times length of scape, 1.56:0.44.

Mesosoma. (23) Light areas yellow. (24) As in *hondurasica.* Scutellar hair pads dark grayish brown, confined to entire lateral portion of scutellum, not completely hidden by base of wing. Metanotal hair pads same color, large, oval, separated by less than 1 mow. (25) Scutal disc punctures larger than in *hondurasica,* shallower, 1 pwa or less, interspaces as in *hondurasica.* (26) Dorsal enclosure of propodeum covered by metanotal hair pad except for medial portion which is gradually elevated; a single, prominent, mesally oblique ridge on each side of the center line, enclosing area with several small, indistinct ridges. (27) Legs with light color the same as on face. Foreleg yellow except base of coxa brown. (28) Middle leg yellow except base of coxa brown, apicotarsus testaceous. (29) Hind leg yellow except base of coxa brown, dorsal apex of femur, and basal rim of basitibial plate testaceous, apicotarsus testaceous. (32) Marginal cell 6-9 subequal to, and 3-4 less than 9-wt, 0.77:0.61:0.78.

Metasoma. (34) As in *granti*. (35) Tergum 1 with punctures of median area very fine, indistinct, interspaces roughened, dull. (37) Sterna brown.

TYPE MATERIAL. Holotype male, from Rio Mayo, Sonora, Aug. 25, 1935 (collector unknown), is in Dr. G. E. Bohart's collection, Logan, Utah. Allotype female and one female paratype, from Rio Mayo, San Bernardino, Sonora, same date (J. J. du Bois), are at the University of California, Riverside, California.

DISCUSSION. Apparently this species is an offshoot of *hondurasica* adapted to the arid Sonoran area where *hondurasica* does not occur.

One female specimen, from Canipole (about 100 mi. S.E. of San Ignacio), Baja California Sur, Oct. 2, 1941 (E. S. Ross and R. M. Bohart), may be this species. Its salient differences from the type material of *sonora* are the *presence* of a yellow spot on the tegula, basal labial palpomere 2.2 times length of others combined and 0.66 times length of scape, galeal length equal to scape length (much greater in *sonora*), interantennal less than antennocular, antennocular greater than inner subantennal sutural, scutal punctures shallower, less distinct, interspaces smoother and duller. Other characteristics are virtually identical, and this is so for numerous body measurements except the highly variable head width.

CALLIOPSIS (CALLIOPSIS) EMPELIA, new species

(Figs. 38-41; Map 2)

The specific name is from the Greek, *empelios*, meaning gray, which is applied with reference to the large gray metanotal hair pads.

It is closest to *sonora* and the female is distinguished from it by the yellow dot on the brown tegula, by the extremely dull interspaces between scutal punctures, by the non-metallic frons, and by the flagellar length being markedly shorter than the minimum interocular distance.

FEMALE. Length, 7.2 mm; forewing length, 4.4 mm; hindwing length, 2.40 mm; clypeal length, 0.53 mm; scutal length, 1.27 mm.

Head. Yellow areas: (1) paraocular area as in *sonora;* (2) clypeus as in *hondurasica;* (4) supraclypeal area as in *sonora;* (5) subantennal plate entirely. (8) Hair faded, but as in *sonora*. (10) Punctures along ocellocular line coarser, shallower than others in *hondurasica* group, less than 1 pwa, interspaces very dull, most coarsely roughened of *hondurasica* group; impunctate area dull, roughened; upper frontal punctures less than 0.5 pwa, interspaces heavily roughened. (12) Clypeus with punctures of disc about size of upper frontal punctures, 2-3 pwa, interspaces roughened, except shiny in median apical portion. (13) Orbital convergence ratio as 1.31:1.26,1.04. Facial fovea distinct, broader medially, tapering strongly above. (14) Galea faintly pebbled (30×); length less than antennocular; galeal gap subequal to length of galea exposed beyond closed mandibles. (15) Head width to head length as 2.30: 1.72,1.34. (17) Eye length, mio, and flagellar length as 1.26:1.26:1.02. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.36:0.39:0.32:0.31. (19) Ocellolabral greater than clypeal width, 1.45:1.39,1.03. (20) Clypeocellar to outer subantennal sutural as 0.92:0.70,1.31. (21) Basal labial palpomere 1.8 times length of others combined; ventral hairs somewhat thickened but much less than in *hondurasica*. (22) Flagellar length about 1.8 times length of scape, 1.02:0.56.

Mesosoma. (23) Light areas yellow; medial interruption of pronotal stripe about 1.5 mow. (24) As in *andreniformis*. (25) Scutal disc with punctures of moderate size, much larger and closer than preceding species, 1 pwa or less, interspaces heavily roughened. (26) Dorsal enclosure of propodeum as in *hondurasica* except dull and more sharply carinate posteriorly. (27) Foreleg with yellow on extreme apex of femur. (28) Middle leg without yellow on extreme apex of femur; spur length about 0.64 times length of middle basitarsus. (30) Tegula brown with anterior yellow dot. (32) Marginal cell 6-9 greater than, and 3-4 less than 9-wt, 1.11:0.85:1.00.

Metasoma. (34) Tergal hair bands white. (35) Tergum 1 with punctures of median area fine, about 1 pwa, interspaces heavily roughened, dullest of subgenus.

Male. Length, 5.3 mm; forewing length, 4.0 mm; hindwing length, 2.89 mm; clypeal length, 0.41 mm; scutal length, 0.85 mm.

Head. Yellow areas: (1) paraocular area as described for subgenus, upper boundary relatively straight; (2) clypeus, dots black; frontoclypeal suture pale; (4) supraclypeal area, summit at level of upper border of antennal socket; (5) subantennal plate. (7) As in *hondurasica*, except brown area of scape extending to base of scape. (8) Hair as in *hondurasica*. (10) Punctures of upper frons almost as fine as in *hondurasica*, less distinct than in *hondurasica*, 1-2 pwa, interspaces smooth, dull. (11) Frontal line with lower portion as in *sonora* except lower. (13) Orbital convergence ratio as 1.11:0.90, 1.22. (14) Galea shiny, faintly pebbled, broader than *hondurasica* and *sonora*, tip less narrowly rounded; galeal gap greater than length of galea exposed beyond closed mandibles. (15) Head width to head length as 2.13:1.63,1.30. (17) Eye length, mio, and flagellar length as 0.99:0.90:1.79. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.29:0.34:0.20:0.24. (19) Ocellolabral slightly less than clypeal width, 1.16:1.19,0.97. (20) Clypeocellar to outer subantennal sutural as 0.75:0.56,1.33. (21) Basal labial palpomere about 1.2 times length of others combined. (22) Flagellar length about 4.0 times length of scape, 1.79:0.44.

Mesosoma. (23) Light areas yellow. (24) As in *hondurasica.* Scutellar hair pad as in *sonora* except dark gray. Metanotal hair pad as in *sonora* except dark gray, contiguous medially on posterior border, separated anteriorly leaving a triangular area with broad apex from which arises a tuft of long white hairs. (25) Scutal disc with punctures as in *sonora* except interspaces shinier. (26) Dorsal enclosure of propodeum as in *sonora.* (27) Legs with light color the same as on face. Foreleg yellow except extreme base of coxa brown. (28) Middle leg colored like foreleg except apicotarsus testaceous. (29) Hind leg as in *hondurasica.* (32) Marginal cell 6-9 greater than, and 3-4 less than 9-wt, 0.82:0.61:0.77.

Metasoma. (34) Tergal hair bands sparse but lateral portions somewhat more plumose and denser than other species of *hondurasica* group. (35) Tergum 1 with punctures of median area very fine, indistinct, interspaces roughened, somewhat shiny. (37) Sterna brown.

Type Material. Holotype male, from Mt. Lemmon Road, Mt. Lemmon, Arizona, 3500 ft., Aug. 15, 1954 (R. M. Bohart), and allotype female, from Douglas, Arizona, Aug. 2, 1940 (W. W. Jones), are in the Timberlake collection at the University of California, Riverside, California.

Discussion. The sexes were associated on the basis of punctation, sculpturing, similarity of mouthparts, and size difference as compared with that for *sonora* and *hondurasica.* The species probably occurs in that rich area for the genus—the Chiricahua Mountain region in the vicinity of Portal, Arizona.

CALLIOPSIS (CALLIOPSIS) ZORA, new species

(Map 2)

The specific name is from the Greek *zoros,* meaning strong, and is applied because this species is the largest and most robust bee in its subgenus.

Apparently closest to *empelia* from which it is distinguished by the completely brown tegula, by the moderately shiny interspaces between the scutal punctures, and by the faint greenish metallic color on the frons.

Female. Length, 7.5 mm; forewing length, 5.0 mm; hindwing length, 3.62 mm; clypeal length, 0.58 mm; scutal length, 1.38 mm.

Head. Yellow areas: (1) paraocular area as in *sonora* but ending on orbit at about level of upper rim of antennal socket; (2) clypeus with median stripe as in *hondurasica* except reaching to preapical groove; (3) labrum with median apical spot on labral plate; middle portion of labral plate strongly depressed, sunken well below usual level in *Calliopsis s.s.;* (4) supraclypeal area, apex reaching to slightly above midlevel of antennal socket; (5) subantennal plate as in *empelia.* (8) Hair as in *hondurasica.* (10) Punctures along ocellocular line fine, 2 pwa, interspaces faint greenish metallic, moderately shiny; impunctate area laterally adjacent to posterior ocellus dull, finely roughened; upper frontal punctures extremely fine, indistinct, shallow, less than 1 pwa, interspaces faint greenish metallic, interspaces smooth, moderately shiny. (12) Clypeus with punctures of disc larger than upper frontal punctures, 2-3 pwa, interspaces roughened beside subantennal plate, shiny elsewhere (30×). (13) Orbital convergence ratio as 1.45:1.33,1.09. Facial fovea with indistinct mesal border, broader medially narrowed above and below. (14) Galea faintly pebbled basad; length subequal to antennocellar; galeal gap and length of galea exposed beyond closed mandibles N. A. (15) Head width to head length as 2.36:1.87,1.36. (17) Eye length, mio, and flagellar length as 1.33:1.33:1.33. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.34:0.44:0.32:0.36. (19) Ocellolabral greater than clypeal width, 1.55:1.43,1.08. (20) Clypeocellar to outer subantennal sutural as 0.97:0.78,1.24. (21) Basal labial palpomere about 1.5 times length of others combined; ventral hairs thickened but less than in *hondurasica,* only 4-5 present. (22) Flagellar length about 2.2 times length of scape, 1.33:0.61.

Mesosoma. (23) Light areas yellow; medial interruption of pronotal stripe about 4 mow. (24) Longer scutal and scutellar hairs dark brown, longer and more prominently branched than in preceding species. Hairs of metanotum fulvous, others as in *hondurasica.* (25) Scutal disc with punctures moderately large, about as in *empelia,* less than 0.5 pwa, interspaces shiny although finely roughened, punctures becoming crowded anteriorly, to contiguous. (26) Dorsal enclosure of propodeum shiny, with numerous fine, reticulated ridges; posterior border carinate, a small median portion of border raised distinctly upward; median portion about as long as lateral portion. (27) Foreleg without yellow on femur. (28) Middle leg colored like foreleg; spur length about 0.65 times length middle basitarsus. (30) Tegula blackish brown. (32) Marginal cell 6-9 less than, and 3-4 less than 9-wt, 1.04:0.88:1.09.

Metasoma. (34) Tergal hair bands white. (35) Tergum 1 with punctures of median area fine, about 1 pwa, interspaces moderately shiny, finely roughened.

TYPE MATERIAL. Holotype female, El Salto (6 mi. N.E.), Durango, México, 8500 ft., Aug. 10, 1947 (Gertsch, David Rockefeller Expedition), is in the American Museum of Natural History.

CALLIOPSIS (CALLIOPSIS) HELENAE, new species

(Map 1)

This species is named for my wife, Helen, who has helped in many ways to make the completion of this revision possible. The species has no apparent close relative and is quite distinctive by virtue of the yellow markings on the lateral portions of the clypeus and on the tegula.

FEMALE. Length, 6.5 mm; forewing length, 4.1 mm; hindwing length, 2.98 mm; clypeal length, 0.48 mm; scutal length, 1.16 mm.

Head. Cream colored areas: (1) paraocular area, below a sinuous line originating in upper half of outer subantennal suture and extending diagonally upward to a point on orbit about 0.4 of eye length below summit of eye; (2) clypeus with a broad, vertical median area from base bordering supraclypeal and subantennal areas to preapical groove and with irregular splotches contiguous to median area; (3) labrum with spot on apex of labral plate; (4) supraclypeal area to level of middle of antennal socket; (5) subantennal plate; (6) mandible possibly with a faint basal spot. (8) Hair on vertex, frons, and clypeus fulvous. (10) Punctures of vertex and along ocellocular line with interspaces shiny (30×). Median punctures of frons coarse, deep, less than 1 pwa, interspaces shiny (30×). (11) Frontal line with lower portion sulcate ending at level of middle of antennal socket. (13) Orbital convergence ratio as 1.22:1.19,1.03. Facial fovea elongate, length about 1.5 mow. (14) Galea entirely pebbled, galeal gap less than length of galea exposed beyond closed mandibles, 0.31:0.58. Glossa, length 1.62 (paratype). (15) Head width to head length as 2.06:1.65,1.25. (17) Eye length, mio, and flagellar length as 1.22:1.19:1.21. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.34:0.34:0.31:0.30. (19) Ocellolabral greater than clypeal width, 1.34:1.29, 1.32. (21) Basal labial palpomere about 2.0 times length of others combined. (22) Flagellar length about 2.3 times length of scape, 1.22:0.54.

Mesosoma. (23) Light areas cream colored; medial interruption of pronotal stripe about 2 mow. (24) Scutum and scutellum with short and long fulvous hairs (long hairs may be faded brown hairs!). Hair of metanotum fulvous. (25) Scutal disc with punctures fine, 2-3 pwa, interspaces shiny, smooth (30×), but roughened on anterior slope of scutum. (26) Dorsal enclosure of propodeum with median portion a dull reticulum of close transverse ridges, the lateral portion shiny with ridges becoming longitudinal. (27) Legs with light color the same as on face. Foreleg with cream color on dorsal apex of femur and knee of tibia. (28) Middle leg colored like foreleg; spur finely, uniformly pectinate; length of spur to basitarsal length of paratype as 0.46:0.71,0.69. (30) Tegula transparent testaceous with anterior patch of cream color. (32) Marginal cell 6-9 and 3-4 both shorter than 9-wt, 0.82: 0.75:0.87.

Metasoma. (34) Tergal hair bands moderately dense, white, appressed. (35) Tergum 1 with punctures of median area finer than on scutum, mostly 2 pwa, interspaces shiny (30×). Declivity of tergum 1 finely lineolate. (37) Sternum 6 brown without a median, clear, subcircular area.

TYPE MATERIAL. Holotype female, Alice (10 mi. S.), Texas, July 17, 1956 (University of Kansas Mexican Expedition), is in the Snow Entomological Museum at The University of Kansas. One female paratype, Piedras Negras, Coahuila, 1300 ft., Aug. 25, 1949 (G. M. Bradt), is at the American Museum of Natural History.

Subgenus PERISSANDER Michener

Perissander Michener, 1942, New York Ent. Soc. Jour., 50:275; Michener, 1951, *in* Muesebeck *et al.*, U.S. Dept. Agric., Monogr. No. 2:1104.

Type species. Calliopsis anomoptera Michener, 1942, monobasic and original designation.

This subgenus seems to be a derivative of the *hondurasica* group of *Calliopsis s.s.* The entire subgenus is restricted to the arid northwestern Mexico and southwestern United States. The species prefers flowers of *Euphorbia* to which the short, stubby mouthparts seem adapted. *Calliopsis gilva, C. fulgida,* and *C. yalea* are slightly different from the *anomoptera* group (which includes *rogeri, syphar,* and *limbus*) largely by reason of the elongate cylindrical glossae. The floral records for *gilva* and *fulgida* include *Verbesina* and *Tidestromia,* members of the Compositae and Amaranthaceae, respectively, which also suggest an ecological separation from the *anomoptera* group.

Perissander differs from the other subgenera as follows. Males lack the scutellar and metanotal hair pads, yet have the type of genital capsule described for *Calliopsis s.s.* Both males and females have the galeae hidden in repose by the closed mandibles, or in *gilva, fulgida,* and *yalea* have the length of the galea exposed beyond closed mandibles less than 1 mow. The peculiar, flat, short, truncate glossa of the *anomoptera* group occurs elsewhere only in *squamifera* and *peninsularis.*

FEMALE. Length, 4.5-7.5 mm.

Head. Light colored areas: (1) paraocular area below a line originating on outer subantennal suture slightly below its upper origin, and extending laterally from 0.50-0.75 times width of paraocular area, thence dorsally to, or close to, lower margin of facial fovea, thence laterally ending on orbit at level of it; in *gilva,* upper border runs sinuously from about midpoint of outer subantennal suture (to near upper end) to lower border of facial fovea ending at level above it on orbit. (2) Clypeus with a median area with base adjacent to frontoclypeal suture, shape variable, from a relatively narrow horizontal strip or trianguliform area, to longitudinal band with laterally expanded base, length about 0.66 times length of clypeus; *gilva* with spot in lower lateral corner; (3) absent on labrum; (4) supraclypeal area pentagonal or semilunar with apex at or below midlevel of antennal socket; (5) subantennal plate; (6) absent on mandible (basal dot in *fulgida* and *yalea*). (7) Scape and pedicel brown to black, flagellum dark above, tan below on at least apical 7 flagellomeres. (8) Hair on vertex, frons, and clypeus variable, of gena white.

(10) Punctures along ocellocular line variable, interspaces variable; impunctate area lateral to posterior ocellus shiny (roughened and dull in *limbus*); punctures of frons with shiny interspaces (roughened in *limbus*). (11) Frontal line with lower portion a sharp carina or a finely sulcate carina. (12) Clypeus with punctures of disc somewhat eccentric; disc very little protuberant; apical portion adjacent to medial area bent about 45° posteriad as seen from below, projection of apical border smoothly rounded, not tooth-like. (13) Inner orbits subparallel to divergent below. Facial fovea shallow to deep, smaller than in other subgenera, usually oval. (14) Galea short, not visible with mandibles closed except in *gilva, fulgida,* and *yalea,* where length of galea exposed beyond closed mandibles is less than 1 mow. Glossa flat, short, truncate, abruptly broadened medially, flabellum absent except in *gilva, fulgida,* and *yalea* which have short, cylindrical, flabellate glossae. (15) Head width/head length 1.3-1.5. (17) Eye length slightly less than mio, subequal to or more than a tenth less than flagellar length. (18) Antennocellar about twice antennocular; interocellar two-thirds of, to equal to ocellocular. (19) Ocellolabral equal to or greater than mio, subequal to clypeal width. (21) Basal labial palpomere slightly less than, or subequal to, length of others combined in *anomoptera* group, about 1.7 times length of others in *gilva*. (22) Flagellomere 1 slightly shorter than flagellomere 9. Flagellar length 2.1-2.8 times length of scape.

Mesosoma. (23) Light colored areas: medial interruption of pronotal stripe 2-3 mow; apex of pronotal lobe; scutellar crest. (24) Scutal and scutellar hairs of two kinds, longer ones fulvous to black, shorter ones fulvous. (25) Scutal disc with punctures distinct, interspaces polished to dulled by fine roughening. (26) Dorsal enclosure of propodeum variously sculptured, always with some ridges, often quite low. (27) Legs with light color the same as on face. Foreleg as in *Calliopsis s.s.* (28) Middle leg as in *Calliopsis s.s.,* except spur of *gilva* almost bare, with a few coarse teeth apicad. (29) Hind leg brown (yellow band on trochanter of *yalea*). (30) Tegula brown to transparent straw color, with anterolateral patch of yellow or cream color. Humeral plate brown, or testaceous with apical half yellow. (31) Wing at least partly smoky apically beyond cells. Stigma brown. (32) Marginal cell 6-9 variable, 3-4 less than 9-wt.

Metasoma. (34) Tergal hair bands white, dense, appressed. Band of tergum 1 broadly interrupted medially, of tergum 2 much less so, of other terga complete, except all bands complete on *rogeri,* white to fulvous. Suberect hair of discs of terga 4-5 dark brown to black. Prepygidial and pygidial fimbriae smoky to dark brown. (35) Tergum 1 with punctures of median area subequal to or smaller than those on scutum, uniformly distributed, distinct, interspaces dull to shiny. Declivity of tergum 1 variable. (37) Sterna orange-red, brown, or black.

MALE. Length, 4.0-5.5 mm.

Head. Light colored areas: (1) paraocular area upper limit varying between lower and upper border of facial fovea, in latter case indented by facial fovea; (2) clypeus; (3) labrum; (4) supraclypeal area apex between three-fourths length of scape above upper rim of antennal socket to about 0.02 mm below middle ocellus, joined with paraocular area to make a continuous light colored area; (5) subantennal plate; (6) base of mandible; (7) scape, pedicel (tan dorsally in *limbus*), flagellomere 1, remaining flagellomeres tan. (8) Hair of vertex, frons, and clypeus white or fulvous. (10) Punctures of upper frons, fine, dense, fairly regularly distributed, 1 pwa or less. (11) Frontal line with lower portion as in female. (13) Inner orbits moderately convergent below. Facial fovea tiny, less than area of middle ocellus in some cases. (14) Galea as in female. (15) Head width/head length 1.2-1.4. (17) Eye length subequal to or greater than mio; flagellar length variable. (18) Interocellar to ocellocular variable; antennocular equal to or greater than interantennal. (21) Basal labial palpomere 0.5-1.8 times length of others combined. (22) As in female but flagellar length 3.1-3.8 times length of scape.

Mesosoma. (23) Light colored areas: as in female but also ventral surface of mesosoma extending upward to lower third or half of mesepisternum. (24) Hair as in female except long and short scutal and scutellar hairs concolorous. Scutellar and metanotal hair pads absent. (25) Scutal disc with punctures deep and distinct, or shallow and indistinct; interspaces smooth or finely roughened. (26) Dorsal enclosure of propodeum with fine ridges, vertical triangular portion delimited very faintly. (27) Legs with light color the same as on face. Foreleg yellow except minute spot of brown on posterior dorsal surface of trochanter, distitarsus testaceous. (28) Middle leg colored like foreleg except brown trochanteral spot larger, apicotarsus testaceous. (29) Hind leg colored like middle leg. (30) Tegula brown to colorless with anterior patch or spot of yellow. Humeral plate basally brown, apically yellow. (31) Wing with apical portion beyond cells clear to distinctly light brown to naked eye. Costal vein testaceous to yellowish white. Stigma pale testaceous. (32) As in female.

Metasoma. (34) Similar to female. (35) Tergum 1 with punctures variable. (36) Pygidial plate sunken medially, broadly rounded to somewhat truncate apically. (37) Sternal color similar to that of female. Shapes of sterna 5, 6, and 8 similar to those in *Calliopsis s.s.* (38) Sterna and genitalia as illustrated (Figs. 46-57).

CALLIOPSIS (PERISSANDER) ANOMOPTERA Michener

(Figs. 7, 46-49; Map 4)

Calliopsis (Perissander) anomoptera Michener, 1942, Jour. New York Entom. Soc., 50: 275-277; Michener, 1951, *in* Muesebeck *et al.*, U.S. Dept. Agric., Monogr. No. 2: 1104; Krombein, 1961, Ent. News, 72: 82-83 (biology).

The specific name obviously was applied because of the anomalous shape of the apical portion of the wing of the male which is unique among the

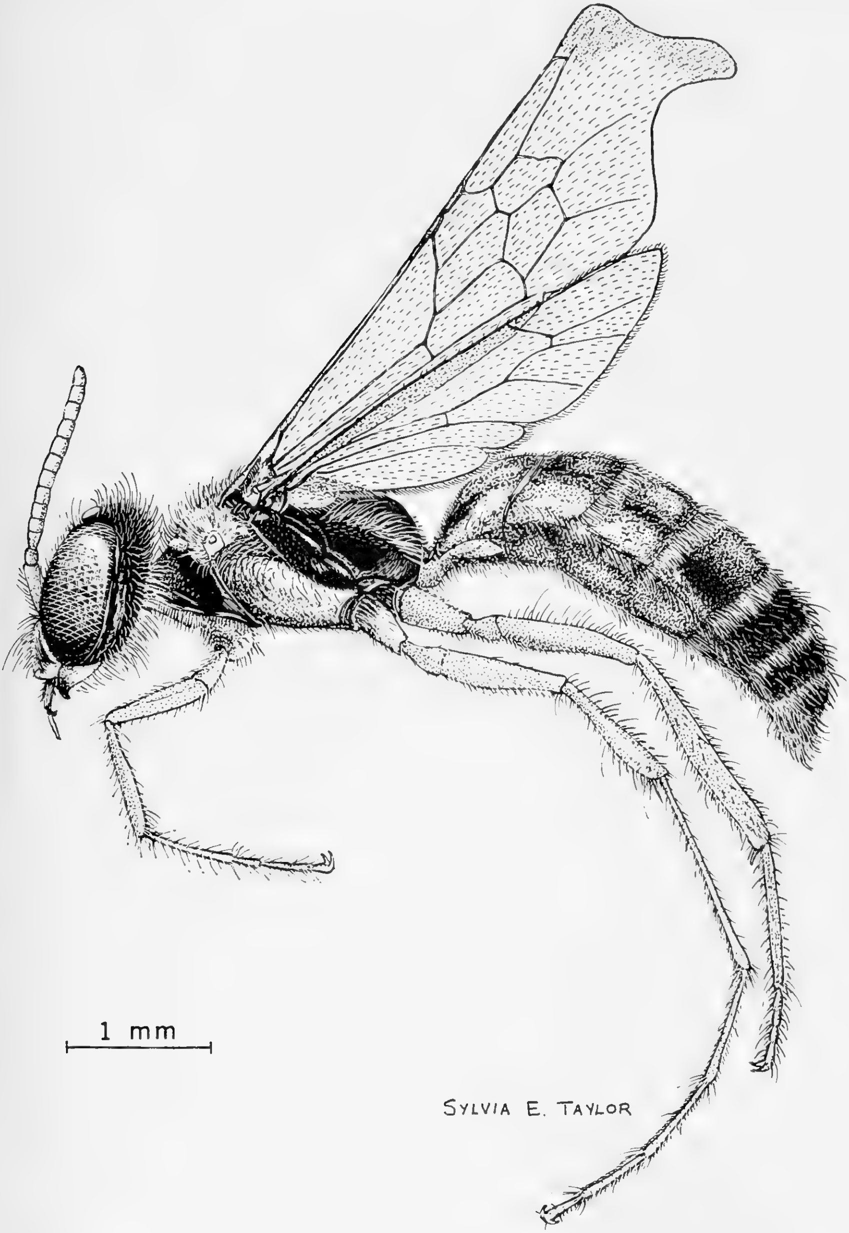


FIG. 7. Lateral view of male *Calliopsis (Perissander) anomoptera* Michener. Note the great elongation of the middle tarsus which is characteristic of the subgenus.

Apoidea. The closest relative is *rogeri* from which *anomoptera* is readily distinguished by the larger size and by the orange or orange-red metasomal terga. In fact, *anomoptera* is distinguished from all other species of *Calliopsis* by the orange or orange-red metasoma.

FEMALE. Length, 5.5 mm; forewing length, 3.6 mm; hindwing length, 2.4 mm; clypeal length, 0.34 mm; scutal length, 0.78 mm.

Head. Integumental background color black (faintly metallic in some specimens). Yellow areas: (1) paraocular area below a sinuous line originating slightly below upper origin of outer subantennal suture and extending concavely upward to ventral margin of facial fovea and laterally to a point on the orbit about same level which is about 0.4 of eye length below summit of eye; (2) clypeus with a subtriangular spot with base bordering supraclypeal area and apex reaching about 0.6 of distance to clypeal apex (to all yellow except for brown splotching along apical margin medially; (7) scape brown (some specimens with extreme apex and base including basal bulb pale testaceous). (8) Hair of vertex, frons, and clypeus fulvous. (10) Punctures of midvertex and along ocellocular line fine, 1-2 pwa, interspaces shiny (30×). (11) Frontal line with lower portion carinate, ending in a slightly raised prominence at level of upper rim of antennal socket. (13) Orbital convergence ratio as 1.00:0.97,1.04. Facial fovea ellipsoidal, short, only slightly longer than mow, length to width as 0.17:0.09. (15) Head width to head length as 1.60:1.16,1.39. (17) Eye length, mio, and flagellar length as 0.90:0.97:0.90. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.27:0.44:0.27:0.22. (19) Ocellolabral subequal to clypeal width, 0.97:0.99. (20) Clypeocellar to outer subantennal sutural as 0.63:0.46,1.37. (21) Basal labial palpomere subequal to length of others combined. (22) Flagellar length about 2.1 times length of scape, 0.90:0.42.

Mesosoma. (23) Light areas yellow; medial interruption of pronotal stripe about 2 mow. (24) Scutum and scutellum with numerous short, fulvous hairs and less numerous, long, brownish hairs. Hair of metanotum fulvous medially, white laterad. (25) Scutal disc with punctures fine, 1-2 pwa, interspaces shiny, smooth (30×). (26) Dorsal enclosure of propodeum with curved lines radiating anterolaterad from the median apical border, interspaces shiny, remainder of propodeum smooth, highly polished. (27) Foreleg with yellow on extreme dorsal apex of femur (sometimes absent) and basal third to half of tibia. (28) Middle leg colored like foreleg except tibial yellow slightly less extensive; spur finely, evenly pectinate, testaceous, its length slightly less than half of basitarsal length, 0.29:0.60. (30) Tegula transparent, straw colored with anterior patch of yellow. Humeral plate testaceous with small patch of light color. (32) Marginal cell 6-9 and 3-4 both longer than 9-wt, 0.76:0.70:0.66.

Metasoma. (33) Terga 1-4 reddish-orange, sometimes with irregular patches of reddish-black, tergum 4 often with posterior margin black; terga 5-6 black. (35) Tergum 1 with punctures of median area much finer than on scutum, densely, regularly distributed, less than 1 pwa, interspaces shiny (30×). Declivity of tergum 1 somewhat shiny. (37) Sterna orange except sternum 6 dark brown to black.

MALE. Length, 5.1 mm; forewing length, 4.5 mm; hindwing length, 3.0 mm; clypeal length, 0.34 mm; scutal length, 0.75 mm.

Head. Yellow areas: (1) paraocular area ending between middles of facial foveae, indented by them, or extending above facial foveae, surrounding them continuous with supraclypeal area; (4) supraclypeal area and entire frons to about 0.02 mm below middle ocellus. (13) Orbital convergence ratio as 1.00:0.87,1.15. Facial fovea ovoid, tiny, a fourth to third area of middle ocellus. (15) Head width to head length as 1.65:1.24,1.33. (17) Eye length, mio, and flagellar length as 0.94:0.87:1.29. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.27:0.29:0.22:0.20. (19) Ocellolabral subequal to clypeal width, 0.99:1.00,1.00. (20) Clypeocellar to outer subantennal sutural as 0.65:0.46,1.41. (21) Basal labial palpomere about 0.66 times length of others combined. (22) Flagellar length about 3.6 times length of scape, 1.29:0.36.

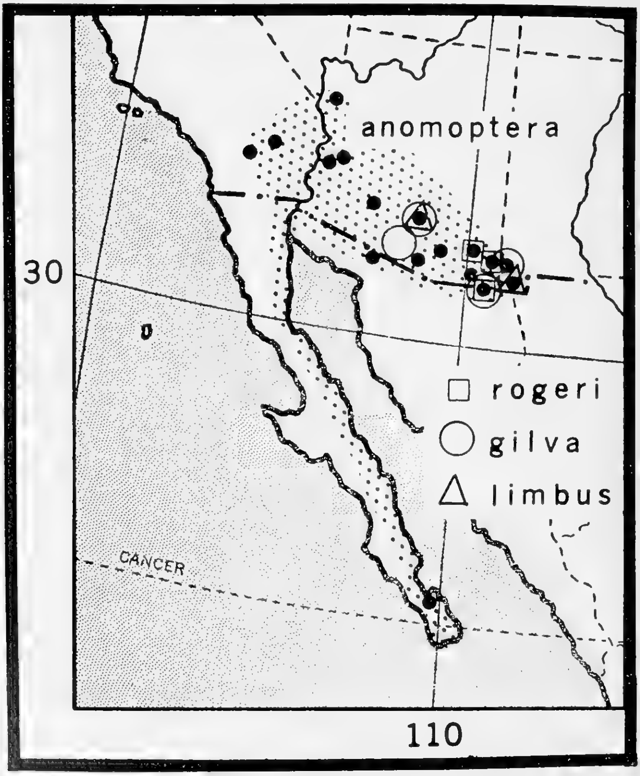
Mesosoma. (23) Yellow area of mesepisternum usually covering approximately lower half, sometimes with yellow reaching pronotal lobe. (24) Short scutal hairs many-branched, appearing moss-like and partially hiding surface viewed from directly above. (25) Scutal disc with punctures fine, deep, distinct, 2 pwa, interspaces smooth, shiny. (26) Dorsal enclosure of propodeum declivous, sunken, with rolled porterior border; median portion much longer than lateral portions, with fine ridges originating in strong emargination along posterior border, diverging laterally towards anterior border; lateral portions with low, fine ridges separated by about 2 ridge widths, interspaces slightly roughened but shiny. (28) Length of middle tibia, basitarsus, mediotarsus, and apicotarsus as (0.95:1.21:1.38:1.65), basitarsus distinctly shorter than mediotarsus, ratio of tibia to basitarsus 0.79. (30) Tegula colorless to pale straw color with anterior yellow patch. (31) Forewing of unique shape among Apoidea (Fig. 6), apical portion beyond marginal cell bent abruptly posteriad, drawn into a broad, posteriorly-directed tip, brown apical portion in form of a band. Costal vein yellowish white. (32) Marginal cell long, very slender, parallel-sided apically, 6-9 about 3 times, and 3-4 about 2 times greater than 9-wt, 1.09:0.85:0.39; 11-12 less than 0.7 times 13-14.

Metasoma. (33) Terga 1-3 orange, sometimes with reddish-brown areas; tergum 2 with lateral fovea reddish-brown; terga 4-6 reddish-brown to black. (35) Tergum 1 with punctures of median area fine, distinct, regularly distributed, 0.5 pwa or less, interspaces smooth, dull (30×). (37) Sterna orange, except sternum 8 dark brown.

TYPE MATERIAL. Holotype male and allotype female from Picacho Pass, Arizona, Aug. 7, 1940 (C. D. Michener), on a small *Euphorbia,* are at the American Museum of Natural History. The above description of the female is primarily based on a specimen from Douglas (1 mi. E), Arizona, Aug. 16, 1962 (M. Statham), and that of the male on a paratype specimen.

DISTRIBUTION. The southwestern United States and northwestern Mexico, including Baja California. It occurs from the first week of July to the last week of September in New Mexico and Arizona, and has been taken in California from early September to early October. The latest date of capture is at La Paz, Baja California Sur, on Oct. 10, 1955 (F. X. Williams). It is a sonoran desert form which occurs where *Euphorbia* flourishes.

Approximately 255 specimens were examined from the following localities which include the type: ARIZONA: Apache (5 mi. S.E.), Cochise Co.; Brenda (2 mi. W.), Yuma Co.; Douglas (1, 17 mi. E.; 3 mi. N.; 16 mi. N.E.), Cochise Co.; Gila Bend (18 mi. S.), Maricopa Co.; Kingman (10



MAP 4. Map showing the known distributions of *Calliopsis (Perissander) anomoptera* Michener, *C. (P.) rogeri* Shinn, *C. (P.) gilva* Shinn, and *C. (P.) limbus* Shinn.

mi. N.W.), Mohave Co.; Lowell (5 mi. E.), Cochise Co.; Picacho Pass; Portal, Chiricahua Mts., Cochise Co.; Sabino Canyon, near Tucson; Santa Rita Mts., 5000 ft. to 8000 ft.; Sells, Pima Co.; Tucson (10, 23 mi. S.); Wenden; Willcox, Cochise Co. CALIFORNIA: Palm Springs, Riverside Co.; Twentynine Palms. NEW MEXICO: Granite Pass, Hidalgo Co.; Rodeo (11, 18 mi. N.), Hidalgo Co.; Rodeo, Cienaga Lake, Hidalgo Co.; Willow Creek Mts. BAJA CALIFORNIA: La Paz. SONORA: Sonoita (26 mi. E.).

BIONOMICS. This species is one of several which favor *Euphorbia* for a food plant for both pollen and nectar. Krombein (1961) reported that he found it in abundance on *Euphorbia albomarginata* from July 23 to 31, 1959, and that P. D. Hurd collected it at the same place and flower August 9 to 15, 1958, both at Portal, Arizona, 4000 ft. altitude, near the S. W. R. S., American Museum of Natural History. Krombein *(op. cit.)* mentioned that only males were taken on July 23 and 24, most of them newly emerged, and that freshly emerged females were present on the flowers on July 26th. Two of the females captured bore pollen masses composed entirely of *Euphorbia* pollen.

FLOWER RECORDS. *Cladothrix lanuginosa, Eriogonum, Euphorbia albomarginata, E. capitellata, E. hirtella, E. pleniradiata, E. polycarpa hirtella, E. polycarpa typica, Lepidium thurberi, Tidestromia.*

CALLIOPSIS (PERISSANDER) ROGERI, new species

(Figs. 50-53; Map 4)

I take pleasure in naming this smallest species of *Calliopsis* after my son, Roger, who has helped me in many ways during the study, both in the field and the laboratory.

The species is closest to *anomoptera* and *syphar*, but both sexes are readily distinguished from *anomoptera* by their black, metallic integument, and total absence of any trace of integumental orange-red color. The male of *syphar* is unknown but the female of *rogeri* differs from that of *syphar* by the strong brassy tints on head, mesosoma, and especially the metasomal terga.

FEMALE. Length, 4.6 mm; forewing length, 3.1 mm; hindwing length, 2.2 mm; clypeal length, 0.31 mm; scutal length, 0.82 mm. Integumental background color black with faint greenish metallic tint on head, strong brassy metallic tint on mesosomal dorsum, very strong brassy tint on metasomal terga.

Head. Yellow areas: (1) paraocular area as described for subgenus; (2) clypeus with T-shaped median figure, ventral end of shaft of T extending to middle of clypeus (T often filled in to form a triangular patch). (8) Hair of vertex, frons, and clypeus fulvous. (10) Punctures along ocellocular line fine, dense, regularly distributed, 1 pwa, interspaces shiny. (11) Frontal line with lower portion a finely sulcate carina. (13) Orbital convergence ratio as 1.02: 0.94,1.09. Facial fovea ovoid, short, only slightly longer than mow. (15) Head width to head length as 1.56:1.12,1.39. (17) Eye length, mio, and flagellar length as 0.83:0.94:0.88. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.31:0.25:0.27:0.18. (19) Ocellolabral equal to clypeal width, 0.95: 0.95,1.00. (20) Clypeocellar to outer subantennal sutural as 0.65:0.44,1.46. (21) Basal labial palpomere about 0.85 times length of others combined. (22) Flagellar length about 2.2 times length of scape, 0.88:0.39.

Mesosoma. (23) Light areas yellow; medial interruption of pronotal stripe about 2 mow. (24) Scutal black hairs twice length of short, fulvous hairs, or more. (25) Scutal disc with punctures almost hidden, viewed from above, by plumosity of short, fulvous hairs; punctures fine, deep, distinct, 1-2 pwa, interspaces shiny, metallic. (26) Dorsal enclosure of propodeum with fine, low ridges originating along posterior, median border, passing anterolaterally in parallel, symmetrical, curves. (27) As in *anomoptera* but only basal fourth to third of tibia yellow. (28) Middle leg colored like foreleg; spur evenly, finely pectinate, length of spur about half of basitarsal length, 0.27:0.56. (30) Tegula brown with anterolateral patch of yellow. Humeral plate brown. (32) Marginal cell 6-9 subequal to, and marginal cell 3-4 distinctly shorter than 9-wt, 0.68:0.53:0.66.

Metasoma. (34) All tergal hair bands complete. (35) Tergum 1 with punctures of median area smaller than on scutum, very fine, dense, regularly distributed, 0.5 pwa, interspaces moderately shiny. Declivity of tergum 1 dull. (37) Sterna black (to dark brown).

MALE. Length, 4.5 mm; forewing length, 3.3 mm; hindwing length, 2.15 mm; clypeal length, 0.34 mm; scutal length, 0.65 mm.

Head. Yellow areas: (1) paraocular area extending to lower border of facial fovea, indented by it (usually), continuous with supraclypeal area; (4) supraclypeal area extending above to same level as (to slightly below) paraocular yellow, both well below middle ocellus. (11) Frontal line with lower portion a sharper carina than in *anomoptera*. (13) Orbital convergence ratio as 0.95:0.82,1.16. Facial fovea ovoid to tear drop shaped, area about half area of middle ocellus. (15) Head width to head length as 1.50:1.11,1.35. (17) Eye length, mio, and flagellar length as 0.82:0.82:1.11. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.26:0.29:0.23:0.17. (19) Ocellolabral greater than clypeal width, 0.94:0.90,1.03. (20) Clypeocellar to outer subantennal sutural as 0.60:0.53,1.40. (21) Basal labial palpomere about 0.85 times length of others combined. (22) Flagellar length about 3.4 times length of scape, 1.11:0.32.

Mesosoma. (23) Yellow area of mesepisternum covering somewhat less than lower half, less extensive than in *anomoptera*. (24) As in *anomoptera* except denser. (25) As in *anomoptera* but punctures 1 pwa. (26) Dorsal enclosure of propodeum subhorizontal, not sunken, posterior border weakly or not defined; median portion as in *anomoptera*, lateral portions roughened with few mesally oblique ridges. (28) Lengths of middle tibia, basitarsus, mediotarsus, and apicotarsus as 0.78:0.97:1.19:1.36, basitarsus distinctly shorter than mediotarsus, ratio of tibia to basitarsus 0.81, about as in *anomoptera.* (30) Tegula pale straw color with anterior yellow patch. (31) Forewing normal, brown apical portion in form of a round spot, slightly flattened on side toward wing base. Costal vein pale testaceous. (32) Marginal cell 6-9 longer than, and 3-4 shorter than 9-wt, 0.71:0.58:0.66; 11-12 equal to or only slightly shorter than 13-14.

Metasoma. (33) Terga black with brassy tints. (34) As in female. (35) Tergum 1 with punctures of median area fine, shallower and not so distinct as in *anomoptera,* less regularly distributed, 0.5 pwa or less. Interspaces roughened, dull (30×). (37) Sterna brown to black.

Type Material. Holotype male and allotype female from Douglas (1 mile E.), Cochise Co., Arizona, Aug. 16, 1962 (M. Statham), are at the American Museum of Natural History.

Twelve male and 10 female paratypes were collected at the following localities: Arizona: Apache (5 mi. S.E.), Cochise Co., 1 male, Aug. 11, 1958 (D. D. Linsdale), 5 males, same date (R. M. Bohart), *Euphorbia; idem* (14 mi. S.W.), 2 males, 2 females, Aug. 7, 1961 (J. G. Rozen), *Euphorbia;* Douglas (1 mi. E.), Cochise Co., 2 males, 1 female, Aug. 16, 1962 (M. Statham); *idem* (3 mi. N.), 4 males, 1 female, Aug. 4, 1961, *Euphorbia,* 2 males, 2 females, Aug. 8, 1961 (all J. G. Rozen); *idem* (17 mi. E.), 1 male, Aug. 4, 1958 (D. D. Linsdale); *idem,* 4 males, 1 female, Aug. 8, 1958, *Euphorbia,* 1 male, same date, *Lepidium thurberi* (all P. D. Hurd); *idem,* 2 females, Aug. 8, 1958 (R. M. Bohart), *Euphorbia;* Lowell (5 mi. E.), Cochise Co., 1 male, Aug. 15, 1958 (P. M. Marsh); Portal, Cochise Co., 1 male, Aug. 12, 1958 (P. D. Hurd), *Euphorbia; idem,* 1 female, July 23-31, 1959 (K. V. Krombein), *Euphorbia albomarginata; idem* (2 mi. N.E.), "Site B", 1 female, Sept. 25, 1961 (M. A. Cazier); Willcox, Cochise Co., 1 male, Aug. 14, 1958 (D. D. Linsdale), *Euphorbia; idem* (1 mi. S.), 1 female, Sept. 8, 1959 (G. I. Stage). Paratypes will be deposited in the collection of P. H. Timberlake, University of California, Riverside, California, the California Academy of Science, the University of California at Berkeley, the American Museum of Natural History, and the personal collections of Dr. Karl V. Krombein of the U.S. National Museum, Mr. Roy E. Snelling, Los Angeles, California, and The University of Kansas, Lawrence.

Distribution. Known only from the southeastern corner of Arizona but probably will be found in at least the adjacent parts of México and New Mexico. Its flight season is in August and September.

Flower Records. *Euphorbia albomarginata, E.* sp., and *Lepidium thurberi.* It has been taken with *Calliopsis anomoptera* on these plants. A study of the competition between these two species would be enlightening.

CALLIOPSIS (PERISSANDER) SYPHAR, new species

(Map 3)

The specific name is derived from the Greek, *sypharos,* meaning wrinkled skin, in allusion to the appearance of the dorsal enclosure of the propodeum which suggests the wrinkled character of the elephant's skin. The specimens exhibit strong similarities to *C. (Perissander) rogeri,* notably in the characteristic of the dorsal enclosure of the propodeum, though expressed more strongly than in *rogeri. C. syphar* is readily distinguished from *rogeri* by the non-metallic integument, larger size, proportionately longer mesotibial spur, and by the marginal cell 6-9 being about the same length as 3-4 and 9-wt.

FEMALE. Length, 5.5 mm; forewing length, 3.5 mm; hindwing length, 2.5 mm; clypeal length, 0.39 mm; scutal length, 0.85 mm.

Head. Cream colored areas: (1) paraocular area below a line originating at upper end of outer subantennal suture and extending horizontally to about midline of area thence curving sharply upward to level of lower margin of facial fovea, ending on orbit about half eye length below summit of eye. (2) Clypeus with a broad T-shaped maculation (to only the vertical stem of T present), the crossbar of the T along the border of the supraclypeal area (to along supraclypeal area and both subantennal plates), the vertical stem extending about two-thirds of distance to clypeal apex. (8) Hair of vertex fulvous (to light brown), twice length of longer scutal hairs, of frons and clypeus fulvous. (10) As in *rogeri.* (11) Frontal line with lower portion a barely discernible (30×) sulcus becoming obsolete about midlength of scape, frontal prominence with a minute point. (13) Orbital convergence ratio as 1.11:1.07, 1.02. Facial fovea ovoid, very shallow, width about half length, shallower and broader than *rogeri.* (15) Head width to head length as 1.75:1.22,1.43. (17) Eye length, mio, and flagellar length as 0.97:1.07:1.05. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.34:0.31:0.31:0.22. (19) Ocellolabral slightly greater than clypeal width, 1.09:1:04,1.05. (20) Clypeocellar to outer subantennal sutural as 0.70:0.51,1.36. (21) Basal labial palpomere about 1.1 times length of others combined. (22) Flagellar length about 2.4 times length of scape, as 1.05:0.44.

Mesosoma. (23) Light areas cream colored; medial interruption of pronotal stripe about 2 mow. (24) As in *rogeri.* (25) Scutal disc with punctures finer than in *rogeri,* deep, about 2 pwa, interspaces shiny, smooth. (26) Dorsal enclosure of propodeum with fine lines radiating anterolaterad from the median apical border as in *rogeri* but more pronounced, numerous, longer, and originating along a broader part of rear border of dorsal enclosure, interspaces roughened, and remainder of propodeal triangle finely roughened. (27) Foreleg with cream color on dorsal apex of femur and basal third of tibia, tarsus brown. (28) Middle leg colored like foreleg; spur linely, evenly pectinate, testaceous, its length about 0.6 times basitarsal length, 0.37:0.61. (30) Tegula transparent, almost colorless, with small anterior patch of cream color. Humeral plate testaceous. (32) Marginal cell 6-9 and 3-4 greater than 9-wt, 0.73:0.71:0.68.

Metasoma. (35) Tergum 1 with punctures of median area smaller than on scutum, densely, regularly distributed, 1 pwa or less, interspaces shiny (30×). Declivity of tergum 1 finely lineolate, shiny. (36) As in *rogeri.*

TYPE MATERIAL. Holotype female from San Ignacio (15 mi. N.), Baja California Sur, Sept. 29, 1941 (E. S. Ross and R. M. Bohart) is in the California Academy of Sciences, San Francisco.

Five female paratypes are from the localities below: BAJA CALIFORNIA SUR: Canipole, 2 females, Oct. 2, 1941 (Ross and Bohart); La Paz, 1 female, Oct. 10, 1955 (F. X. Williams); San Ignacio (15 miles N.), 1 female, Sept. 29, 1941 (Ross and Bohart); San Pedro, 1 female, Oct. 7, 1941 (Ross and Bohart).

CALLIOPSIS (PERISSANDER) LIMBUS, new species

(Map 4)

The species name is from the Latin, *limbus,* meaning border, in reference to its occurrence near the Mexican and United States borders. It is closest to *C. rogeri* but the male is readily distinguished from *rogeri* by the faintly smoky wing tip and the finely roughened interspaces between mesoscutal punctures. The abdomen of the male holotype is missing. Both the female allotype and single female paratype are the same species, but since they were not collected with the male, the association of the sexes is tentative. The female of *limbus* differs from that of *rogeri* by the higher ratio of flagellar length to scape length (average 2.7 to 2.3 for *rogeri*), by the marginal cell 6-9 being less than 9-wt, and by the lack of metallic sheen on the dorsum of the thorax and abdomen.

FEMALE. Length, 4.4 mm; forewing length, 3.1 mm; hindwing length, 2.19 mm; clypeal length, 0.34 mm; scutal length, 0.82 mm.

Head. Pale yellow areas: (1) paraocular area as described for subgenus; (2) clypeus, narrow strip extending along frontoclypeal suture between middles of subantennal plates, with a broad, ventrally directed median projection of light color. (8) Hair of vertex, frons, and clypeus white. (10) Punctures along ocellocular line as in *rogeri* except interspaces roughened, impunctate area beside lateral ocellus roughened. (11) Frontal line with lower portion a low, sharp carina. (13) Orbital convergence ratio as 0.97:0.95,1.02. Facial fovea elliptical, minute, area smaller than that of lateral ocellus; length slightly greater than mow. (14) Glossa narrower medially than that of *rogeri,* shape somewhat intermediate between *rogeri* and *fulgida.* (15) Head width to head length as 1:53:1.16,1.32. (17) Eye length, mio, and flagellar length as 0.87:0.95:1.02. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.29:0.29:0.27:0.20. (19) Ocellolabral slightly greater than clypeal width, 1.00:0.95,1.05. (20) Clypeocellar to outer subantennal sutural as 0.66:0.44,1.50. (21) Basal labial palpomere 1.8 times length of others combined. (22) Flagellar length about 2.5 times length of scape, 1.02:0.39.

Mesosoma. (23) Light areas pale yellow; medial interruption of pronotal stripe 1-2 mow. (24) Scutal dark hairs only slightly longer than short, fulvous hairs. (25) Scutal disc with punctures not obscured by hair; punctures finer than in *rogeri,* 2 pwa, interspaces faintly roughened, shiny, becoming crowded with more distinct roughening of interspaces anteriad. (26) Dorsal enclosure of propodeum with about 18 longitudinal or obliquely longitudinal ridges with interspaces heavily roughened. (27) Foreleg with yellow on extreme dorsal apex of femur and base of tibia. (28) Middle leg colored like foreleg; spur evenly, finely pectinate, length of spur about 0.6 (to 0.5) times basitarsal length, 0.31:0.51. (30) Tegula pale brown with anterolateral patch of pale yellow. Humeral plate pale brown. (32) Marginal cell 6-9 less than, and 3-4 much less than 9-wt, 0.63:0.53:0.68.

Metasoma. (35) Tergum 1 with punctures of median area very fine, dense, regularly distributed, 0.5 pwa, interspaces roughened, quite dull. Declivity of tergum 1 as in *rogeri.* (37) Sterna black.

MALE. Length, N. A. (abdomen missing); forewing length, 3.3 mm; hindwing length, 2.4 mm; clypeal length, 0.34 mm; scutal length, 0.78 mm.

Head. Yellow areas: (1) paraocular area as in *rogeri* but separated from supraclypeal area by intervening black less than 0.02 mm wide at antennal socket; (4) supraclypeal area extending above to a level 0.8 mow below summit of paraocular yellow. (11) Frontal line with lower portion as in *rogeri.* (13) Orbital convergence ratio as 1.04:0.90,1.15. Facial fovea elliptical, area about half of area of middle ocellus. (15) Head width to head length as 1.53: 1.22,1.25. (17) Eye length, mio, and flagellar length as 0.88:0.90:1.14. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.29:0.32:0.26:0.22. (19) Ocellolabral longer than clypeal width, 1.02:0.97,1.05. (20) Clypeocellar to outer subantennal sutural as 0.68:0.46,1.48. (21) Basal labial palpomere about 1.1 times length of others combined. (22) Flagellar length about 3.2 times length of scape, 1.14:0.36.

Mesosoma. (23) Yellow area of mesepisternum covering less than lower one-third, less extensive than either *rogeri* or *anomoptera.* (24) As in *rogeri.* (25) Scutal disc with punctures fine, shallow, larger than *rogeri* or *anomoptera,* 1 pwa, interspaces finely roughened, moderately shiny. (26) Dorsal enclosure of propodeum subhorizontal, slightly sunken, posterior border defined by low carina; median and lateral portions with numerous, slightly vermiform, longitudinal ridges separated by 1-2 ridge widths, dull. (28) Lengths of middle tibia, basitarsus, mediotarsus, and apicotarsus as 0.83:0.94: 0.99:1.17, basitarsus only slightly shorter than mediotarsus, ratio of tibia to basitarsus 0.89, higher than in *rogeri* and *anomoptera.* (30) Tegula pale straw color with anterior yellow patch. (31) Forewing normal, apical portion beyond cells clear to naked eye, slightly smoky beyond marginal cell (30×). Costal vein pale testaceous. (32) Marginal cell 6-9 and 3-4 both shorter than 9-wt, 0.68:0.56:0.75; 11-12 slightly longer than 13-14.

Metasoma. Missing.

TYPE MATERIAL. Holotype male from Sabino Canyon, near Tucson, Arizona, July 31, 1941 (L. H. Banker), and allotype female from Granite Pass, 15 mi. N.E. Rodeo, Hidalgo Co., New Mexico, Aug. 25, 1958 (P. D. Hurd), on *Euphorbia,* are in the Snow Entomological Museum at The University of Kansas, Lawrence, and at the University of California, Berkeley, respectively. One female paratype, Mt. Lemmon Road, Arizona, 3500 ft. altitude, Aug. 15, 1954 (R. M. Bohart), is at the University of California, Riverside.

DISTRIBUTION. Known only from southeastern Arizona and southwestern New Mexico.

FLOWER RECORDS. *Euphorbia.*

CALLIOPSIS (PERISSANDER) GILVA, new species

(Figs. 54-57; Map 4)

The specific name from the Latin, *gilvus,* meaning pale yellow, is applied in reference to the large amount of pale yellow color on the male face, antenna, and legs.

The species is closest to *limbus.* The female is readily separated from all others of the genus by its unique mesotibial spur which is bare except for 2-4 coarse teeth on the apical four-tenths; both male and female are separated from *limbus* by the shiny, non-roughened interspaces on the head and scutum. The male is readily separated from *limbus* also by the non-metallic integument on the body.

FEMALE. Length, 7.5 mm; forewing length, 4.4 mm; hindwing length, 3.1 mm; clypeal length, 0.49 mm; scutal length, 1.19 mm.

Head. Yellow areas: (1) paraocular area below a sinuous line originating at about middle (to upper origin) of outer subantennal suture and extending obliquely upward ending on orbit about 0.4 of eye length below summit of eye, slightly above lower rim of facial fovea; (2) clypeus with a vertical stripe from margin below supraclypeal area to within less than mow of apex, width of stripe slightly less than width of supraclypeal area (and a small dot in lower corner of clypeus in some specimens); (8) Hair of vertex and clypeus both brown and fulvous, of frons fulvous. (10) Punctures of midvertex with interspaces shiny, along ocellocular line 2 pwa, interspaces shiny (30×). Median punctures of frons fine, deep, mostly 1 pwa, interspaces shiny (30×). (11) Frontal line with lower portion sulcate, ending at level of middle of antennal socket. (13) Orbital convergence ratio as 1.36:1.34,1.01. Facial fovea elongate, length about 2 mow. (14) Galea pebbled apically, shiny medially, length exposed beyond closed mandibles to galeal gap as 1.10:0.56. (15) Head width to head length as 2.23:1.62,1.38. (17) Eye length, mio, and flagellar length as 1.24:1.34:1.22. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.37:0.39:0.37:0.31. (19) Ocellolabral less than clypeal width, 1.34:

1.41,0.95. (20) Clypeocellar to outer subantennal sutural as 0.85:0.70,1.22. (21) Basal labial palpomere about 1.5 times length of others combined. (22) Flagellar length about 2.2 times length of scape, 1.22:0.57.

Mesosoma. (23) Light areas yellow; medial interruption of pronotal stripe about 2 mow. (24) Scutum and scutellum with similarly sized, short fulvous hairs and brown hairs twice as long. Hair of metanotum fulvous except long, posteriorly directed hair whitish. (25) Scutal disc with fine punctures mostly 1 pwa, interspaces shiny, smooth (30×). (26) Dorsal enclosure of propodeum a reticulum of fine, vermiform ridges, dull medially but with interspaces shiny laterad, remainder of propodeal triangle shiny. (27) Foreleg with yellow on extreme dorsal apex of femur and knee of tibia. (28) Middle leg colored like foreleg; spur bare basally, with three sharp teeth on apical 0.4; length of spur about 0.7 times basitarsal length, 0.56:0.83. (30) Tegula transparent testaceous with anterior patch of yellow. Humeral plate testaceous, broadly margined with yellow. (32) Marginal cell 6-9 slightly longer than, and 3-4 much shorter than 9-wt, 0.90:0.65:0.88.

Metasoma. (35) Tergum 1 with punctures of median area finer than on scutum, somewhat irregularly distributed, less than 1 pwa, interspaces shiny (30×). Declivity of tergum 1 finely lineolate. (37) Sterna brown.

MALE. Length, 4.7 mm; forewing length, 3.7 mm; hindwing length, 2.6 mm; clypeal length, 0.37 mm; scutal length, 0.80 mm.

Head. Yellow areas: (1) paraocular area as in *limbus* (to broadly continuous with supraclypeal area); (4) supraclypeal area extending above to level of summit of paraocular yellow (to 0.02-0.03 mm below). (11) Frontal line with lower portion as in *rogeri*. (13) Orbital convergence ratio as 0.99: 0.82,1.20. Facial fovea elliptical, less distinct than in other *Perissander* species, area as in *limbus*. (15) Head width to head length as 1.65:1.24,1.33. (17) Eye length, mio, and flagellar length as 0.95:0.82:1.39. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.31:0.31:0.20:0.20. (19) Ocellolabral greater than clypeal width, 1.05:0.97,1.09. (20) Clypeocellar to outer subantennal sutural as 0.68:0.44,1.54. (21) Basal labial palpomere about 1.7 times length of others combined. (22) Flagellar length about 3.7 times length of scape, 1.39:0.37.

Mesosoma. (23) Yellow area of mesepisternum covering approximately lower half (variable, from less than lower third to more than lower half). (24) Short scutal hairs not many-branched, not moss-like nor partially hiding surface viewed from directly above. (25) As in *anomoptera*. (26) Dorsal enclosure of propodeum subhorizontal, slightly sunken, with rolled posterior border, area much reduced compared with other *Perissander* species; median and lateral portions with numerous, slightly vermiform, longitudinal ridges separated by 1 ridge width, moderately shiny. (28) Lengths of middle tibia, basitarsus, mediotarsus, and apicotarsus as 0.97:1.11:0.87:1.09, basitarsus distinctly longer than mediotarsus, slightly longer than (to subequal to) apicotarsus, ratio of tibia to basitarsus 0.87. (30) Tegula pale straw color with anterior yellow patch (to spot). (31) Forewing normal, apical portion beyond cells faintly smoky to naked eye. Costal vein yellowish white basally to testaceous apically. (32) Marginal cell 6-9 subequal to, and 3-4 much shorter than 9-wt, 0.78:0.58:0.77.

Metasoma. (35) Tergum 1 with punctures of median area fine, larger than in other species of *Perissander,* deep, distinct, regularly distributed, 0.5-1 pwa, interspaces smooth, shiny (30×). Declivity of tergum 1 somewhat shiny. (37) Sterna brown.

TYPE MATERIAL. Holotype male from Douglas (17 mi. E.), Cochise Co., Arizona, August 8, 1958 (R. M. Bohart), on *Euphorbia,* is in the collection of P. H. Timberlake at the University of California, Riverside, California. Allotype female from Douglas (1 mi. E.), Arizona, August 16, 1962 (M. Statham), is at the American Museum of Natural History.

Two male and seven female paratypes were collected from the following localities: ARIZONA: Douglas (1 mi. E.), 4 females, Aug. 16-17, 1962 (M. Statham); Quijotoa (30 mi. E.), Pima Co., 1 male, 1 female, Aug. 28-29, 1927 (Cornell University, Lot 542 Sub 336); Tucson (10 mi. S.), 1 male, Aug. 7, 1940 (C. D. Michener), on *Verbesina.* NEW MEXICO: Rodeo (4.5 mi. N.), Hidalgo Co., 1 female, Aug. 21, 1962 (J. G. Rozen, M. Statham, S. J. Hessel); *idem* (4.8 mi. N), 1 female, Sept. 4, 1961 (P. D. Hurd), on *Tidestromia lanuginosa.* Paratypes will be deposited at Cornell University, the Snow Entomological Museum of The University of Kansas, the University of California at Berkeley, the American Museum of Natural History, and in the author's collection.

DISTRIBUTION. Known only from southeastern Arizona and southwestern New Mexico. Its flight season is August and early September, which is similar to that of *rogeri* and *limbus.*

FLOWER RECORDS. *Euphorbia, Verbesina,* and *Tidestromia lanuginosa.* These records represent three families, viz., Euphorbiaceae, Compositae, and Amaranthaceae. Although taken mostly on *Euphorbia,* this bee apparently visits other plants, perhaps more extensively than *Euphorbia.* Its mouthparts are short as in the other species of *Perissander,* but the glossa is cylindrical and the labial palp is much longer and with segments of different proportions than the other species. A comparison of mouthparts of *Euphorbia*-visiting bees to discover the adaptations necessary for visiting this flower would be interesting.

CALLIOPSIS (PERISSANDER) FULGIDA, new species

(Map 3)

The specific name is from the Latin *fulgidus,* meaning shining, and is applied because of the overall high lustre of the black integument—the shiniest of the genus. Its closest relative is *gilva,* from which it is easily distinguished by the impunctate posterior area on the first metasomal tergum. It is distinguished from all other species of *Calliopsis s.s.* and *Perissander* by the impunctate posterior area on metasomal tergum 2 as well. A fundamental difference between *fulgida* and *gilva* occurs in the mouthparts. *C. fulgida* has a cylindrical, flabellate glossa which is shorter than the maxillary palp, whereas *gilva* has the same type of glossa but it is distinctly longer than the maxillary palp.

FEMALE. Length, 6.4 mm; forewing length, 4.3 mm; hindwing length, 3.1 mm; clypeal length, 0.48 mm; scutal length, 1.02 mm.

Head. White to cream colored areas: (1) paraocular area below a sinuous line originating at about middle (to upper origin) of outer subantennal suture and extending diagonally upward ending on orbit about 0.4 of eye length below summit of eye, slightly above level of lower rim of facial fovea; (2) clypeus with a median T-shaped mark (one arm of crossbar partially missing in type), the crossbar adjacent to supraclypeal and subantennal areas, the vertical portion reaching to preapical groove; small dots adjacent to apical border laterally; (6) mandible with a faint basal dot. (8) Hair of vertex and clypeus both brown and fulvous, of frons fulvous. (10) Punctures of mid-vertex with interspaces shiny, along ocellocular line 3 pwa, interspaces shiny (30×), both areas with punctures finer than in *gilva*. Median punctures of frons finer than *gilva,* 2 pwa, interspaces shiny (30×). (11) Frontal line with lower portion sulcate, much wider and deeper than in *gilva*. (13) Orbital convergence ratio as 1.24:1.21,1.03. Facial fovea as in *gilva*. (14) Galea pebbled, length exposed beyond closed mandibles to galeal gap as 0.07:0.56 (0.09:0.44). (15) Head width to head length as 2.06:1.51,1.36. (17) Eye length, mio, and flagellar length as 1.16:1.21:1.09. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.39:0.32:0.34:0.31. (19) Ocellolabral slightly shorter than clypeal width, 1.28:1.29,0.99. (20) Clypeocellar to outer subantennal sutural as 0.77:0.54,1.40. (21) Basal labial palpomere about 1.5 times length of others combined. (22) Flagellar length about 2.1 times length of scape, 1.09:0.51.

Mesosoma. (23) Light areas cream colored; medial interruption of pronotal stripe 1.8 mow. (24) As in *gilva* except brown hairs faded to fulvous on type. (25) Scutal disc with fine punctures 2-3 pwa, interspaces highly polished (30×). (26) Dorsal enclosure of propodeum with longitudinal, shiny ridges and interspaces, remainder of propodeal triangle highly polished. (27) Foreleg with cream color as in *gilva*. (28) Middle leg colored like foreleg; spur with about 7 fine, uniformly-spaced teeth, length of spur about 0.6 times basitarsal length, 0.43:0.68. (30) Tegula transparent testaceous with anterior patch of cream color. Humeral plate as in *gilva*. (32) Marginal cell 6-9 longer than, and 3-4 shorter than 9-wt, 0.90:0.77:0.85.

Metasoma. (35) Tergum 1 with punctures of anterior half of median area finer than on scutum, 1-3 pwa, of posterior half virtually absent, interspaces highly polished. Declivity of tergum 1 smooth, finely punctate. (37) As in *gilva*.

TYPE MATERIAL. Holotype female, from Rodeo (4.8 mi. N.), Hidalgo Co., New Mexico., Sept. 4, 1961 (P. D. Hurd), on *Tidestromia lanuginosa,* is in the collection of the California Insect Survey, University of California, Berkeley. One female paratype from Portal (5 mi. E.), Arizona, Sept. 16, 1956 (G. E. Bohart), on *Euphorbia,* is in the collection of the collector at Logan, Utah.

DISCUSSION. P. D. Hurd has taken both *gilva* and *fulgida* on *Tidestromia,* and both have been taken on *Euphorbia,* records which support the placement of *fulgida* as a close relative of *gilva.*

CALLIOPSIS (PERISSANDER) YALEA, new species

(Map 3)

The specific name is from the Greek, *yaleos,* meaning highly polished. The species has no close affinities and although the facial marking is similar to *C. syphar,* it is readily distinguished from *syphar* by the much larger size. The stout setae of the ventral surface of the basal labial palpomere are similar to those of the *Calliopsis hondurasica* group, but they are much shorter, thicker, and straighter.

FEMALE. Length, 7.5 mm; forewing length, 5.2 mm; hindwing length, 3.5 mm; clypeal length, 0.59 mm; scutal length, 1.36 mm.

Head. Yellowish areas: (1) paraocular area below a line originating on outer subantennal suture about at level of middle of antennal socket and extending dorsally 0.03 mm then laterally slightly more than half width of area, curving concavely upward to just below facial fovea and ending on orbit about at level of lower border of facial fovea, 0.44 times length of eye below summit of eye; lower mesal portion of area somewhat tumid; (2) clypeus with a broad T-shaped area adjacent to subantennal plates and supraclypeal area, the lower part of vertical bar 2 times mow, extending to within 0.5 mow of clypeal apex; (6) mandible, a more or less indistinct spot. (8) Hair of vertex brown, of frons white, of clypeus both fulvous and brown. (10) Punctures of midvertex with interspaces roughened, along ocellocular line of mixed sizes, 1-2 pwa, interspaces slightly roughened. (11) Frontal line with lower portion a sulcus, frontal prominence ending about level of middle of antennal socket. (13) Orbital convergence ratio as 1.53:1.46,1.04. Facial fovea as in *syphar.* (14) Galea shiny, length exposed beyond closed mandibles to galeal gap as 0.15:0.65. (15) Head width to head length as 2.50:1.87,1.32. (17) Eye length, mio, and flagellar length as 1.39:1.46:1.33. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.43:0.43:0.39:0.36. (19) Ocellolabral less than clypeal width, 1.55:1.63,0.95. (20) Clypeocellar to outer subantennal sutural as 0.97:0.77,1.26. (21) Basal labial palpomere about 1.7 times length of others combined; seven stout setae ventrally on basal five-eighths, two additional setae paired apically, the mesoapical seta longer, thicker, all setae proportionately shorter and thicker than those of *Calliopsis (C). hondurasica* group. (22) Flagellar length about 2.1 times length of scape, 1.33:0.65.

Mesosoma. (23) Light areas yellowish; medial interruption of pronotal stripe about 2 mow. (24) Scutal and scutellar longer hairs brown, others N. A. Hair of metanotum white. (25) Scutal disc with punctures very fine, 1 pwa, interspaces shiny. (26) Dorsal enclosure of propodeum with medial portion dull with fine, low, interconnecting ridges, lateral portions shiny with a few prominent, shiny ridges. (27) Legs with light color the same as on face. Foreleg with a narrow yellow band on ventral apex of trochanter, yellow on dorsal apex of femur and basal fourth to third of tibia. (28) Middle leg colored like foreleg; spur finely, evenly pectinate, testaceous, its length about 0.5 times basitarsal length, 0.49:0.97. (29) Hind leg brown except trochanter colored as in foreleg but band narrower. (30) Tegula transparent, testaceous, with small anterior patch of yellow. Humeral plate brown. (32) Marginal cell 6-9 longer than, and 3-4 slightly shorter than 9-wt, 1.05:0.90:0.92.

Metasoma. (35) Tergum 1 with punctures of median area about the same size as on scutum, densely, regularly distributed, 1-2 pwa, interspaces shiny (30×). Declivity of tergum 1 rather dull with numerous fine punctures. (37) Sterna dark brown.

TYPE MATERIAL. Holotype female, from Apatzingan (11 miles E.), Michoacan, Aug. 20, 1954 (E. G. Linsley, J. W. MacSwain, and R. F. Smith), is in the California Academy of Sciences, San Francisco.

Subgenus CALLIOPSIMA, new subgenus

Type species. Calliopsis rozeni Shinn.

This subgenus is composed of closely related species which are sharply separated from the other subgenera. No specimens which might represent annectent forms have been discovered. Several species of the South American panurgine genus *Acamptopoeum* have color markings almost identical with the males of many species of *Calliopsima*. The deep, distinct punctures with smooth, shiny interspaces found in *Calliopsima* are also typical of *Acamptopoeum*. *Calliopsima* seems to have a mixture of the characters found in *Acamptopoeum* and *Calliopsis s.s.*, and is judged to be closest to *Calliopsis s.s.*

Four groups of species occur within this subgenus. They are: 1) the *crypta* group including *rozeni, unca, azteca,* and *chlorops;* 2) the *pectidis* group including *timberlakei* and *bernardinensis;* 3) the *coloratipes* group including *deserticola, pugionis,* and possibly *coloradensis;* and 4) the *hurdi* group including *quadridentata* and *kucalumea.*

Calliopsima occurs only from Canada to near the border between Mexico and Guatemala. The locality for *Acamptopoeum* which is closest to this area is for *A. colombiensis* Shinn (Shinn, 1965) in northern Colombia. [The record of *A. maculatum* (Smith) in Florida is almost certainly erroneous.] *Calliopsima* predominately visits flowers of the Compositae and Leguminosae.

The males of *Calliopsima* differ from those of *Calliopsis* and *Perissander* by the relatively flat clypeus, the non-tumid paraocular area, and the different shapes of the posterior projections of sterna 5 and 8. Sternum 5 of *Calliopsima* has a relatively large median, posterior projection which is club-shaped or parallel-sided; sternum 8 has a long, slim club-shaped projection. The females differ from those of *Calliopsis* and *Perissander* by the white to amber prepygidial and pygidial fimbriae (smoky in *hurdi* group) and the light hairs of the discs of terga 4-5 (a few brown hairs occasionally). Both sexes differ from the above subgenera by having maxillary palpomere 2 longer than 3, and by having coarse, deep, pleural punctures with smooth, usually shiny interspaces.

FEMALE. Length 6.5-10.0 mm.

Head. Light colored areas: (1) paraocular area below a sinuous line originating between middle of outer subantennal suture and upper end of suture and extending diagonally upward to lower inner margin of facial fovea, thence laterally, tangent to fovea, ending on orbit well above level of upper border of antennal socket, usually about level of middle of facial fovea; very shiny; (2) clypeus variable from completely yellow except for two small clypeal dots, to yellow on lateral portions with a median longitudinal band extending from frontoclypeal suture a variable distance towards the clypeal apex; (3) labrum variable, all black to yellow; (4) supraclypeal area pentagonal to trianguliform with apex between middle of and a third mow above antennal socket; (5) subantennal plate variable, black to yellow; (6) mandible with basal portion variable. (7) Scape reddish brown to blackish brown dorsally (except basal and apical yellow areas in *timberlakei*), pedicel and dorsal surface of flagellum brown to black extending part way onto ventral surface of flagellomeres 1-4, or latter all black, remaining flagellomeres tan ventrally. (8) Hair of vertex colorless or mixed light and dark, or all dark, of frons whitish, of clypeus fulvous. (10) Punctures along ocellocular line medium sized to very fine. Interspaces shiny; impunctate area, lateral to posterior ocellus shiny; punctures beside lower half of frontal line fine to large, interspaces smooth, dull to shiny. (11) Frontal line with lower portion a narrow, sulcus, sometimes interrupted, rising gradually to a low summit on frontal prominence between antennal sockets slightly above their midline. (12) Clypeus with punctures of disc more distinct than in *Calliopsis s.s.,* clypeus relatively much flatter than in *Calliopsis s.s.* but somewhat protruding in *deserticola*. Projections beside apical emargination of clypeus smoothly rounded. (13) Inner orbits slightly convergent below. Facial fovea deep, upper end slightly below middle ocellus, lower end about 1 mow above level of upper border of antennal socket, somewhat tear-drop shaped or broadened medially, tapered above and below. (14) Galea of moderate length, proportionately longer than in *Calliopsis s.s.* (except *hondurasica* group). Galeal gap less than inner subantennal sutural. (15) Head width/head length 1.2-1.5. (17) Eye length subequal to or less than mio or flagellar length. (18) Interocellar subequal to ocellocular except greater in *pectidis* group; antennocular greater than interantennal (less than in *deserticola*). (19) Ocellolabral subequal to or greater than clypeal width except distinctly less in *hurdi*. (21) Basal labial palpomere 2.1-3.3 times length of others combined. *Maxillary palpomere 2 longer than 3.* (22) Flagellomere 1 about twice length of flagellomere 2, subequal to flagellomere 9; flagellar length 2.0-2.3 times length of scape.

Mesosoma. (23) Light colored areas: medial interruption of pronotal stripe 0.5-3 mow, variable within species; apex pronotal lobe, sometimes absent; scutellar crest variable. (24) Scutal and scutellar hairs of two kinds, longer ones fulvous to black, shorter ones fulvous. Hairs of scutellar crest and of posterolateral border of metanotum as in *Calliopsis s.s.* (25) Scutal disc with punctures deeper, mostly larger, more distinct than in *Calliopsis s.s.*, interspaces smooth, either shiny or dull. (26) Dorsal enclosure of propodeum with longitudinal ridges, sometimes vermiform, posterior border at least carinate laterally, medial portion usually prolonged posteriorly, interspaces shiny. (27) Foreleg with at least basal spot of yellow on tibia, on apex of femur (absent in *hurdi* and *kucalumea*), and on base of basitarsus in *pectidis* group. (28) Middle leg colored like foreleg. Spur with extremely minute teeth or without evident teeth (20×), covered with fine, abundant, short fulvous or white hair. (29) Hind leg usually brown except yellowish on apex of femur and base of tibia in *pectidis, timberlakei,* and some specimens of *bernardinensis*. (30) Tegula colorless to dark brown with light colored anterior patch or spot. Humeral plate brown or light colored apically. (31) Wing slightly smoky (to naked eye or at 30×) apically beyond cells. Stigma testaceous to brown. (32) Marginal cell 6-9 greater than (subequal to in *pectidis*), and 3-4 much less than (subequal to or greater than in *deserticola, bernardinensis,* and *kucalumea*) 9-wt.

Metasoma. (34) Tergal hair bands white, appressed, dense to sparse. Band of tergum 1 broadly interrupted, of tergum 2 less so (except both may be continuous in *pectidis* and *bernardinensis*). Suberect hair of discs of terga 4-5 whitish to fulvous, a few brown hairs in some cases. Prepygidial and pygidial fimbriae white to fulvous (smoky in *hurdi* group). (35) Tergum 1 with punctures of median area as in *Calliopsis s.s.* but interspaces shiny to highly polished (dull in *hurdi*), puncture size variable with respect to punctures on scutum. Declivity of tergum 1 with a highly polished mirror-like surface, bearing few to no punctures.

MALE. Length, 5.2-8.0 mm.

Head. Yellow areas: (1) paraocular area as in female, except upper border usually straight, mesal origin of dorsal boundary line usually higher than in corresponding female, yellow ending in more of a point on orbit; (2) clypeus with testaceous apical border; (3) labrum; (4) supraclypeal area as in female; (5) subantennal plate in some cases with small black area, black border, or all black (some *hurdi*); (6) mandible a basal spot to basal two-thirds; (7) scape entirely, through lesser amounts of yellow, to all brown; pedicel, sometimes; flagellum as in female except lighter throughout, flagellomeres 1-3 sometimes yellow. (8,10) As in female. (11) Frontal line with lower portion a slightly elevated, low, non-sulcate, somewhat rounded, never sharp, rather broad ridge, summit as in female. (12) As in female. (13) Inner orbits moderately to strongly convergent below. Facial fovea usually distinct. (14) As in female. (15) Head width/head length 1.30-1.48. (17) Eye length greater than (barely so in *hurdi* and *quadridentata*) mio, and much less than flagellar length. (18) Interocellar subequal to ocellocular (greater in *timberlakei, bernardinensis,* less in *hurdi, kucalumea, quadridentata*); antennocular less than interantennal; antennocellar subequal to outer subantennal sutural. (21) Basal labial palpomere 1.6-3.2 times length of others combined. *Maxillary palpomere 2 longer than 3.* (22) As in female except flagellar length 2.8-3.3 times length of scape.

Mesosoma. (23) Yellow areas as in female, except more extensive, richer yellow. (24) As in female unless otherwise stated. (25) Scutal disc with punctures deeper, larger, more distinct than in *Calliopsis s.s.,* more abundant than in female, interspaces smooth, dull or shiny. (26) Dorsal enclosure of propodeum similar to that of female except median portion more prolonged and ridges usually straighter, farther apart. (27) Legs with light color the same as on face. Foreleg with highly variable color pattern among species. (28) Middle leg colored like foreleg, but less extensive light color. (29) Hind leg usually colored like middle leg. (30) As in female (*azteca, hurdi,* and *kucalumea* without light color on tegula). (31) As in female. (32) Marginal cell 6-9 greater than, and 3-4 equal to or less than (more than, in *hurdi, kucalumea, quadridentata*) 9-wt; 11-12/13-14 variable.

Metasoma. (34) As in female. (35) Tergum 1 with punctures of median area as described for *Calliopsis s.s.,* tergum sometimes dull; puncture size smaller than to larger than that of scutum. Declivity of tergum 1 usually smooth, dull, sometimes shiny, bearing several to many punctures (none in *azteca*) (30×). Pygidial plate plane to convex, not abruptly sunken medioapically as in *Calliopsis s.s.* (37) Sterna brown to testaceous. Sternum 5 produced posteriorly into a blunt, rounded, often club-like projection. Sternum 6 with a broadly concave, median bilobed portion, each lobe flattened from base to apex or apex bent abruptly ventrad to produce a pair of ventral "prongs" usually tilted slightly towards each other. Sternum 8 with a long, median projection drawn gradually or abruptly into a terminal club. (38) Sterna and genitalia as illustrated (Figs. 58-122).

CALLIOPSIS (CALLIOPSIMA) ROZENI Shinn

(Figs. 58-62; Map 5)

Calliopsis rozeni Shinn, 1965, Amer. Mus. Novitates, 2211:2.

This species is named for Dr. Jerome G. Rozen, Jr., who has lent numerous specimens for my study of the genus. The species is closest to *C. coloradensis* and *C. kucalumea.* Superficially, it bears a striking resemblance to *C. crypta.* The male of *rozeni* has the tips of the projections beside the apical portion of metasomal sternum 6 flat, whereas in *coloradensis, kucalumea,* and *crypta* they are bent ventrad. The female of *rozeni* is distinguished from *crypta* by the fine head punctures described in (10) below and by the possession of fulvous long hairs on the scutum and scutellum, whereas in *crypta* the head punctures are coarse and the long hairs on the scutum and scutellum are brown. The female of *coloradensis* has fine, dense punctures, regularly spaced about 2 pwa on the disc of metasomal tergum 1, but those of *kucalumea* are regularly spaced less than 1 pwa, and those of *rozeni* are larger, sparse, irregularly spaced about 0.5-3 pwa.

Female. Length, 8.0 mm; forewing length, 5.5 mm; hindwing length, 3.8 mm; clypeal length, 0.60 mm; scutal length, 1.43 mm.

Head. Cream colored areas: (1) paraocular area below a sinuous line originating at middle of outer subantennal suture and extending to lower inner margin of facial fovea, thence bordering fovea ventrally, ending on orbit slightly below middle of fovea; (2) clypeus except for narrow brown apical border and two vertical bars of brown originating at dorsolateral corners of clypeal emargination, extending dorsally about five-sevenths of median length of clypeus; (3) absent on labrum; (5) subantennal plate (to all black or with irregularly shaped cream colored area); (6)absent on mandible. (7) Flagellomeres 1-4 brown and tan ventrally. (8) Hair of vertex fulvous. (10) Punctures beside lower half of frontal line large, 1-2 pwa, interspaces shiny. (13) Orbital convergence ratio as 1.68:1.55,1.09. (14) Galea finely pebbled, galeal gap subequal to length of galea exposed beyond closed mandibles, 0.37: 0.39. (15) Head width to head length as 2.64:1.82,1.45. (17) Eye length, mio, and flagellar length as 1.39:1.55:1.39. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.48:0.48:0.41:0.36. (19) Ocellolabral equal (to subequal) to clypeal width, 1.53:1.53. (20) Clypeocellar to outer subantennal sutural as 0.92:0.82,1.12. (21) Basal labial palpomere about 2.8 times length of others combined. (22) Flagellar length about 2.0 times length of scape, 1.38: 0.68.

Mesosoma. (23) Cream colored areas: a dot on right pronotal lobe (a dot on each, or none); scutellar crest. (24) Scutal and scutellar hair fulvous, long hair concolorous with short. (25) Scutal disc with punctures about the same size as on midvertex, 0.5 pwa or less, interspaces shiny (30×). (26) Dorsal enclosure of propodeum somewhat declivous with sharp, carinate posterior border, enclosure with longitudinally vermiform ridges medially, straighter longitudinal ridges laterad. (27) Legs with light color the same as on face. Foreleg with cream color on apex of femur and knee of tibia and adjacent area subequal to it. (28) Spur with many short hairs, finely pectinate (to no distinct teeth); spur length less than half of length of middle basitarsus, 0.44:0.94. (30) Tegula transparent testaceous. Humeral plate with cream-colored apex. (31) Stigma tan. (32) Marginal cell 6-9 longer than, and 3-4 shorter than (to equal to) 9-wt, 1.17:0.99:1.02.

Metasoma. (34) Suberect hairs of discs of terga 4-5 white. (35) Tergum 1 with punctures of median area smaller than on scutum, deep, irregularly spaced, sparse medially, dense laterally, less than 1 pwa.

MALE. Length, 6.5 mm; forewing length, 4.7 mm; hind wing length, 3.2 mm; clypeal length, 0.55 mm; scutal length, 1.27 mm.

Head. Yellow areas: (1) paraocular area below diagonal line originating at upper rim of antennal socket to lower margin of facial fovea ending on orbit about third of eye length below summit of eye; (6) mandible basal half to two-thirds; (7) scape with broad lateroventral stripe; a mere dot on lateroventral surface of flagellomere 1. (10) Punctures beside lower half of frontal line large, 1-2 pwa, interspaces shiny. (13) Orbital convergence ratio as 1.53: 1.14,1.34. (14) As in female but galeal gap slightly more than half of length of galea exposed beyond closed mandibles (0.26:0.44). (15) Head width to head length as 2.35:1.70,1.38. (17)) Eye length, mio, and flagellar length as 1.31:1.14:1.53. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.43:0.41:0.29:0.32. (19) Ocellolabral greater than clypeal width, 1:41:1.26, 1.12. (20) Clypeocellar to outer subantennal sutural as 0.82:0.71,1.14. (21) Basal labial palpomere about 2.6 times length of others combined. (22) Flagellar length about 3.0 times length of scape, 1.55:0.51.

Mesosoma. (24) Scutal and scutellar hair pale grey (to pale fulvous), otherwise as in female. (25) Scutal disc with punctures slightly larger than on midvertex, 0.5-1 pwa, interspaces shiny (30×). (27) Foreleg with yellow on dorsoapical third of femur, anterior surface of tibia, basitarsus and second tarsomere entirely; third to fifth tarsomeres successively darker, testaceous to light brown; posterior surface of tibia brown. (28) Middle leg colored like foreleg but yellow on dorsoapical fifth of femur; lengths of tibia, basitarsus, and apicotarsus as 1.09:0.87:1.00. (29) Hind leg colored like middle leg, narrow brown margin may occur on anterior surface of basitarsus, apicotarsus brown. (32) Marginal cell 6-9 greater than, and 3-4 less than 9-wt, 0.99:0.83: 0.92.

Metasoma. (34) Suberect hairs of discs of terga 4-5 fulvous. (35) Tergum 1 with punctures of median area larger than in female, smaller than on scutum, deep, fairly regularly spaced, less than 1 pwa, interspaces shiny.

TYPE MATERIAL. Holotype male, from Rodeo, Hidalgo County, New Mexico, August 22, 1962 (J. G. Rozen, M. Statham, S. J. Hessel) on *Heterotheca subaxillaris,* and allotype female, from Portal (5 mi. W.), S. W. R. S., Cochise Co., Arizona, 5400 ft., Aug. 10, 1956 (Ellen Ordway), on *Melilotus alba,* are at the American Museum of Natural History.

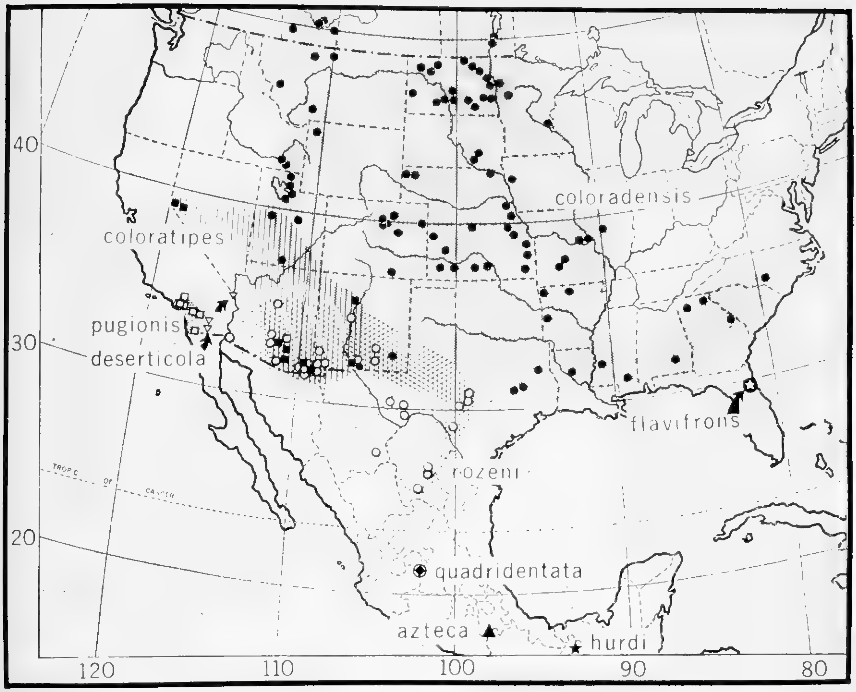
In addition, 154 male and 120 female paratypes are from the following localities: ARIZONA: Apache and vicinity; Skeleton Canyon, Benson, Bisbee, Portal and vicinity, all in Cochise Co.; Flagstaff; Mt. View; Phoenix; Santa Rita Mountains; San Xavier Mission; Superior, Pinal Co.; Tucson; Warren; Yuma: Yuma Test Station. NEW MEXICO: Granite Pass, Peloncillo Mts., Hidalgo Co.; High Rolls, Otero Co.; Lordsburg; Filmore Canyon and Soledad, Organ Mountains; Road Forks, Hidalgo Co.; Rodeo and vicinity, Hidalgo Co.; Roswell; Socorro. TEXAS: Coopers Store, Big Bend National Park, Brewster Co.; Davis Mts., Jeff Davis Co.; Marathon (20 mi. S.); Stonewall; Uvalde. CHIHUAHUA: Salaices. COAHUILA: La Gloria, south of Monclova, 3300 ft.; Paila, 3900 ft.; Piedras Negras (192 km. S.), 1300 ft.

DISTRIBUTION. The southwestern United States and north central Mexico. In addition to the type material, 4 females have been examined from 5 miles west of Junction, Kimble Co., Texas, April 15, 1961 (Rozen and Schrammel).

This species is active in April, May, June, July, August, September, and October.

GEOGRAPHIC VARIATION. Three characters are conspicuously variable in female *rozeni:* 1) the amount of yellow color on the pronotal lobe, 2) the amount of yellow on the subantennal plate, and 3) the density of the punctures of the median area of metasomal tergum 1. The first two do not appear to be clinal, but the third may be so. Specimens from Texas exhibit denser punctation than more western ones, and females from Junction, Texas, have been excluded from the type series primarily for this reason since no males were collected to confirm the determination.

DISCUSSION. It is unusual for two solitary bees of different species to be taken *in copulo,* and this has almost always been interpreted to mean that the two specimens are not, indeed, different species. One male of *rozeni* was collected *in copulo* with a female of *crypta* by J. G. Rozen (Portal, S. W. R. S., Arizona, September 14, 1962, on *Heterotheca subaxillaris*), and one pair of *rozeni* was taken *in copulo* by G. I. Stage, Rodeo (2.5 miles north), New Mexico, September 7, 1959, on *Baileya pleniradiata.* Both collectors had observed the specimens carefully prior to collection. Inasmuch as I have an interspecific mating pair of *Calliopsis chlorops* with *Calliopsis coloradensis,* I believe the phenomenon may be more common than preserved specimens indicate. Nevertheless, I have not yet seen a specimen of either sex of any of these species which can be considered an intermediate, or hybrid, form. It is



MAP 5. Map showing the known distributions of *Calliopsis (Calliopsima) coloradensis* Cresson, *C. (C.) coloratipes* Cockerell, *C. (C.) pugionis* Cockerell, *C. (C.) deserticola* Shinn, *C. (C.) rozeni* Shinn, *C. (C.) quadridentata* Shinn, *C. (C.) azteca* Shinn, and *C. (C.) hurdi* Shinn. The presumptive collection locality for *Calliopsis flavifrons* Smith is also shown.

possible that the males can be deceived by some of the females of these closely related and superficially indistinguishable pairs of species. I conclude that no viable offspring are produced.

FLOWER RECORDS. *Baccharis, Baileya pleniradiata, Chamaesaracha conioides, Eriocarpum gracile, Eriogonum, Gaillardia, Helianthus, Heterotheca subaxillaris, Hymenoxys odorata, Melilotus alba, Parkinsonia, Pectis papposa, Psilostrophe cooperi, Sphaeralcea emoryi?, Verbesina exauria.* Taken primarily on *Heterotheca subaxillaris* which is a favorite flower among its relatives also.

CALLIOPSIS (CALLIOPSIMA) COLORADENSIS Cresson

(Figs. 63-66; Map 5)

Calliopsis coloradensis Cresson, 1878, Trans. Amer. Ent. Soc., 7:63, female, male; Patton, 1879, Bull. U.S. Geol. Survey, 5:366; Cockerell, 1897, Canad. Ent., 29:290; 1897, Bull. Univ. New Mexico, 24:19; 1897, Proc. Acad. Nat. Sci. Phila., 49:350; 1898, Trans. Amer. Ent. Soc., 25:196, 1898, Bull. Sci. Labs. Denison Univ., 11:52; 1898, Zoologist, (4) 2:313; 1899, Ent. News, 10:4; Bridwell, 1899, Trans. Kans. Acad. Sci., 16:210; Cockerell, 1901, Ann. Mag. Nat. Hist., (7) 7:128; Cockerell and Atkins, 1902, Ann. Mag. Nat. Hist., (7) 10:44; Cockerell, 1906, Trans. Amer. Ent. Soc., 32:299; 1906, Bull. Amer. Mus. Nat. Hist., 22:440; Swenk and Cockerell, 1907, Ent. News, 18:178; 1908, Canad. Ent., 40:147-148; Crawford, 1912, Canad. Ent., 49:359; Robertson, 1914, Ent. News, 25:70; Cresson, 1916, Mem. Amer. Ent. Soc., 1:115; Stevens, 1919, Canad. Ent., 51:210; Cockerell, 1919, Jour. N.Y. Ent. Soc., 27:299; 1921, Amer. Mus. Nov., 24:13; Robertson, 1922, Psyche 29(4):169; Robertson, 1926, Ecology, 7:379 (anthecology); Hicks, 1926, Univ. Colo. Studies, 15:223; Robertson, 1928, Flowers and Insects, p. 10+ (anthecology); 1929, Psyche, 36(2):115 (anthecology); Stevens, 1950, North Dakota Agric. Exp. Sta. Bimon. Bull., 12:90,93 (biol.); Rozen, 1951, Jour. Kans. Ent. Soc., 24(4):142+(male genitalia); Linsley, 1958, Hilgardia, 27:561; Mitchell, 1960, North Carolina Agric. Exp. Sta. Tech. Bull. No. 141:288-289, 291-294.

coloradensis coloratipes; Pierce, 1904, Stud. Univ. Nebraska, 4:23. (misidentification)
coloratipes fedorensis; Cockerell, 1909, Ann. Mag. Nat. Hist. (8) 4:28. (misidentification)
coloradensis fedorensis; Cockerell, 1921, Amer. Mus. Novitates, 24:14.
C. sp.?, Michener, 1947, Amer. Midl. Nat., 38:447.

The species is closest to *rozeni* and *coloratipes.* It is separated in the male from them by the long ventral prongs on sternum 6, by having the volsella much expanded, and by having the punctures of tergum 1 much smaller than in *rozeni* and larger than in *coloratipes.* It is separated in the female from *coloratipes* by the dark mandibular base, from *rozeni* by the much finer punctures of tergum 1, and from both species by the regularly distributed punctures of tergum 1, which are sparse medially in them.

Female. Length, 8.8 mm; forewing length, 5.8 mm; hindwing length, 4.1 mm; clypeal length, 0.62 mm; scutal length, 1.60 mm.

Head. Cream colored areas: (1) as in *rozeni;* (2) clypeus with a broad T with convex crossbar bordering entire length of horizontal portion of frontoclypeal suture (to somewhat less), bottom of the T with adjacent small spot (more typically, clypeus light colored except for testaceous apical border and wide, twin, vertical bars of brown arising from its median portion); (3) absent on labrum; (5) subantennal plate with dot (to entirely); (6) absent on mandible. (7) As in *rozeni.* (8) Hair of vertex fulvous. (10) Punctures beside lower half of frontal line slightly smaller than in *rozeni,* 1-2 pwa, interspaces shiny. (13) Orbital convergence ratio as 1.82:1.70,1.07. (14) Galea finely pebbled, dull, galeal gap about half length of galea exposed beyond closed mandibles, (0.31:0.58). (15) Head width to head length as 2.77:1:89, 1.47. (17) Eye length, mio, and flagellar length as 1.46:1.70:1.48. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.51:0.51:0.48:0.43. (19) Ocellolabral slightly greater than clypeal width, 1.62:1.56,1.03. (20) Clypeocellar to outer subantennal sutural as 0.99:0.87,1.14. (21) Basal labial palpomere about 2.5 times length of others combined. (22) Flagellar length about 2.1 times length of scape, 1.48:0.71.

Mesosoma. (23) Yellowish areas: apex of pronotal lobe, scutellar crest. (24) As in *rozeni,* except hairs longer. (25) Scutal disc with punctures slightly larger than those of vertex, 1 pwa or less. (26) As in *rozeni* except ridges narrower, more abundant, shinier. (27) Foreleg with yellow at apex of femur and knee of tibia. (28) Spur exceedingly finely pectinate on apical half, bearing about 10 short teeth, barely distinguishable (30×); spur length about half of length of middle basitarsus, 0.48:0.94. (30) Tegula transparent, light amber. Humeral plate with anterior half yellow. (31) Wing clear (to faintly smoky apically, not so smoky as in *rozeni*). Stigma tan. (32) Marginal cell 6-9 greater than, and 3-4 less than 9-wt, 1.33:0.90:1.14.

Metasoma. (34) As in *rozeni* but hairs longer. (35) Tergum 1 with punctures of median area slightly finer than on scutum, fairly regularly spaced, 2-3 pwa.

MALE. Length, 6.3 mm; forewing length, 4.9 mm; hindwing length, 3.52 mm; clypeal length, 0.58 mm; scutal length, 1.41 mm.

Head. Yellow areas: (1) paraocular area below diagonal line originating at upper end (or between upper end and middle) of outer subantennal suture and extending tangent to facial fovea ending on orbit below midlevel of fovea, angle of upper corner about 40° (or 10°); (4) supraclypeal area in some cases with black border between frontoclypeal suture and yellow supraclypeal area; (5) subantennal plate, sometimes reduced to basal spot; (6) mandible basal half; (7) scape with ventral surface yellow except dark brown mesally and apically (through various states of reduction of yellow to all brown scape); yellowish ventral dots on flagellomeres 1-2 (sometimes absent). (10) As in female. (13) Orbital convergence ratio as 1.60:1.22,1.30. (14) As in female. (15) Head width to head length as 2.41:1:70,1.42. (17) Eye length, mio, and flagellar length as 1.33:1.22:1.51. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.46:0.46:0.31:0.36. (19) Ocellolabral greater than clypeal width, 1.43:1.26,1.13. (20) Clypeocellar to outer subantennal sutural as 0.85:0.68,1.25. (21) Basal labial palpomere about 2.0 times length of others combined. (22) Flagellar length about 2.9 times length of scape, 1.51: 0.53.

Mesosoma. (25) Scutal disc with punctures slightly larger than in *rozeni*, 0.5-1 pwa, interspaces shiny. (27) Foreleg with yellow on dorsoapical half (or less) of femur, tibia, basitarsus and second tarsomere, remaining tarsomeres tinged testaceous. (28) Middle leg colored like foreleg but less yellow on femur, brown patch on posterior surface of tibia (sometimes); lengths of tibia, basitarsus, and apicotarsus 1.04:0.94:0.99. (29) Hind leg colored like middle leg. (32) Marginal cell 6-9 greater than, and 3-4 less than 9-wt, 1.12: 0.87:0.99.

Metasoma. (35) Tergum 1 with punctures of median area slightly smaller than on scutum, deep, crowded medially, contiguous, interspaces shiny.

TYPE MATERIAL. Lectotype female, 1 female and 2 male paratypes, Colorado (Ridings and Morrison), with no further label data, are at the Academy of Natural Sciences of Philadelphia, Types 2187, 2187.2, 2187.4, and 2187.5, respectively. Paratype 2187.3, same data, is a female specimen of *C. chlorops*. I suggest that the indefinite type locality be restricted to the Colorado counties of Denver, northern half of Jefferson, and eastern half of Boulder, where specimens taken agree exactly with the types. The description of the male is principally based on paratype No. 2187.2.

Distribution. Alberta to southern Utah and southern New Mexico, east to the Mississippi River, thence through eastern Texas and the Gulf States to the east slope of the Appalachian Mountains in North Carolina. Not yet found in Florida, although it has likely occurred there in the past (cf. remarks regarding *Calliopsis flavifrons* Smith under the following section, Geographic variation). It is a late summer-early autumn bee collected between June 27, 1918, at Winnfield, Louisiana, and Oct. 10, 1961, at Nacogdoches, Texas, but most records are in July and August.

In addition to the type specimens, about 490 others have been studied from the following localities: Alberta: Lethbridge; Medicine Hat; Scandia; Tilley. Manitoba: Balmoral; Stony Mountain; Stormy Mountain; Winnipeg. Alabama: Pickett Springs, Montgomery Co. Arkansas: Chessman Ferry, Stone Co.; Fayetteville, Washington Co.; Polk Co. Colorado: Boulder; Denver; Hoehne; Limon; Loveland; Roggen; Wray. Georgia: Augusta, Richmond Co.; Cartersville, Bartow Co.; Nacoochee Valley. Idaho: Downey; Fort Hall. Illinois: Carlinville. Iowa: Sioux City. Kansas: Blue Rapids; Dodge City (8 mi. N.E.); Douglas Co.; Garnett; Hutchinson; Lakin (4 mi. E.); Riley Co.; Scott Co., 2970 ft.; Sherman Co., 3690 ft.; Smith Co., 1800 ft.; Stafford Co.; Yates Center. Louisiana: Winnfield, Winn Co. Minnesota: Detroit; Moorhead; Powder Plant Woods, Ramsey Co.; University Farms, Ramsey Co. Mississippi: Hattiesburg; Utica. Missouri: Conway (10 mi. N.); Gilmore; High Hill; Lebanon (12 mi. E.). Montana: Bozeman; Hill Co.; Missoula; Pompey's Pillar, Yellowstone Co.; Pondera Co. Nebraska: Crofton (2 mi. W.; 7 mi. N.W.); Gordan, Sheridon Co.; Harrison (13 mi. N.); Lincoln; West Point. New Mexico: Organ Mountains, Filmore Canyon, Dona Ana Co., 5400 ft.; Roswell (5 mi. E.), Chaves Co. North Carolina: Aberdeen, Moore Co. North Dakota: Beach, Bismarck; Carpio; Crary; Devils Lake; Edgeley; Fargo; Glen Ullin (10 mi. E); Grand Forks; Granville; Hatton; Jamestown; Lakota; McKenzie; Mandan; Minot; Mott; Perth; Sentinel Butte; Valley City; Williston. South Dakota: Geddes (5 mi. E.); Fort Thompson. Texas: Brazos Co.; Fedor; Lee Co.; Nacogdoches. Utah: Farr West; Garfield; Knaub; Magna; Petersboro; Price; Topaz; Williard. Wyoming: Waltman, Natrona Co.; Yellowstone National Park.

Geographic Variation. This species is more variable than any other species of *Calliopsima*. The subgenus as a whole consists of rather more closely related species than does either *Calliopsis s.s.* or *Perissander*. It is about the same in this respect as *Verbenapis* whose species are possibly even more closely related than those in *Calliopsima*.

The most obvious variation is in size. The size grades from the large robust specimens of Canada and the Rocky Mountain States to the small specimens from the Missouri and Mississippi River valleys from Missouri to Mississippi.

Seven characteristics were investigated for use as total size indicators because of the high variability of total length. These characteristics were measured for 33 male specimens from all parts of the range of the species and the correlations were calculated among them with the results shown in Table 2.

These results suggest that scutal length, clypeal length, and flagellar length are most highly correlated with all the other variables, and that eye length has the smallest correlation with all the others.

Based upon these data and similar ones for *C. andreniformis,* wing length,

TABLE 2. Correlation Coefficients of Characteristics for Expressing Total Size of a Bee Based on *Calliopsis coloradensis*

	Hindwing Length	Scutal Length	Head Length	Clypeo-cellar	Clypeal Length	Eye Length	Flagellar Length
Hindwing Length	1.000	.884	.817	.870	.900	.639	.864
Scutal Length		1.000	.883	.888	.948	.693	.935
Head Length			1.000	.779	.888	.637	.830
Clypeo-cellar				1.000	.863	.657	.838
Clypeal Length					1.000	.653	.931
Eye Length						1.000	.639
Flagellar Length							1.000
Multiple Correlation of each variable with all the others	.92	.97	.90	.91	.97	.70	.95

scutal length, and clypeal length were chosen as suitable measures of the total size of a bee. These are the introductory measurements given for each species treated in this genus.

A summary of the salient differences between male topotypical specimens of *coloradensis* and those of the Missouri and Mississippi River basins is given in Table 2. The measurements are for the male allotype from Colorado, and for a Missouri River specimen from Gilmore, Missouri. The latter is representative of the specimens from the two river systems and from the southeastern United States. I do not feel that there is an adequate basis to consider these latter specimens as a species separate from *coloradensis*. I would like to see more specimens and comparative ecological data before reaching a decision on their status. If they eventually are shown to be a distinct species there is every reason to use the available name *Calliopsis flavifrons* Smith, 1853. Smith's description of the *flavifrons* collected in East Florida would fit only this form of *Calliopsis* which is the only representative of its subgenus in the southeastern United States. Specimens from localities between Colorado and the Mississippi are somewhat variable with respect to the characters given below. However, no clear clinal changes have been uncovered although the average size of males increases steadily from Missouri to Colorado and from North Carolina to Texas. The typical southeastern male is only slightly more than three-fourths the length of the typical Colorado male.

TABLE 3. Comparison of Rocky Mountain forms of *C. coloradensis* with forms from the southeastern United States

Character	Colorado	Missouri
Hind wing length	1.17	0.97
Head length	1.70	1.36
Inner subantennal sutural/galeal gap	>1	$\leqq 1$
Galeal length/clypeocellar	>1	$\leqq 1$
Basal labial palpomere length/clypeocellar	$\geqq 1$	<1
Eye length/scutal length	<1 (1.33:1.41)	$\cong 1$ (1.02:1.04)
Eye profile width/antennocellar	$\leqq 1$ (0.71:0.73)	>1 (0.61:0.53)
Eye profile width/outer subantennal sutural	>1 (0.73:0.68)	<1 (0.53:0.56)
Midocellar interocular/flagellar length	>1 (1.60:1.51)	<1 (1.26:1.34)
Fore basitarsal length/clypeocellar	<1 (0.85:0.94)	<1 (0.68:0.71)
Dorsal propodeal enclosure, hind border of median portion	Weakly carinate	Rolled anteriad, or obscurely carinate
Punctures of frons	Finer	Coarser
Hind tibia, posterior surface	Mostly yellow	Mostly brown
Outline of vertex in facial aspect	Flat	Arched
Penis valve length/volsella length	Greater	Lesser
Apodemes of penis valves	Shorter	Longer

FLOWER RECORDS. *Anthemis cotuia, Aplopappus pluriflorus, Aster dumosus, A. praetus, Bidens laevus, B. aristosa, Boltonia asteroides, Chrysopsis, Chrysothamnus nauseosus, Coreopsis tripteris, Eriocarpum gracile, Grindelia perennis, G. squarrosa, Helenium nudiflorum, Heterotheca subaxillaris, Macrotera, Rudbeckia triloba, Silphium, Solidago rigida, S. serotina.*

Robertson (1922) studied the anthecology of this species at Carlinville, Illinois. His results are given below:

FEMALES COLLECTING POLLEN	MALES SUCKING NECTAR	MALE-FEMALE IN COPULO
Astereae:		
Boltonia asteroides	*Boltonia asteroides*	*Boltonia asteroides*
Solidago canadensis	*Solidago canadensis*	*Solidago canadensis*
Heliantheae:		
Bidens aristosa	*Bidens aristosa*	*Bidens aristosa*
Rudbeckia triloba	*Rudbeckia triloba*	
Coreopsis tripteris		

CALLIOPSIS (CALLIOPSIMA) PECTIDIS Shinn

(Figs. 67-71; Map 6)

Calliopsis pectidis Shinn, 1965, Amer. Mus. Novitates, 2211:10.

This species is named for one of the genera of plants, *Pectis,* used as its food source, and is adopted from the manuscript name proposed for it by

Prof. P. H. Timberlake who recognized it as a new form more than a decade ago. The closest relatives are *C. timberlakei* and *C. bernardinensis*. All three species comprise a closely related group which has close affinities with *rozeni*.

The male is separated from other species of *Calliopsima* by the yellow scape with light brown apical rim and by the shape of the ventral protuberance of the apical portion of the penis valve (Fig. 71). The female is distinguished by the presence of large amounts of cream coloration on the tibiae and basitarsi as described in (27), (28), and (29) below, and by the characteristic nap-like vestiture of the scutum as described in (24) below.

FEMALE. Length, 7.7 mm; forewing length, 5.0 mm; hindwing length, 3.4 mm; clypeal length, 0.56 mm; scutal length, 1.49 mm.

Head. Cream colored areas: (1) paraocular area as described for subgenus, sinuous line originating at a point about two-thirds up outer subantennal suture and ending on orbit at about level of middle of fovea; (2) as in *rozeni* except brown clypeal bars narrower, extending dorsally about five-eighths (or less) of median length of clypeus; (3) labrum except for testaceous rim of labral plate and median area apical to it; (5) subantennal plate; (6) mandible about basal fourth; (7) scape with small apicoventral dot, base testaceous ventrally; pedicel and flagellum as in *rozeni* except lighter brown. (8) Hair color as in *rozeni* but all areas with shorter, more plumose hair. (10) Punctures beside lower half of frontal line larger than in *rozeni,* 1-2 pwa, interspaces shiny. (13) Orbital convergence ratio as 1.60:1.51,1.05. (14) Galea shinier, more finely pebbled than in *rozeni*. (15) Head width to head length as 2.58:1.79,1.45. (17) Eye length, mio, and flagellar length as 1.36:1.51:1.45. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.53:0.43: 0.41:0.37. (19) Ocellolabral greater than (to subequal to) clypeal width, 1.48:1.45,1.02. (20) Clypeocellar to outer subantennal sutural as 0.90:0.75,1.20. (21) N. A., measured on paratype of equivalent size: basal labial palpomere about 2.3 times length of others combined. (22) Flagellar length 2.1 times length of scape, 1.45:0.68.

Mesosoma. (23) Cream colored areas: apex of pronotal lobe, scutellar crest. (24) Hair about half length of that of *rozeni,* more plumose. Scutal and scutellar hair color as in *crypta* except long dark hairs of lighter brown hue; short hairs dense, profusely branched concealing scutal punctures, appearing like a closely applied nap at 10×, highly distinctive, unique in its group. (25) Scutal disc with punctures contiguous, smaller than in *rozeni*. (26) As in *rozeni* but enclosure shorter. (27) Foreleg with cream color at apex of femur, most of anterior and posterior surfaces of tibia dorsally, and basal half of anterior surface of basitarsus. (28) Spur length half of length of middle basitarsus, 0.41:0.82. (29) Hind leg colored like foreleg but anterior surface of basitarsus entirely light with brown rim. (30) Tegula hyaline laterally, straw color posteriorly. Humeral plate as in *rozeni.* (31) As in *rozeni.* (32) Marginal cell 6-9 less than (to subequal to), and 3-4 shorter than 9-wt, 0.92:0.82:0.95.

Metasoma. (34) Tergal hair bands denser than in *rozeni,* more plumose, hence much more distinct. Suberect hairs of discs of terga 4-5 brownish (almost always whitish). (35) As in *rozeni* but much smaller, regularly spaced, less than 1 pwa.

MALE. Length, 7.2 mm; forewing length, 4.3 mm; hindwing length, 2.9 mm; clypeal length, 0.56 mm; scutal length, 1.37 mm.

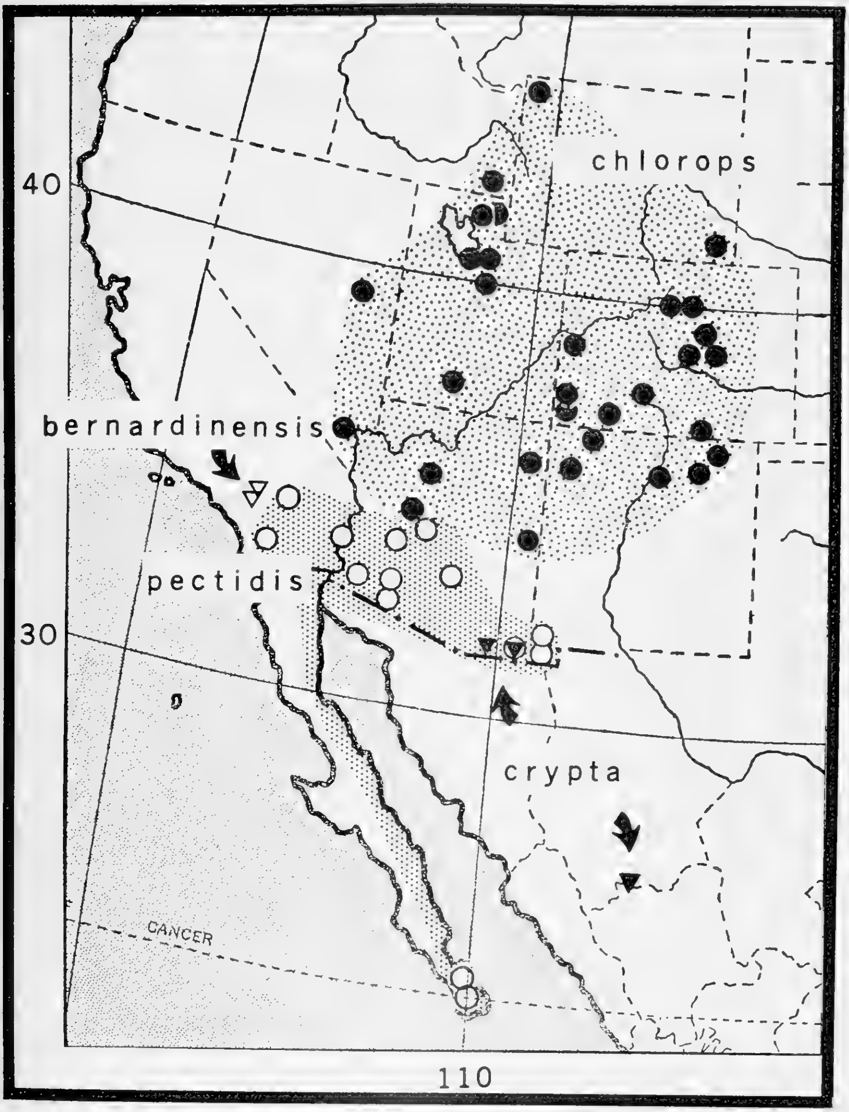
Head. Yellow areas: (1) paraocular area below a dorsally convex line originating at upper rim of antennal socket and extending to lower inner margin of facial fovea ending on orbit at about level of lower margin of fovea; (6) as in *rozeni;* (7) scape entirely (or with a longitudinal streak of brown on dorsal surface); pedicel and flagellomere 1 on ventrolateral surfaces. (10) As in *rozeni.* (13) Orbital convergence ratio as 1.46:1.14,1.28. (14) As in female. (15) Head width to head length as in *rozeni,* 2.35:1.70,1.38. (17) Eye length, mio, and flagellar length as 1.22:1.14:1.62. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.41:0.43:0.28:0.32. (19) Ocellolabral greater than clypeal width, 1.38:1.14,1.21. (20) Clypeocellar to outer subantennal sutural as 0.80:0.68,1.18. (21) N. A., taken on paratype of equivalent size: basal labial palpomere about 1.6 times length of others combined. (22) Flagellar length about 3.3 times length of scape, 1.62:0.49.

Mesosoma. (25) As in *rozeni* but smaller, less than half pwa, interspaces shiny. (27) Foreleg with coxa yellow on apical half of ventral surface, trochanter with yellow patch apicoventrally, femur with yellow on apical three-fourths of anterodorsal surface and apical third of posterior surface, tibia and tarsomeres 1-4 yellow, tarsomere 5 testaceous. (28) Middle leg with coxal yellow reduced to apical fourth of ventral surface, trochanter with apicoventral yellow patch smaller than that of foreleg, femur and tibia with yellow pattern similar to that of foreleg, tarsomeres 1-3 yellow, tarsomeres 4-5 successively darker testaceous; lengths of tibia, basitarsus, and apicotarsus as 0.95:0.90:0.95. (29) Hind leg with yellow color pattern of trochanter, femur, and tibia similar to those of middle leg; coxa with yellow as on front trochanter; tarsomeres 1-2 yellow, tarsomeres 3-5 successively darker testaceous. (32) Marginal cell 6-9 equal to (to subequal to), and 3-4 shorter than 9-wt, 0.87:0.78:0.87.

Metasoma. (34) As in female but very few erect, brownish hairs. (35) Tergum 1 with punctures of median area smaller than on scutum or in *rozeni,* regularly spaced, contiguous, interspaces shiny.

TYPE MATERIAL. Holotype male and allotype female, from Portal (2 miles N.E.), Cochise Co., Arizona, August 21, 1962 (J. G. Rozen, M. Statham, S. J. Hessel), are at the American Museum of Natural History.

In addition 65 males and 47 female paratypes are from the following localities: Arizona: Ajo; Aguila; Brenda (2 mi. W.), Yuma Co.; Congress (4 mi. S.W.); Florence Junction (3.1 mi. S.), Pinal Co.; Gila Bend and 28 mi. E., Maricopa Co.; Portal and vicinity, Cochise Co.; Salome (2.3 mi. N.). California: Blythe (10 mi. N.); Julian (12 mi. E.); San Diego Co.; Twentynine Palms. New Mexico: Carrizozo, Lincoln Co. ; Lordsburg (11 mi. N.W.); Road Forks; Rodeo. Baja California Sur: San Pedro; Sierra de la Laguna Mountains, Big Canyon (about latitude 23° 34′ N., longitude 110° 00′ W.).



Map 6. Map showing the known distributions of *Calliopsis (Calliopsima) chlorops* Cockerell, *C. (C.) bernardinensis* Michener, *C. (C.) pectidis* Shinn, and *C. (C.) crypta* Shinn.

Discussion and Distribution. Dr. Paul D. Hurd, Jr., has informed me (in litt.) that two female *Holcopasites arizonicus* (Linsley) were taken in association with a female *C. pectidis* by Dr. Mont A. Cazier, 2 mi. N.E. of Portal, Arizona, Sept. 24, 1961. This is the second species record of a *Calliopsis-Holcopasites* association, the other being of *H. calliopsidis* (Linsley) with *C. andreniformis* Smith. *C. pectidis* is apparently widespread from southern New Mexico to the Mohave and Colorado Deserts in California and south to near the tip of Baja California. I anticipate its discovery in the Sonoran Desert of northern Mexico. The species is active from August to October.

Flower Records. *Aplopappus, Baccharis, Baileya pleniradiata, Helianthus, Heterotheca subaxillaris, Hymenothrix wislizeni, Melilotus alba, Pectis angustifolia, P. papposa, Tidestromia lanuginosa, Verbesina encelioides.* Seven of the same genera and four of the same species are visited by *pectidis* and *rozeni.*

CALLIOPSIS (CALLIOPSIMA) TIMBERLAKEI, new species

(Figs. 72-76; Map 7)

The specific name is given to honor Mr. P. H. Timberlake, Associate Entomologist, Emeritus, of the University of California, Riverside, who lent me his entire collection of *Calliopsis* including several new, unpublished species he had earlier recognized.

Calliopsis timberlakei is closest to *pectidis.* It is separated in the male by the sparser, longer, scutal hair which does not conceal the scutal punctation, and by the partially yellow pedicel. The female is distinguished by the entirely yellow clypeus which lacks brown clypeal bars.

Female. Length, 7.7 mm; forewing length, 4.8 mm; hindwing length, 3.47 mm; clypeal length, 0.58 mm; scutal length, 1.33 mm.

Head. Yellow areas: (1) paraocular area as described for subgenus, sinuous line originating near upper end of subantennal suture; (2) clypeus except for brown markings near anterior tentorial pit, black subtriangular area with anterior tentorial pit as center, and testaceous apical border; (3) labrum except brown spot medioapically beyond labral plate (sometimes along apical border of labral plate); (5) subantennal plate; (6) mandible basal half; (7) scape a tiny area on extreme dorsolateral surface and at base, flagellomeres 1-4 tan ventrally. (8) Hair of vertex fulvous. (10) Punctures beside lower half of frontal line slightly smaller than in *coloradensis,* 1-4 pwa, interspaces shiny. (13) Orbital convergence ratio as 1.56:1.48,1.06. (14) Galea finely pebbled, shiny basally, dull apically. (15) Head width to head length as 2.47:1.72,1.44. (17) Eye length, mio, and flagellar length as 1.34:1.48:1.38. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.49:0.41:0.39:0.36. (19) Ocellolabral greater than clypeal width, 1.48:1.41,1.05. (20) Clypeocellar to outer subantennal sutural as 0.90:0.77,1.18. (21) Basal labial palpomere about 2.5 times length of others combined. (22) Flagellar length about 2.2 times length of scape, 1.36:0.61.

Mesosoma. (23) Yellowish areas: apex pronotal lobe; scutellar crest. (24) Color as in *rozeni,* length of shorter hairs intermediate between *rozeni* and *coloradensis.* (25) Scutal disc with punctures finer than in *rozeni* and *bernardinensis,* 0.5-1 pwa. (26) Dorsal enclosure of propodeum as in *rozeni* except ridges more regularly spaced, slightly farther apart. (28) Foreleg with yellow at dorsal apex of femur, dorsal surface of tibia, and base (to all) of basitarsus. (28) Middle leg colored like foreleg but tibial and basitarsal yellow less extensive, not reaching apices of segments; spur length half of length of middle basitarsus, 0.43:0.85. (29) Hind leg with yellow patch on femur dorsosubapically and on tibia anterobasally. (30) Tegula testaceous. Humeral plate yellowish apically. (31) Wing not noticeably smoky to naked eye. Stigma testaceous. (32) Marginal cell 6-9 greater than, and 3-4 less than 9-wt, 0.66:0.77:0.94.

Metasoma. (34) As in *rozeni* but hair longer and denser. (35) Tergum 1 with punctures of median area smaller than on scutum, deep, fairly regularly spaced, 1-2 pwa.

MALE. Length, 5.5 mm; forewing length, 4.0 mm; hindwing length, 2.80 mm; clypeal length, 0.51 mm; scutal length, 1.12 mm.

Head. Yellow areas: (1) paraocular area below diagonal line originating at upper end of outer subantennal suture and extending dorsolaterally tangent to facial fovea, ending on orbit at about midlevel of facial fovea; (6) mandible basal half; (7) scape, except for brown dorsoapical band with streak; pedicel, ventrolaterally; flagellomeres 1-3, ventrally. (10) As in female. (13) Orbital convergence ratio as 1.33:1.02,1.30. (14) As in female. (15) Head width to head length as 2.11:1.46,1.44. (17) Eye length, mio, and flagellar length as 1.17:1.02:1.43. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.41:0.37:0.27:0.34. (19) Ocellolabral greater than clypeal width, 1.28:1.11, 1.15. (20) Clypeocellar to outer subantennal sutural as 0.77:0.63,1.21. (21) Basal labial palpomere about 1.8 times length of others combined. (22) Flagellar length about 3.2 times length of scape, 1.43:0.44.

Mesosoma. (25) Scutal disc with punctures 1 pwa or less, interspaces dull. (27) Foreleg with yellow on coxa apically, femur dorsoapically, extending onto anterior and posterior surfaces, tibia (a dot of brown on posterior surface sometimes), basitarsus and mediotarsus, distitarsus testaceous. (28) Middle leg colored like foreleg but less yellow on femur and entire apicotarsus testaceous; lengths of tibia, basitarsus, and apicotarsus as 0.85:0.66:0.78. (29) Hind leg colored like middle leg. (32) Marginal cell 6-9 greater than, and 3-4 less than 9-wt, 0.83:0.70:0.78.

Metasoma. (34) As in female. (35) Tergum 1 with punctures of median area medium sized, less than 1 pwa, interspaces shiny.

TYPE MATERIAL. Holotype male and allotype female, from Three Rivers (7.5 m. S.), Otero Co., New Mexico, Sept. 9, 1961 (P. D. Hurd), on *Gutierrezia microcephala,* are in the collections of the California Insect Survey, University of California, Berkeley.

In addition, 24 males and 37 female paratypes are from the following localities: ARIZONA: Chambers, 1 female, Sept. 19, 1938 (I. H. McCracken), *Helianthus;* Coconino Co., 1 female, Aug. 19, 1927 (P. A. Readio); Petrified Forest, 1 female, Aug. 27, 1931 (P. H. Timberlake), *Gutierrezia sarothrae;* Taylor, Navajo Co., 1 male, Sept. 14, 1961 (P. D. Hurd), *Gutierrezia;* Tucson (9 mi. S.E.), 1 female, Sept. 3, 1961 (P. D. Hurd), *Bahia absinthifolia.* NEW MEXICO: Carlsbad (5 mi. N.), Eddy Co., 1 female, Sept. 21, 1956 (J. W. MacSwain); Carrizozo, 1 male, 1 female, Sept. 10, 1961 (P. D. Hurd), *Gutierrezia microcephala; idem* (8 mi. N.), 1 male, *Aplopappus spinulosus;* Correo, 1 female, Sept. 4, 1930 (Timberlake), *Gutierrezia sarothrae;* Laguna, 2 males, Sept. 4, 1930 (Timberlake), *Isocoma wrighti;* Mesilla Park (8.5 mi. E.) Dona Ana Co., 1 male, Sept. 5, 1961 (P. D. Hurd), *Gutierrezia lucida;* Rinconada, 1 female, Sept. 26 (T. D. A. Cockerell, No. 5547), tall *Bigelovia;* Roswell, Chaves Co., 2 males, Sept. 11, 1961 (P. D. Hurd), *Gutierrezia longifolia;* Roswell, 3 males, 1 female, Sept. 12, 1937 (R. H. Crandall); Three Rivers (7.5 mi. S.), Otero Co., 11 males, 27 females, Sept. 9, 1961 (P. D. Hurd), *Gutierrezia microcephala.* TEXAS: The Basin, Big Bend National Park, 1 male, 1 female, *in copulo,* Oct. 4, 1956 (J. W. MacSwain). UTAH: Wildcat Canyon (N. of Beaver), 1 male, Sept. 7, 1954 (G. F. Knowlton), *Chrysothamnus nauseosus.*

DISTRIBUTION. Extreme western Texas, northwest through New Mexico to northern Arizona, the range is allopatric to that of the close relative *pectidis. C. timberlakei* occurs generally in more mountainous localities, whereas *pectidis* is more of a desert form.

FLOWER RECORDS. *Haplopappus spinulosus, Bahia absinthifolia, Bigelovia* (tall), *Chrysothamnus nauseosus, Gutierrezia longifolia, G. microcephala, G. sarothrae, Isocoma wrightii. C. timberlakei* shares one genus, *Haplopappus,* with *C. pectidis,* and one genus, *Gutierrezia,* with *bernardinensis.*

CALLIOPSIS (CALLIOPSIMA) BERNARDINENSIS Michener

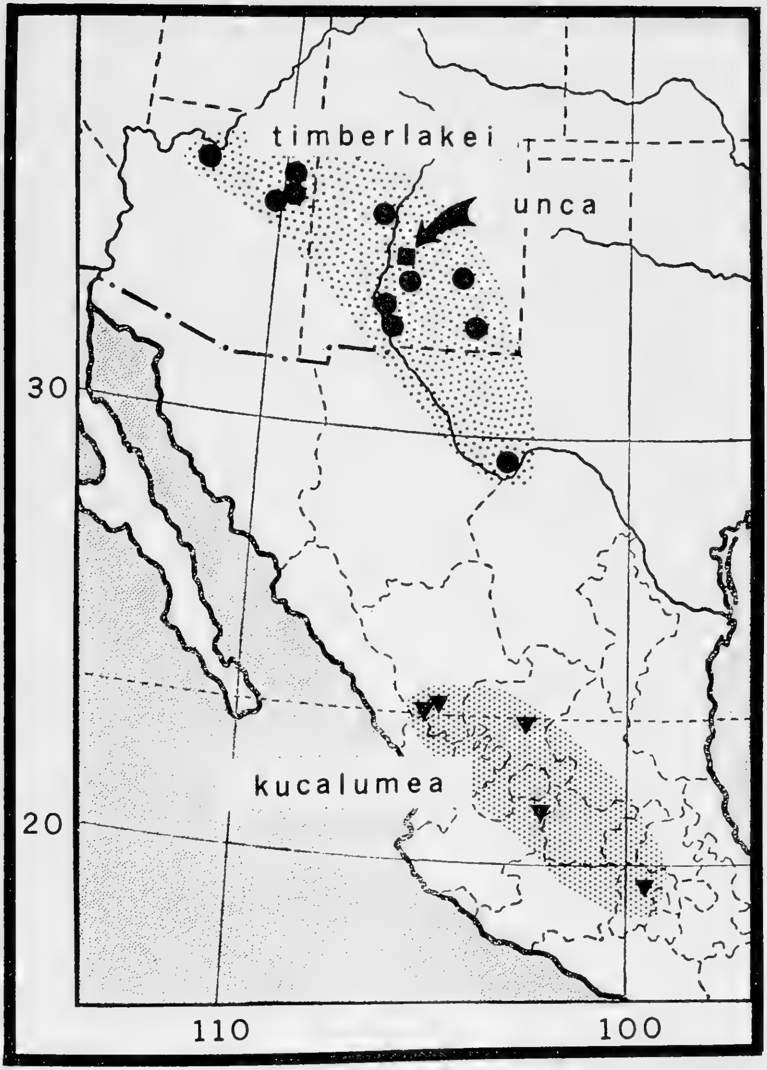
(Figs. 77-82; Map 6)

Calliopsis bernardinensis Michener, 1937, Ann. Mag. Nat. Hist., (10)19:323; Michener, 1951, *in* Muesebeck *et al.,* U.S. Dept. Agric., Monogr. No. 2:1103.

This species is closest to *timberlakei* and *pectidis.* The male is distinguished by the densely punctured, dull, tergum 1, with interspaces about 0.33 pwa, by the flagellum with posterior surface brown, and by the large patches of brown color on the posterior surfaces of the tibiae. The female is distinguished by the completely yellow labrum and the brown hind leg which sometimes bears a small yellow spot near the base of the tibia beside the basitibial plate.

FEMALE. Length, 7.6 mm; forewing length, 5.2 mm; hindwing length, 3.50 mm; clypeal length, 0.58 mm; scutal length, 1.33 mm.

Head. Yellow areas: (1) as in *timberlakei;* (2) as in *timberlakei;* (3) labrum entirely; (5,6,7,8) as in *timberlakei.* (10) Punctures beside lower half



MAP 7. Map showing the known distributions of *Calliopsis (Calliopsima) timberlakei* Shinn, *C. (C.) unca* Shinn, and *C. (C.) kucalumea* Shinn.

of frontal line smaller than those of *pectidis* or *timberlakei*, 1 pwa or less, interspaces shiny. (13) Orbital convergence ratio as 1.58:1:43,1.11. (14) As in *timberlakei*. (15) Head width to head length as 2.48:1.77,1.40. (17) Eye length, mio, and flagellar length as 1.34:1.43:1.36. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.48:0.44:0.39:0.39. (19)Ocellolabral greater than clypeal width, 1.50:0.80,1.87. (20) Clypeocellar to outer subantennal sutural as 0.92:0.77,1.20. (21) Basal labial palpomere about 2.5 times length of others combined. (22) Flagellar length about 2.2 times length of scape, 1.36:0.61.

Mesosoma. (23) Yellowish areas: apex pronotal lobe; scutellar crest. (24) Color as in *timberlakei*, length of shorter hairs intermediate between *pectidis* and *timberlakei;* some specimens with shorter hairs dense, profusely branched, obscuring scutal surface as in *pectidis*. (25) Scutal disc with punctures smaller than in *pectidis,* larger than in *timberlakei,* slightly more than 0.5 pwa. (26) Dorsal enclosure of propodeum as in *timberlakei* except ridges slightly further separated. (27) Foreleg with yellow on femur dorsoapically, dorsal surface of tibia, basal half or less of anterior surface of basitarsus. (28) Middle leg with yellow on femur dorsoapically, on basal half of dorsal surface of tibia, sometimes a spot on basitarsus basally; spur length about half of basitarsal length, 0.39:0.80. (29) Hind leg brown, rarely with yellow basal spot anterior to basitibial plate. (30) Tegula pale straw color to colorless. Humeral plate yellow apically. (31) As in *timberlakei*. (32) Marginal cell 6-9 longer than, and 3-4 equal to 9-wt, 1.11:0.94:0.94.

Metasoma. (34) Tergal hair bands entire although somewhat sparser medially and sparser than in *pectidis;* suberect hair of discs of terga 4-5 white. (35) Tergum 1 with punctures of median area smaller than on scutum, smaller than in *pectidis,* larger than in *timberlakei,* deep, regularly spaced, 0.5-1 pwa.

MALE. Length, 6.4 mm; forewing length, 4.2 mm; hindwing length, 2.80 mm; clypeal length, 0.51 mm; scutal length, 1.10 mm.

Head. Yellow areas: (1) paraocular area as in *timberlakei;* (6) mandible basal half; (7) scape, except dorsally; pedicel, ventrolaterally, much less distinct than in *timberlakei* (absent in some cases); flagellomere 1, ventrally (sometimes). (10) Punctures beside lower half of frontal line slightly larger than in *timberlakei,* 0.5 pwa or less, interspaces shiny. (13) Orbital convergence ratio as 1.34:1.00,1.34. (14) As in female. (15) Head width to head length as 2.07:1.53,1.36. (17)) Eye length, mio, and flagellar length as 1.17:1.00:1.50. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.39:0.37:0.22:0.32. (19) Ocellolabral greater than clypeal width, 1.28:1.11, 1.15. (20) Clypeocellar to outer subantennal sutural as 0.77:0.63,1.22. (21) Basal labial palpomere about 2.3 times length of others combined. (22) Flagellar length about 3.4 times length of scape, 1.50:0.44.

Mesosoma. (25) Scutal disc with punctures fine, slightly larger than in *timberlakei,* mostly 0.5 pwa, interspaces moderately shiny. (27) Foreleg with yellow as in *timberlakei* but sometimes absent on coxa, tibia except large posterior patch of brown reaching almost to apex. (28) Middle leg colored like foreleg but yellow absent from coxa, apicotarsus pale brown; lengths of tibia. basitarsus, and apicotarsus as 0.87:0.73:0.77. (29) Hind leg colored like middle leg, brown patch of tibia covering most of posterior surface. (32) Marginal cell 6-9 greater than, and 3-4 subequal to 9-wt, 0.87:0.78:0.80.

Metasoma. (35) Tergum 1 with punctures of median area largest, deepest of the *pectidis* group, crowded, contiguous, giving surface a definite bumpy character.

TYPE MATERIAL. Holotype male and allotype female, from Erwin Lake, San Bernardino Mountains, California, Aug. 22, 1932 (C. D. Michener), are at the California Academy of Science, San Francisco. I have not seen the types. The above description of the female is principally based on a paratype with the same label data as the type, while that of the male is based on a specimen from the Upper Santa Ana River, San Bernardino Co., California, Sept. 1, 1946 (Grace H. and John L. Sperry), on *Senecio ionophyllus*.

DISTRIBUTION. A late-summer, early-autumn bee.

Fourteen males and eight females have been studied from the following localities, which include the type locality: CALIFORNIA: Erwin Lake, San Bernardino Mts., Aug. 16, 22, 1932 (C. D. Michener); Riverside, Sept. 26-28, 1934 (P. H. Timberlake), on *Gutierrezia sarothrae;* Santa Ana River (upper), San Bernardino Co., Aug. 23, 1946 (Grace H. and John L. Sperry), on *Senecio ionophyllus.*

DISCUSSION. This species is probably a form isolated from an originally continuous range of *C. timberlakei.*

FLOWER RECORDS. *Gutierrezia sarothrae* and *Senecio ionophyllus,* both Compositae. *Gutierrezia* is also used by *timberlakei.*

CALLIOPSIS (CALLIOPSIMA) UNCA, new species

(Figs. 83-86; Map 7)

The specific name is from the Latin *uncus,* a hook, named for the hooklike projection on the outer posterior corner of the male volsella. It is closest to *crypta* and *chlorops* but is distinguished by the shape of the male volsella, and by the large amount of yellow on the ventral surface of the scape as described below in (7).

MALE. Length, 6.8 mm; forewing length, 4.5 mm; hindwing length, 3.10 mm; clypeal length, 0.54 mm; scutal length, 1.19 mm.

Head. Yellow areas: (1) paraocular area below diagonal line originating at antennal socket above upper end of outer subantennal suture and extending concavely dorsolaterally tangent to facial fovea, ending on orbit slightly above level of lower border of facial fovea; (6) mandible basal half; (7) scape except dorsal surface and apex ventromesally; flagellomeres 1-2 both with tiny patch ventrally. (8) Hairs of vertex fulvous with dark tips, of frons and clypeus white, more plumose than in *chlorops* or in *crypta.* (10) Punctures beside lower half of frontal line larger than those of *azteca* or *chlorops,* about the same size as those of *crypta,* 1 pwa, interspaces shiny. (13) Orbital convergence ratio as 1.43:1.11,1.29. (14) Galea shiny, apical pebbling barely perceptible (30×). (15) Head width to head length as 2.23:1.60,1.39. (17) Eye length, mio, and flagellar length as 1.21:1.11:1.56. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.43:0.41:0.27:0.34. (19) Ocellolabral less than clypeal width, 1.16:1.21,0.96. (20) Clypeocellar to outer subantennal sutural as 0.80:0.66,1.20. (21) Basal labial palpomere about 2.4 times length of others combined. (22) Flagellar length about 3.0 times length of scape, 1.53:0.51.

Mesosoma. (24)) Scutal and scutellar shorter hairs grayish-fulvous, longer hairs amberish, dark when viewed from behind. (25) Scutal disc with punctures deepest, most distinct in its group, relatively large, 0.33 pwa, interspaces moderately shiny. (26) Dorsal enclosure of propodeum with carinate border, shiny (30×) with high, narrow, strongly vermiform longitudinal ridges medially, somewhat straighter longitudinal ridges laterally, median portion produced posteriorly. (27) Foreleg with yellow as in *bernardinensis* but absent from coxa. (28) Middle leg with yellow on femur dorsoapically, tibia except large median brown patch on posterior surface, basitarsus and following two tarsomeres, last two testaceous; lengths of tibia, basitarsus, and apicotarsus as 1.02:0.78:0.94. (29) Hind leg colored like middle leg but tibia with only tiny, pale brown patch medially. (30) Tegula transparent light brown with anterior yellow patch. Humeral plate yellow apically. (32) Marginal cell 6-9 and 3-4 both less than 9-wt, 0.88:0.78:0.94.

Metasoma. (34) Tergal hair bands indistinct, hairs fine, appressed, whitish. Suberect hairs of discs of terga 5-6 white. (35) Tergum 1 with punctures of median area smaller than on scutum, deep, distinct, about 0.33 pwa, interspaces moderately shiny.

TYPE MATERIAL. Holotype male, from Bingham (3 mi. W.), Socorro Co., New Mexico, Sept. 12, 1961 (P. D. Hurd), on *Baileya pleniradiata,* is the property of the California Insect Survey, University of California, Berkeley.

DISTRIBUTION. The type locality of this species is a relatively short distance from the site of the world's first atomic bomb explosion near Alamogordo, New Mexico, in July, 1945. It seems unlikely, however, that this man-made radiation has created a mutated population from which this unique specimen has arisen. Persistent collecting from central to southern New Mexico and adjacent Mexico will probably be necessary to get a good study series of specimens.

CALLIOPSIS (CALLIOPSIMA) AZTECA, new species

(Figs. 91-94, Map 5)

The specific name is from the Nahuatlan, *Azteca,* meaning an Indian of the Nahuatlan tribe which founded the Mexican Empire, and is given because of the occurrence of the species in the heart of the former Aztec territory in Mexico. It is closest to *unca* but is easily distinguished by the wide, impunctate shiny area adjacent to the upper rim of the anterior declivity of metasomal tergum 1, by the yellow color on the scape being reduced to a small ventrobasal patch, and by the much finer, more widely separated punctures of the frons at the middle of the frontal line.

MALE. Length, 6.0 mm; forewing length, 4.1 mm; hindwing length, 3.0 mm; clypeal length, 0.46 mm; scutal length, 1.10 mm.

Head. Yellow areas: (1) paraocular area below diagonal line originating just below upper end of outer subantennal suture and extending convexly dorsolaterally tangent to facial fovea, ending on orbit slightly above level of lower border of facial fovea; (6) as in *unca;* (7) scape a small patch on ventral surface basally; flagellomeres 1-3 with tiny, successively larger patches ventrally. (8) Hairs of vertex and frons fulvous, of clypeus whitish. (10) Punctures beside lower half of frontal line, finest in the subgenus, somewhat irregularly distributed, 2-4 pwa, interspaces shiny (30×); punctures half to third of diameter of those of *unca,* much farther apart. (13) Orbital convergence ratio as 1.29:0.99,1.30. (15) Head width to head length as 2.06:1.53,1.35. (17) Eye length, mio, and flagellar length as 1.22:0.99:1.39. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.34:0.37:0.24:0.27. (19) Ocellolabral greater than clypeal width, 1.24:1.04,1.19. (20) Clypeocellar to outer subantennal sutural as 0.78:0.51,1.53. (21) Basal labial palpomere about 2.0 times length of others combined. (22) Flagellar length about 3.0 times length of scape, 1.39:0.46. (24) Scutal and scutellar shorter and longer hairs whitish to fulvous, longer hairs amberish, not dark when viewed from behind. (25) Scutal disc with punctures deep, distinct, medium sized, about two-thirds diameter of those of *unca,* 0.33 pwa, interspaces moderately shiny. (26) As in *unca* but ridges lower, fewer medial vermiform ridges, more longitudinal ridges laterally. (27) Foreleg with yellow on femur dorsoapically extending onto anterior and posterior surfaces, less extensive than that of *unca,* tibia except larger brown patch on posterior surface, basitarsus and following tarsomere, other tarsomeres pale testaceous. (28) Middle leg colored like foreleg but less yellow at apex; lengths of tibia, basitarsus, and apicotarsus as 0.90:0.78:0.87. (29) Hind leg colored like foreleg but brown patch of hind tibia much less extensive separated from base of tibia by 2 mow, tarsus brown. (30) Tegula transparent testaceous without yellow maculation. Humeral plate brown. (32) Marginal cell 6-9 and 3-4 both greater than 9-wt, 0.90:0.82: 0.78.

Metasoma. (34) As in *unca.* (35) Tergum 1 with punctures of median area smaller than on scutum, shallow but distinct, 1.5-3 pwa, interspaces moderately shiny. Declivity of tergum 1 shiny, impunctate.

Type Material. Holotype male, from Acatlán, Puebla, Sept. 11, 1948 (H. O. Wagner), is at the University of Michigan, Ann Arbor.

Remarks. This species bears on the outer posterior corner of the male volsella a hook-like projection which is like that of *unca*.

CALLIOPSIS (CALLIOPSIMA) CRYPTA Shinn

(Figs. 87-90; Map 6)

Calliopsis crypta Shinn, 1965, Amer. Mus. Novitates, 2211:15.

The specific name from the Greek *kryptos,* meaning hidden, is applied because this species remained mixed in a series of specimens of *C. chlorops* and *C. rozeni* for a long time prior to its recognition.

The differentiation of *crypta* from *rozeni* is discussed under the latter. The species is closest to *C. chlorops* and *C. kucalumea.* The male of *crypta* has the expanded middle section of sternum 8 with smoothly rounded posterior corners, whereas *chlorops* bears a tiny, posteriorly-directed, sharply-pointed process at each corner. The female of *crypta* has the mandibular base black or brownish black, whereas *chlorops* has the base cream colored. *C. crypta* is best distinguished from *C. kucalumea* by the key characters.

Female. Length, 8.6 mm; forewing length, 5.5 mm; hindwing length, 3.8 mm; clypeal length, 0.60 mm; scutal length, 1.49 mm.

Head. Cream colored areas: (1,2) as in *rozeni;* (3) dot (sometimes absent) dorsally near apex of labral plate; (5) absent on subantennal plate; (6) absent on mandible. (7) As in *rozeni* except tan areas of flagellomeres 1-4 smaller. (8) Hair of vertex mostly brown (view with integument as background). (10) Punctures beside lower half of frontal line larger than those of *rozeni,* less than 1 pwa, interspaces smooth, dull. (13) Orbital convergence ratio as 1.68:1.51,1.11. (14) As in *rozeni.* (15) Head width to head length as 2.60:1.82,1.43. (17) Eye length, mio, and flagellar length as 1.39:1.51:1.50. Flagellum slightly longer than in *rozeni.* (18) Interocellar, ocellocular, antennocular, and interantennal ratios similar to those of *rozeni,* as 0.46:0.49:0.43: 0.36. (19) Ocellolabral distance slightly greater than clypeal width, 1.53:1.45, 1.06. (20) Clypeocellar to outer subantennal sutural as 0.94:0.85, 1.10. (21) As in *rozeni.* (22) Flagellar length about 2.2 times length of scape, 1.50:0.68.

Mesosoma. (23) Cream colored areas: as in *rozeni* except dot on each pronotal lobe. (24) As in *rozeni* but short hairs of scutum fulvous, long hairs brown; short hairs and lateral long hairs of scutellum fulvous, other long hairs brown. (25) Scutal disc with punctures contiguous, larger than in *rozeni,* and larger than on midvertex, interspaces dull. (26) As in *rozeni* but more ridges and enclosure appearing somewhat duller although with interspaces shiny. (27) As in *rozeni.* (28) As in *rozeni* except spur length to length of middle basitarsus as 0.46:0.94. (29,30,31) As in *rozeni*. (32) As in *rozeni* but ratio as 1.14:0.97:1.11 (some specimens with ratios almost identical to those in *rozeni*).

Metasoma. (34) As in *rozeni* but disc of tergum 4 with at least ten brown hairs. (35) Tergum 1 with punctures of median area smaller than on scutum, larger than in *rozeni,* dense, fairly regularly spaced, 1 pwa or less.

MALE. Length, 7.3 mm; forewing length, 4.8 mm; hindwing length, 3.4 mm; clypeal length, 0.52 mm; scutal length, 1.27 mm.

Head. Yellow areas: (1) paraocular area below diagonal line originating on outer subantennal suture at level of middle of antennal socket (or below) and extending to lower margin of facial fovea ending on orbit slightly above level of lower border of facial fovea; (6) as in *rozeni*. (7) Scape entirely black (basal ventral dot or streak of yellow to a basal, ventral, narrow yellow stripe strongly attenuate apically); a dot on lateroventral surface of flagellomere 1. (10) As in female. (13) Orbital convergence ratio as 1.51:1.14,1.33. (14) As in *rozeni*. (15) Head width to head length as 2.33:1.63,1.43. (17) Eye length, mio, and flagellar length as 1.21:1.14:1.62. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.43:0.43:0.31:0.34. (19) Ocellolabral greater than clypeal width, 1.34:1.14,1.18. (20) Clypeocellar to outer subantennal sutural identical to that in *rozeni,* 0.82:0.71,1.14. (21) N. A., measured on paratype: basal labial palpomere about 2.4 times length of others combined. (22) Flagellar length about 3.1 times length of scape, 1.62:0.53.

Mesosoma. (24) As in *rozeni,* except scutal and scutellar short hairs fulvous, long hairs whitish (fulvous, or brown as seen from behind). (25) Scutal disc with punctures larger than in *rozeni* or *chlorops,* mostly 0.5 pwa (or less), interspaces shiny. (26) Dorsal enclosure of propodeum with fewer, higher ridges than that of *rozeni,* median ridges more vermiform and lateral ridges less straight than those of *rozeni*. (27) As in *rozeni*. (28) Middle leg yellow as in *rozeni,* but tibia with anterior surface splotched with brown; lengths of tibia, basitarsus, and apicotarsus about as in *rozeni,* 1.02:0.85:1.09. (29) Hind leg yellow as in *rozeni* but slightly darker, apicotarsus brown. (32) Marginal cell 6-9 greater than, and 3-4 less than 9-wt, 0.99:0.83:0.90.

Metasoma. (34) Suberect hairs of disc of terga 4-5 brownish. (35) Tergum 1 with punctures of median area subequal to those on scutum, larger than those of *rozeni,* contiguous, becoming no more than 0.5 pwa laterad, interspaces shiny. (38) Plane of each ventral prong of sternum 6 perpendicular to surface of sternum whereas ventral prongs of other species of *Calliopsima* are tilted towards sagittal plane of body.

TYPE MATERIAL. Holotype male, from Rustler Park (near Apache), Chiricahua Mts., Cochise County, Arizona, Sept. 5, 1962 (J. G. Rozen, M. Statham, S. J. Hessel), and allotype female, from Portal (5 mi. W.), S.W.R.S., Cochise County, Arizona, 5400 ft., September 3, 1962 (J. G. Rozen, M. Statham), are at the American Museum of Natural History.

In addition 17 male and 28 female paratypes are from the following localities: ARIZONA: Montezuma Pass, Huachuca Mountains, Cochise Co., 6500 ft.; Portal (5 mi. W.); Rustler Park, Chiricahua Mountains, Cochise Co., 8500 ft. CHIHUAHUA: Santa Barbara, 6200 ft.

DISCUSSION AND DISTRIBUTION. An apparent case of interspecific mating with male *rozeni* is discussed above under that species. The one record from Mexico indicates that *crypta* is not strictly an endemic species of southeastern Arizona.

FLOWER RECORDS. *Cirsium*, *Helianthus*, and *Heterotheca subaxillaris*. *Calliopsis crypta* shares *Helianthus* and *Heterotheca* flowers with both *C. rozeni* and *C. pectidis*.

CALLIOPSIS (CALLIOPSIMA) CHLOROPS Cockerell

(Figs. 95-98; Map 6)

Calliopsis chlorops Cockerell, 1899, *in* Cockerell and Porter, Ann. Mag. Nat. Hist., (7)4:413, male; Cockerell and Atkins, 1902, Ann. Mag. Nat. Hist., (7)10:44; Cockerell, 1906, Trans. Amer. Ent. Soc., 32:300; 1908, Canad. Ent., 40:148; 1921, Amer. Mus. Novitates, 24:14.

This species has affinities with *coloratipes*, but the preponderance of morphological similarities are with *crypta* and *unca* from which it is differentiated as discussed under those species.

FEMALE. Length, 7.9 mm; forewing length, 5.6 mm; hindwing length, 3.65 mm; clypeal length, 0.56 mm; scutal length, 1.34 mm.

Head. Yellowish areas: (1) paraocular area as described for subgenus, sinuous line originating at about middle of outer subantennal suture, ending on orbit slightly below level of middle of facial fovea; (2) clypeus, with two longitudinal brown, to black, bars arising above apical margin of disc, or on apical margin, at angles of median emargination, reaching upward close to, to contacting, frontoclypeal suture along subantennal plate and supraclypeal area; frontoclypeal suture black; (3) labrum entirely, to only on median portion of labral plate; (5) absent on subantennal plate, to almost imperceptible dot at 30×; (6) mandible basal half. (7) Flagellomeres 1-3 dark ventrally, with tiny dot of tan, flagellomere 4 tan ventrally. (8) Hair of vertex fulvous. (10) Punctures beside lower half of frontal line smaller than those of *crypta*, larger than those of *coloratipes*, 1 pwa or more, interspaces dull. (13) Orbital convergence ratio as 1.51:1.48,1.02. (14) Galea shiny basally, finely pebbled, dull apically. (15) Head width to head length as 2.57:1.72,1.49. (17) Eye length, mio, and flagellar length as 1.29:1.48:1.43. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.46:0.46.037:0.36. (19) Ocellolabral greater than clypeal width, 1.50:1.41,1.06. (20) Clypeocellar to outer subantennal sutural as 0.94:0.78,1.20. (21) Basal labial palpomere 2.8 times length of others combined. (22)Flagellar length about 2.2 times length of scape, 1.43: 0.65.

Mesosoma. (23) Yellowish areas: apex pronotal lobe; scutellar crest. (24) Scutal and scutellar longer hairs fulvous (to amber). Shorter hairs more plumose than those of *crypta* but scutal surface readily visible. (25) Scutal disc with punctures slightly larger than on frons, deep, crowded, contiguous to 0.5 pwa, interspaces dull. (26) Dorsal enclosure of propodeum with fine, longitudinally vermiform ridges, interspaces shiny, medial portion prolonged posteriorly, posterior border carinate. (27) Foreleg yellowish at dorsal apex of femur, knee of tibia and adjacent area subequal to it. (28) Spur length slightly more than half length of middle basitarsus, 0.44:0.83. (30) Tegula colorless to pale straw color. Humeral plate yellowish apically. (31) Stigma testaceous. (32) Marginal cell 6-9 greater than, and 3-4 less than 9-wt, 1.24: 0.99:1.05.

Metasoma. (34) As in *crypta* but brown hairs often absent. (35) Tergum 1 with punctures of median area larger than on scutum, usually sparsely, irregularly distributed, but rarely relatively regularly distributed medially about 1-2 pwa, interspaces highly polished, mirror-like.

MALE. Length, 5.3 mm; forewing length, 4.1 mm; hindwing length, 2.85 mm; clypeal length, 0.51 mm; scutal length, 1.05 mm.

Head. Yellow areas: (1) paraocular area below diagonal line originating at a point on outer subantennal suture fourth its length below its summit (or from upper end of suture) and extending tangent to facial fovea ending on orbit slightly above level of lower border of facial fovea (to about middle); (5) subantennal plate in some cases with a black triangular area in lowermost outer corner including anterior tentorial pit; (6) mandible basal half; (7) scape, a tiny basal dot (to narrow band or streak reaching as high as middle of scape to all brown). (10) Punctures beside lower half of frontal line of moderate size, smaller than those of *rozeni, unca,* and *crypta,* larger than those of *azteca, coloradensis,* or *pectidis* group, 0.5-1.5 pwa, interspaces shiny. (13) Orbital convergence ratio as 1.29:1.02,1.27. (14) Galea lightly pebbled, dull, tip narrowly rounded. Galeal gap about half length of galea exposed beyond closed mandibles, (0.22:0.48). (15) Head width to head length as 1.96:1.41,1.39. (17) Eye length, mio, and flagellar length as 1.07:1.02:1.38. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.44:0.44: 0.27:0.31. (19) Ocellolabral greater than clypeal width, 1.22:0.97,1.26. (20) Clypeocellar to outer subantennal sutural as 0.71:0.60,1.20. (21) Basal labial palpomere 2.4 times length of others combined. (22) Flagellar length about 2.9 times length of scape, 1.38:0.48.

Mesosoma. (24) Scutal and scutellar hair grayish (to fulvous), longer hairs dark in some specimens. Shorter hairs not so dense nor so plumose as to hide scutal surface. (25) Scutal disc punctures of moderate size, smaller than in *crypta,* mostly contiguous, interspaces shiny. (26) Dorsal enclosure of propodeum concave inward, declivous, bearing distinct, fine, relatively straight, ridges, median portion with vermiform ridges (in some cases). (27) Foreleg with yellow on anterior dorsoapical third (to half) of femur, anterior surface of tibia, all of basitarsus, apicotarsus testaceous. (28) Middle leg colored like foreleg but femoral yellow reduced to sixth (to fourth) of femur; lengths of tibia, basitarsus, and apicotarsus as 0.82:0.68:0.78. (29) Hind leg colored like foreleg but posterior surfaces of tibia and basitarsus all brown (to about four-fifths brown). (32) Marginal cell 6-9 and 3-4 greater than 9-wt, 0.92:0.85:0.80.

Metasoma. (35) Tergum 1 with punctures of median area larger than those of scutum, smaller than those of *crypta* or *rozeni,* deep, about 0.5 pwa, interspaces shiny.

TYPE MATERIAL. Holotype male, from Las Vegas, New Mexico, Aug. 9 (W. Porter), on *Grindelia squarrosa,* is at the University of California, Riverside. A microscope slide of the mouth parts, U. S. N. M. type slide No. 2390, is in the United States National Museum. The above description of the female is principally based on a specimen from Morley, Colorado. The male holotype is exceptionally small.

DISTRIBUTION. The species occurs in the Front Range of the Rocky Mountains from northern New Mexico to northern Wyoming, in the eastern part of the Great Basin, and the upper and middle portion of the Colorado Plateau. It is allopatric with *unca* and *crypta,* but in the western and southern part of its range it is sympatric with *coloratipes,* and also largely with *coloradensis.* It has been collected between July 10 at Petersboro, Utah, and Sept. 27 at Embudo, New Mexico. The highest elevations for it are 9300 and 9200 ft. at Ward, Colorado, and at Warner Ranger Station near Moab, Utah, respectively.

In addition to the type, approximately 115 males and females were examined from the following localities: ARIZONA: Del Rio Verde River vicinity, Yavapai Co.; Eagar; Flagstaff, Coconino Co.; Kirkland, Yavapai Co.; Prescott; Springerville (32 mi. W.), Apache Co. COLORADO: Boulder, 5500 ft.; Coaldale, 7800 ft.; Colorado Springs; Cortez; Durango; Florissant; Manitou; Meeker, 6200 ft.; Morley; Peaceful Valley; Ute Creek, Sage Flats; Ward, 9300 ft. IDAHO: Downey; Franklin, Franklin Co.; NEVADA: Ely (9 mi. W.); Glorieta; Las Vegas; Pecos; Raton; Santa Fe. UTAH: Aspen Grove; Ballard; Devils Slide, Summit Co.; Garfield; Logan; Magna; Moab (28 mi. E.S.E.), Warner Ranger Station, Grand Co., 9200 ft.; Morgan, Morgan Co.; Murray; Petersboro, Cache Co.; Salt Lake City, 5000 ft.; Sandy, Salt Lake Co.; Spanish Fork, Utah Co.; Wellsville, Cache Co. WYOMING: Wheatland; Yellowstone National Park.

FLOWER RECORDS. *Haplopappus gracilis, Chrysopsis, Grindelia squarrosa, Medicago sativa, Ratibida, Verbesina, Viguiera annua.*

CALLIOPSIS (CALLIOPSIMA) COLORATIPES Cockerell

(Figs. 99-192; Map 5)

Calliopsis flavifrons race *coloratipes* Cockerell, 1898, Bull. Denison Univ. Sci. Labs., 11:52, male; *idem,* Bull. Univ. New Mexico, 1:52.

Calliopsis coloradensis coloratipes; Cockerell, 1900, Entomologist, 33:64, female; *idem,* 1906, Trans. Amer. Ent. Soc., 32:300.
Calliopsis coloratipes; Cockerell, 1908, Canad. Ent., 40:148; *idem,* 1921, Amer. Mus. Novitates, 24:14.

Outside of its own group this species is close to *coloradensis* and has morphological similarities to *chlorops.* Within its own group it is closest to *deserticola.* The male is easily distinguished by the mesally-tilted, conspicuous ventral prongs of sternum 6 whereas prongs are absent in *deserticola.* The female is separated from *deserticola* only with difficulty, but the dorsal enclosure of the propodeum is very shiny in *coloratipes* and quite dull in *deserticola* (20×); moreover, the ridges are straight and 1-2 ridge widths apart in *coloratipes,* but are vermiform and run together in *deserticola.*

FEMALE. Length, 7.6 mm; forewing length, 5.3 mm; hindwing length, 3.71 mm; clypeal length, 0.54 mm; scutal length, 1.36 mm.

Head. Cream colored areas: (1) paraocular area as described for subgenus, dorsal boundary a straight, to sinuous, line originating at upper end of outer subantennal suture, ending on orbit at about level of middle of facial fovea; (2) clypeus as in *chlorops* except many specimens without brown bars, with only two small, brown clypeal dots; labrum all yellow to all brown; (5) subantennal plate except for subtriangular black area at lower end of outer subantennal suture, to mostly dark; (6) mandible basal half. (7) Flagellomeres 1-4 black with tiny amount of tan. (8) Hair of vertex fulvous. (10) Punctures beside lower half of frontal line fine, 2-4 pwa, interspaces dull (to shiny). (13) Orbital convergence ratio as 1.60:1.50,1.07. (14) Galea finely pebbled, dull. Galeal length 1.10. (15) Head width to head length as 2.52: 1.72,1.46. (17) Eye length, mio, and flagellar length as 1.26:1.50:1.31. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.48:0.46:0.39:0.36. (19) Ocellolabral greater than clypeal width, 1.46:0.94, 1.56. (20) Clypeocellar to outer subantennal sutural as 0.92:0.80,1.15. (21) Basal labial palpomere 2.4 times length of others combined. (22) Flagellar length about 2.3 times length of scape, 1.31:0.56.

Mesosoma. (23) Cream colored areas: apex pronotal lobe; scutellar crest. (24) Scutal and scutellar longer hairs fulvous (to amber). Shorter hairs more plumose than those of *chlorops,* in some cases hiding scutal surface. (25) Scutal disc with punctures fine, about twice diameter of those on frons, finer than in *chlorops,* deep, crowded, mostly 0.5 pwa, interspaces shiny. (26) Dorsal enclosure of propodeum with relatively straight shiny ridges separated by 1-2 ridge widths, interspaces shiny, median portion prolonged only slightly, posterior border carinate; a highly polished, impunctate band on vertical surface of propodeal triangle adjacent to enclosure. (27) Foreleg cream colored at dorsal apex of femur and basal third to half of dorsal tibial surface. (28) Middle leg colored like foreleg but about half as much cream color. Spur length less than half length of middle basitarsus, 0.44:0.92. (30) Tegula testaceous. Humeral plate cream colored apically. (31) Stigma testaceous. (32) Marginal cell 6-9 and 3-4 both greater than 9-wt, 1.12:1.00:0.94.

Metasoma. (34) Suberect hairs of discs of terga 4-5 white. (35) Tergum 1 with punctures of median area smaller than on scutum, finer than in *chlorops,* very sparsely, irregularly distributed to virtually absent, tergum highly polished, mirror-like.

Male. Length, 6.5 mm; forewing length, 4.4 mm; hindwing length, 4.0 mm; clypeal length, 0.53 mm; scutal length, 1.22 mm.

Head. Yellowish areas: (1) paraocular area below diagonal line originating at upper end of outer subantennal suture (to fourth length of suture below upper end), ending on orbit below level of middle of facial fovea; (6) mandible basal half; (7) scape anterior surface except for narrow brown strip mesally, slightly widened mesoapically. (10) Punctures beside lower half of frontal line extremely fine, 1-2 pwa, interspaces shiny. (13) Orbital convergence ratio as 1.45:1.09,1.33. (14) Galea pebbled, dull apically, tip narrowly rounded. Galeal gap about half length of galea exposed beyond closed mandibles, 0.22:0.44. (15) Head width to head length as 2.26:1.55,1.46. (17) Eye length, mio, and flagellar length as 1.24:1:09:1.45. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.46:0.39:0.26:0.31. (19) Ocellolabral greater than clypeal width, 1.28:1.16,1.10. (20) Clypeocellar to outer subantennal sutural as 0.75:0.66,1.13. (21) Basal labial palpomere about 2.2 times length of others combined. (22) Flagellar length about 2.9 times length of scape, 1.45:0.49.

Mesosoma. (24) Scutal and scutellar shorter hairs fulvous, plumose, tending to hide scutal surface. (25) Scutal disc with punctures smaller than those of *chlorops,* mostly 0.5 pwa, interspaces shiny. (26) Dorsal enclosure of propodeum as in *chlorops* except ridges finer, straighter, much shinier; median portion barely (or not) produced posteriorly, medial length about 0.26, or about 1.5 mow. (27,28,29) As in *chlorops* but posterior surface of hind tibia sometimes half yellow basally; lengths of tibia, basitarsus, and apicotarsus as 0.87:0.77:0.77. (32) Marginal cell 6-9 greater than, and 3-4 subequal to 9-wt, 1.04:0.83:0.82.

Metasoma. (35) Tergum 1 with punctures of median area smaller than those of scutum, smaller than those of *chlorops,* about 0.5 pwa, interspaces shiny.

Type Material. Holotype male, from Mesilla, New Mexico, Aug. 12 (T. D. A. Cockerell), is at the University of California, Riverside. The above description of the female is principally based on a specimen of a pair taken *in copulo* at Mesilla Park, New Mexico, Sept. 1 (T. D. A. Cockerell), on *Bigelovia wrighti.*

DISTRIBUTION. The southern Great Basin and the Colorado Plateau. Its range is partially sympatric with *coloradensis* and *chlorops,* but it is wholly allopatric with *deserticola* and *pugionis.* It has been collected from July 2, at Carson City, Nevada, to Oct. 23, at Phoenix, Arizona, a distinct difference from its nearest relative, *deserticola,* which is a spring bee.

In addition to the type approximately 41 specimens have been examined from the following localities: ARIZONA: Apache (6 mi. S.E.), Skeleton Canyon; Cochise (2 mi. N.); Florence; Phoenix; San Xavier Mission; Tempe; Tucson; Willcox; "Southern Arizona." NEVADA: Carson City, Ormsby Co.; Yerrington (8.5 mi. S.), Lyon Co. NEW MEXICO: Jemez Springs, Sandoval Co.; Mesilla; Mesilla Park. UTAH: Hinckley, Millard Co.; Milford, Beaver Co.; Topaz, Juab Co.

GEOGRAPHIC VARIATION. Specimens from Utah and Nevada have a longer galea, a more protruding clypeus in the female, and tend to be darker than those from Arizona and New Mexico. Two male specimens from Willcox, Arizona, Aug. 1956 (Ellen Ordway) and 1958 (E. G. Linsley), the latter on *Baileya pleniradiata,* differ from other *coloratipes* by having white face markings with scape yellow, a combination also found in *squamifera.*

DISCUSSION. *C. coloratipes* appears to have given rise to *deserticola* in the southwestern extreme of its range. The basal cream color of the mandible and the sparsely punctate median portion of tergum 1 indicate a relationship to *chlorops.* The cream colored subantennal plates of *coloratipes* are correspondingly black in *chlorops* and either black or partly cream-colored in *coloradensis.* The smaller punctures of *coloratipes* and the straight-ridged character of the dorsal enclosure of the propodeum betoken a relationship with *coloradensis.*

FLOWER RECORDS. *Asclepias subverticillata, in copulo* on both *Bigelovia hartwegi* and *B. wrightii, Chrysothamnus* sp., *C. nauseosus consimilis, Heterotheca.*

CALLIOPSIS (CALLIOPSIMA) DESERTICOLA, new species

(Figs. 103-106; Map 5)

The specific name is compounded from the Latin *desertum,* a waste place, and *-cola,* dwelling in, in reference to its occurrence in the Colorado Desert in California. The species was recognized as new by P. H. Timberlake a number of years ago, and his manuscript name is used here.

Judged by the male it is closest to *pugionis,* but judged by the female it is closest to *coloratipes.* The male is distinguished by the ratio of the length of galea exposed beyond closed mandibles to the galeal gap being 3.5-4.5, whereas in *pugionis* it is 2-3; *C. deserticola* is easily distinguished from *coloratipes* by the absence of ventral prongs on sternum 6. The female is easily distinguished from *pugionis* by its cream colored, rather than deep lemon yellow, face. It is distinguished from *coloratipes* only with difficulty as discussed under that species.

FEMALE. Length, 7.5 mm; forewing length, 4.8 mm; hindwing length, 3.30 mm; clypeal length, 0.60 mm; scutal length, 1.22 mm.

Head. Pale yellowish areas: (1) paraocular area, as described for subgenus, sinuous line originating about middle of outer subantennal suture (lower than in *coloratipes!*) and ending on orbit about 0.33 (or less) times length of facial fovea above its lower border; (2) as in *chlorops;* (3) labrum entirely; (5) subantennal plate a spot touching lower border of antennal socket; (6) mandible basal half. (7) As in *coloratipes* but lighter. (8) Hair of vertex pale fulvous. (10) Punctures beside lower half of frontal line exceedingly fine, slightly finer than those of *pugionis,* shallow, 1-3 pwa, interspaces highly polished. (13) Orbital convergence ratio 1.45:1.38,1.05. (14) Galea very finely pebbled, moderately shiny. Galeal length 1.19. (15) Head width to head length as 2.36:1.73,1.36. (17) Eye length, mio, and flagellar length as 1.26:1.38:1.31. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.43:0.41:0.37:0.37. (19) Ocellolabral greater than clypeal width, 1.48: 1.45,1.02. (20) Clypeocellar to outer subantennal sutural as 0.88:0.77,1.15. (21) Basal labial palpomere about 2.2 times length of others combined. (22) Flagellar length about 2.3 times length of scape, 1.31:0.56.

Mesosoma. (23) Yellowish areas: apex pronotal lobe (in some cases); scutellar crest. (24) Scutal and scutellar hairs pale fulvous. Shorter hairs as plumose as in *chlorops,* tending to hide scutal surface; longer hairs shorter, more plumose than in *coloratipes.* (25) Scutal disc with punctures finer, shallower and farther apart, 1-2 pwa, than in *coloratipes,* interspaces shiny. (26) Dorsal enclosure of propodeum with numerous close-packed, ultra fine, vermiform ridges, dull (20×); median portion scarcely (or not at all) prolonged posteriorly, posterior border non-carinate; an impunctate, highly polished adjacent band of propodeal triangle present as in *coloratipes.* (27) Foreleg yellowish at dorsal apex of femur, knee of tibia and adjacent area subequal to it. (28) Middle leg colored like foreleg but about half as much yellow color; spur length about half of length of middle basitarsus, 0.43:0.85. (30) Tegula testaceous. Humeral plate yellowish apically. (31) Stigma brown. (32) Marginal cell 6-9 and 3-4 both greater than 9-wt, 1.12:1.00:0.94.

Metasoma. (34) Tergal hair bands sparser, hairs slimmer, less plumose than in *coloratipes.* Suberect hairs of terga 4-5 white. (35) Tergum 1 with punctures of median area much smaller than on scutum, finer than in *coloratipes,* very sparsely irregularly distributed to virtually absent; tergum highly polished, mirror-like.

MALE. Length, 7.3 mm; forewing length, 4.8 mm; hindwing length, 3.25 mm; clypeal length, 0.56 mm; scutal length, 1.21 mm.

Head. Yellow areas: (1) paraocular area as in *coloratipes* but dorsal boundary line may extend along orbit only to level of lower border of facial fovea; (5) subantennal plate sometimes with yellow reduced by subtriangular black area around anterior tentorial pit; (6) mandible basal half; (7) scape as in *coloratipes,* flagellomere 1 yellow ventrally. (10) Punctures beside lower half of frontal line exceedingly fine, larger than those of *azteca* or *deserticola,* 1-2 pwa, interspaces shiny. (13) Orbital convergence ratio as 1.39:1.16,1.21. (14) Galea pebbled, dull, tip broadly rounded. Galeal gap about fourth of length of galea exposed beyond closed mandibles, 0.15:0.68. (15) Head width to head length as 2.26:1.72,1.31. (17) Eye length, mio, and flagellar length as 1.22:1.16:1.55. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.46:0.39:0.27:0.34. (19) Ocellolabral greater than clypeal width, 1:38:1.22, 1.13. (20) Clypeocellar to outer subantennal sutural as 0.82:0.71,1.14. (21) Basal labial palpomere about 2.1 times length of others combined. (22) Flagellar length about 3.1 times length of scape, 1:55:0.49.

Mesosoma. (24) Scutal and scutellar hair grayish white, shorter hairs somewhat plumose, tending to hide scutal surface as in *coloratipes.* (25) Scutal disc with punctures smaller than in *coloratipes,* mostly 1-1.5 pwa, interspaces shiny. (26) Dorsal enclosure of propodeum declivous, dull, bearing very fine, obscurely vermiform, ridges; enclosure shorter than others in its group, about 1 mow medially, median portion not produced posteriorly. (27) Foreleg as in *coloratipes* but posterior surface of basitarsus sometimes testaceous. (28) Middle leg with yellow on dorsoapical fourth (to third) of femur, a stripe along tibia and basitarsus anteroventrally, apicotarsus testaceous; light coloration sometimes as unevenly splotched areas; length of tibia, basitarsus, and apicotarsus as 0.99:0.88:0.95. (29) Hind leg colored like middle leg but less extensive yellow, absent from basitarsus (in some cases), tarsus brown; light coloration sometimes as unevenly splotched areas. (32) Marginal cell 6-9 and 3-4 both greater than 9-wt, 1.12:0.94:0.82.

Metasoma. (35) Tergum 1 with punctures of median area subequal to those of scutum, smaller than those of *coloratipes,* 0.5-1 pwa, interspaces shiny. Declivity of tergum 1 with more than 25 fine, deep, distinct punctures, mostly grouped laterally below dorsal margin.

Type Material. Holotype male, from Painted Gorge, southeast corner of Anza Desert State Park north of Coyote Wells, Imperial Co., California, April 12, 1949 (R. A. Hoch), on *Encelia farinosa,* and allotype female, Box Canyon, near Mecca, Riverside Co., April 14, 1935 (P. H. Timberlake), on *Encelia farinosa,* are at the University of California, Riverside. Paratypes are at the Snow Entomological Museum of The University of Kansas and in the author's collection.

In addition, 12 male and 4 female paratypes are from the following localities: California: Box Canyon, Riverside Co., 5 males, 3 females, April 14, 1935 (P. H. Timberlake), on *Encelia farinosa;* Needles, San Bernardino Co., 3 males, 2 females, April 3, 1951 (P. D. Hurd), 2 males, same data except (E. G. Linsley); Painted Gorge, Imperial Co., 2 males, April 12, 1949 (R. A. Hoch), on *Encelia farinosa.*

CALLIOPSIS (CALLIOPSIMA) PUGIONIS Cockerell

(Figs. 107-110; Map 5)

Calliopsis pugionis Cockerell, 1925, Proc. California Acad. Sci., (4) 14:197, female.

The specific name is from the Latin *pugio,* meaning dagger, and refers to the dagger-shaped, yellow median line on the clypeus of the female holotype. The species is closest to *deserticola. C. pugionis* is distinguished in the male by the very deep, distinct, large, contiguous punctures of the median portion of tergum 1 whereas those of *deserticola* are not nearly so deep nor distinct, are of medium size and are mostly 1 pwa. The female is easily distinguished by the deep lemon yellow facial coloring in contrast with the cream or pale yellowish facial coloring of *deserticola.* Both sexes are distinguished from *deserticola* by the galeal gap being greater than the middle ocellar width, and by the galeal length being only about six-sevenths that of *deserticola.*

FEMALE. Length, 8.0 mm; forewing length, 5.5 mm; hindwing length, 3.67 mm; clypeal length, 0.58 mm; scutal length, 1.32 mm.

Head. Deep lemon yellow areas: (1) paraocular area as described for subgenus, sinuous line originating slightly above middle of outer subantennal suture, ending on orbit at level of lower third or less of facial fovea; (2) clypeus with wide, twin vertical brown or black bars arising near angles of median apical emargination, frequently joined by subapical brown band, reaching close to frontoclypeal suture, the bars separated by a dagger-shaped yellow area less than 1 mow in width; brown bars strikingly similar to those in *coloradensis;* (3) labrum almost entirely to absent; (5) subantennal plate with small spot, or absent; (6) mandible basal fifth to absent. (7) Flagellomeres 1-4 brown and tan ventrally. (8) Hair of vertex amber with brownish tips. (10) Punctures beside lower half of frontal line exceedingly fine, finest in the subgenus, deep, 2-4 pwa, interspaces highly polished. (13) Orbital convergence ratio as 1:58:1.48,1.07. (14) Galea finely pebbled, dull. Galeal length about six-sevenths that of galeal length of *deserticola,* 1.02. (15) Head width to head length as 2.48:1.80,1.38. (17) Eye length, mio, and flagellar length as 1.36:1.48:1.33. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.49:0.48:0.41:0.37. Antennocular equal to or greater than interantennal! (19) Ocellolabral equal (to subequal) to clypeal width, 1.50:1.50, 1.00. (20) Clypeocellar to outer subantennal sutural as 0.92:0.78,1.17. (21) Basal labial palpomere about 2.5 times length of others combined. (22) Flagellar length about 2.2 times length of scape, 1.33:0.60.

Mesosoma. (23) Yellow areas: apex pronotal lobe; scutellar crest (sometimes), or testaceous. (24) Scutal and scutellar longer hairs amberish, apical portion frequently brownish. Shorter hairs plumose as in *deserticola,* tending to hide scutal surface; longer hairs as in *deserticola.* (25) Scutal disc with punctures finest in subgenus, deep, 1 pwa or less, interspaces shiny. (26)

Dorsal enclosure of propodeum with somewhat fewer, more distinct, very fine vermiform ridges, usually dull but shinier, than in *deserticola;* median portion slightly prolonged posteriorly, posterior border carinate; impunctate, polished adjacent band of propodeal triangle narrower than in *deserticola.* (27) Foreleg deep lemon yellow with same extent as yellowish on foreleg of *deserticola.* (28) Middle leg deep lemon yellow with same extent as yellowish on middle leg of *deserticola;* spur length half of length of middle basitarsus, 0.44:0.88. (30) Tegula testaceous. Humeral plate yellow to testaceous apically. (31) As in *deserticola.* (32) Marginal cell 6-9 greater than, and 3-4 less than 9-wt, 1.09:0.90:1.04.

Metasoma. (34) Tergal hair bands denser than in *deserticola.* Suberect hairs of terga 4-5 white. (35) Tergum 1 with punctures of median area much smaller than on scutum, about same size or larger than those in *deserticola,* very sparsely, irregularly distributed to virtually absent; tergum highly polished, mirror-like.

MALE. Length, 7.5 mm; forewing length, 5.3 mm; hindwing length, 3.6 mm; clypeal length, 0.61 mm; scutal length, 1.34 mm.

Head. Deep lemon yellow areas: (1) as in *deserticola;* (6) mandible basal half; (7) scape as in *deserticola* (variable, to only basal spot with streak extending dorsally from it). (10) Punctures beside lower half of frontal line larger than those of *deserticola,* smaller than those of *coloratipes,* mostly 1 pwa, interspaces shiny. (13) Orbital convergence ratio as 1.58:1.22,1.29. (14) Galea pebbled, dull, tip broadly rounded. Galeal gap about half length of galea exposed beyond closed mandibles, 0.26:0.58. (15) Head width/head length as 2.52:1.87,1.34. (17) Eye length, mio, and flagellar length as 1.43: 1.22:1.62. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.44:0.46:0.27:0.36. (19) Ocellolabral greater than clypeal width, 1.50:1.39, 1.07. (20) Clypeocellar to outer subantennal sutural as 0.88:0.75,1.18. (21) Basal labial palpomere about 2.4 times length of others combined. (22) Flagellar length about 3.0 times length of scape, 1.62:0.54.

Mesosoma. (24) Scutal and scutellar shorter hairs grayish white, non-plumose, not hiding scutal surface as in *deserticola.* (25) Scutal disc with punctures larger than in deserticola, mostly 1-1.5 pwa, interspaces shiny. (26) Dorsal enclosure of propodeum declivous, dull, bearing fine (but coarser than in *deserticola*), obscurely vermiform ridges; enclosure not produced posteriorly but long, length about 0.31, or 1.7 mow. (27) Same note as for *deserticola.* Foreleg colored like that of *deserticola* but basitarsus may be brown. (28) Middle leg colored like that of *deserticola* except tarsus may be brown; lengths of tibia, basitarsus, and apicotarsus as 1.12:0.92:0.99. (29) Hind leg colored like that of *deserticola.* (32) Marginal cell 6-9 longer than, and 3-4 shorter than 9-wt, 1.12:0.90:0.94.

Metasoma. (35) Tergum 1 with punctures of median area larger, deeper than those of scutum, very coarse, larger than those of *coloratipes* or *deserticola,* contiguous, interspaces shiny, but tergum *in toto* rather dull. Declivity of tergum 1 with more than 25 coarse deep, distinct punctures, mostly grouped about third of length of declivity below the dorsal margin.

TYPE MATERIAL. Holotype female, from Soboba Springs, Riverside Co., California, June 3, 1917 (E. P. Van Duzee), is Type No. 1657 at the California Academy of Sciences, San Francisco. The above description of the female is principally based on a specimen from Palm Springs, Taquitz Canyon, California, April 16, 1938 (R. M. and G. E. Bohart) while that of the male is based on a specimen from Riverside, California, May 3, 1928 (P. H. Timberlake), on garden *Coreopsis.*

DISTRIBUTION. Known only from San Diego, Riverside, and Los Angeles counties in southwestern California. It is a spring bee collected from April 6 to June 14.

I have not examined the type but have studied approximately 70 males and females from the following localities: CALIFORNIA: Acton, Mint Canyon, Los Angeles Co., May 3, 1936 (E. G. Linsley), on *Chaenactis;* Dulzura, June 14, 1917; Newhall, Los Angeles Co., April 20, 1940 (R. M. Bohart); Palm Springs, Andreas Canyon, Riverside Co., March 24 and April 11, 1936 (P. H. Timberlake), *Encelia farinosa; idem,* April 10, 1936, *Encelia farinosa,* April 6, 1939 (both C. D. Michener); *idem,* April 7, 1940 (R. M. Bohart); Palm Springs, Palm Canyon, April 15, 1938 (R. M. and G. E. Bohart), *Encelia farinosa;* Palm Springs, Taquitz Canyon, April 16, 1938 (R. M. and G. E. Bohart); Gavilan (between Perris and Lake Mathew), Riverside Co., 2200 feet, May 15, 1936 (P. H. Timberlake), *Chaenactis artemisiaefolia; idem,* but no altitude given, April 18, 1940 (P. H. Timberlake), *Oenothera ocitebrana;* Riverside, April 25, 1929, April 28, 1934, Aug. 5, 1938, all on *Chaenactis glabrisscula,* May 3, 1928, *in copulo* on garden *Coreopsis,* May 17, 1929, June 7, 1927, both on *Coreopsis,* May 12, 1932, May 13, 15, 16, 1929, all on *Coreopsis lanceolata,* May 31 and June 9, 1927, *Hemizonia wrighti* (all P. H. Timberlake).

DISCUSSION. Although Cockerell considered this species as nearest to *coloradensis* it is really a rather distant relative. The color pattern of the legs of the male is very close to that of *deserticola,* and the color patterns of the legs of both species are remarkably similar to those of *hurdi* and *kucalumea.* I believe that *pugionis* is a relict of a formerly widespread population of *deserticola.*

FLOWER RECORDS. *Chaenactis artemisiaefolia, C. glabrisscula, Coreopsis* (cultivated), *C. lanceolata, Encelia farinosa, Hemizonia wrighti, Oenothera ocitebrana.*

CALLIOPSIS (CALLIOPSIMA) HURDI, new species

(Figs. 111-114; Map 5)

This species, the largest one of the genus, is named for Dr. Paul D. Hurd, Jr., in grateful acknowledgement of his loans of many important specimens for my study of the genus.

The closest relative is *kucalumea* from which it is best distinguished by the key characters in couplet 24 for males, and in couplet 32 for females.

Females. Length, 9.8 mm; forewing length, 7.0 mm; hindwing length, 5.00 mm; clypeal length, 0.65 mm; scutal length, 1.78 mm.

Head. Pale yellow areas: (1) paraocular area as described for subgenus, sinuous line originating below middle of outer subantennal suture and ending on orbit at about level of third length of facial fovea above its lower border; (2) clypeus with wide, twin, vertical black bars arising on clypeal apex near angles of median apical emargination, reaching close to frontoclypeal suture, the bars separated by a finger of yellow 1 mow in width; color pattern similar to that of *coloradensis;* (3) absent on labrum; (5) absent on subantennal plate; (6) absent on mandible. (7) Flagellomeres missing. (8) Hair of vertex brown. (10) Punctures beside lower half of frontal line of medium size about the same size as those of *chlorops,* 1 pwa, interspaces shiny. (13) Orbital convergence ratio as 1.96:1.82,1.07. (14) Galea finely pebbled, slightly shiny. Galeal length greatly exceeding that of *kucalumea,* 1.39:0.99. (15) Head width to head length as 3.06:2.12,1.44. (17) Eye length to mio as 1.63:1.82, flagellum missing. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.49:0.58:0.49:0.46. (19) Ocellolabral less than clypeal width, 1.79:1.96,0.91. (20) Clypeocellar to outer subantennal sutural as 1.12:0.95,1.18. (21) Basal labial palpomere about 3.3 times length of others combined. (22) Length of scape 0.82, flagellum missing.

Mesosoma. (23) Yellow areas: absent from apex of pronotal lobe and scutellar crest. (24) Scutal and scutellar longer hairs black. (25) Scutal disc with punctures small, deep, crowded to contiguous, interspaces shiny, scutal surface completely visible from above. (26) Dorsal enclosure of propodeum relatively dull with many longitudinally vermiform, distinctly separated ridges; median portion prolonged posteriorly, posterior border carinate. (27) Foreleg with yellow tibial knee. (28) Spur length slightly more than half of length of middle basitarsus, 0.58:1.10. (30) Tegula brown. Humeral plate brown. (31) Wing brownish. Stigma brown. (32) Marginal cell 6-9 greater than, and 3-4 less than 9-wt, 1.48:1.16:1.33.

Metasoma. (34) Suberect hairs of disc of tergum 4 brown, of disc of tergum 5 smoky. (35) Tergum 1 with punctures of median area smaller than on scutum, absent from narrow band immediately behind declivity, 2 pwa, interspaces minutely roughened, dull. Area immediately behind declivity laterally, impunctate, high polished.

Male. Length, 8.0 mm; forewing length, 5.6 mm; hindwing length, 4.0 mm; clypeal length, 0.63 mm; scutal length, 1.44 mm.

Head. Yellow areas: (1) paraocular area below diagonal line originating slightly below middle of outer subantennal suture and ending on orbit at about level of lower border of facial fovea; (3) labrum except coarsely punctate apical area (to all yellow): (5) absent from subantennal plate (to yellow except for subtriangular black area around anterior tentorial pit); anterior tentorial pit smaller, more distinct than in other groups of *Calliopsima;* (6) mandible basal fourth (to almost absent). (7) Scape brownish black. (10) Punctures beside lower half of frontal line of moderate size, larger than in *chlorops,* mostly 1 pwa, interspaces shiny. (13) Orbital convergence ratio as 1.60:1.33,1.27. (14) Galea almost imperceptibly roughened (30×), shiny, tip narrowly rounded. Galeal gap fourth of length of galea exposed beyond closed mandibles, (0.17:0.68). (15) Head width to head length as 2.58:1.87, 1.38. (17) Eye length, mio, and flagellar as 1.36:1.33:1.75. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.44:0.51:0.32:0.39. Interocellar less than ocellocular! (19) Ocellolabral greater than clypeal width, 1.56:1.41, 1.11. (20) Clypeocellar to outer subantennal as 0.94:0.82,1.14. (21) Basal labial palpomere about 3.2 times length of others combined. (22) Flagellar length about 2.9 times length of scape, 1.75:0.61.

Mesosoma. (24) Scutal and scutellar shorter hairs grayish white, longer hairs brown; longer hairs of metanotum and propodeum more plumose than in *quadridentata* or *kucalumea.* (25) Scutal disc with punctures of moderate size about 0.017-0.025 in diam., deep, distinct, mostly less than 0.5-1 pwa, interspaces shiny. (26) Dorsal enclosure of propodeum subhorizontal, bearing strong distinct, straight, longitudinal ridges laterally with shiny interspaces; median portion with slightly vermiform ridges; median portion produced posteriorly; length about 0.24, or about 1.3 mow. (27) Same note as for *deserticola.* Foreleg colored like that of *pugionis* except light color less extensive, yellow confined to basal half of anterior surface of basitarsus. (28) Middle leg with yellow on tibial knee; lengths of tibia, basitarsus, and apicotarsus as 1.09:0.97:1.05. (29) Hind leg with yellow on disc of basitibial plate (absent sometimes) and irregular splotch and/or dot on anterior surface of tibia preapically (usually). (30) Tegula brown without yellow patch. Humeral plate brown. (32) Marginal cell 6-9 and 3-4 greater than 9-wt, 1.21: 1.07:0.88.

Metasoma. (35) Tergum 1 with punctures of median area subequal to those of scutum, size intermediate between those of *coloratipes* and *chlorops,* 0.5-1 pwa, interspaces shiny (anterior median portion sometimes finely roughened).

Type Material. Holotype male and allotype female, from Soyalo (7 mi. S.E.), Chiapas, (R. C. Bechtel and E. I. Schlinger), are at the University of California, Berkeley. Of four male paratypes, same data as above except Simojovel (4 mi. S.W.), two are at the California Academy of Sciences, San Francisco, one is at the Snow Entomological Museum of The University of Kansas, Lawrence, and one is in the author's collection.

Distribution. This species represents the southernmost record for the subgenus *Calliopsima.* Since habitats similar to those known for *Calliopsima* occur far south of this, and since I feel that *Calliopsima* is an intruder from South America, I anticipate discoveries of other species farther south when collections are made during the proper season.

CALLIOPSIS (CALLIOPSIMA) QUADRIDENTATA, new species

(Figs. 115-118; Map 5)

The specific name is compounded from the Latin words *quatuor,* four, and *dentata,* toothed, and is given in reference to the four tooth-like projections of the genital capsule, a condition unique in the genus and possibly in the Panurginae.

It is probably closest to *hurdi* but is easily separated from it by the yellow coloration on the anterior portion of the tegula and the more extensive yellow of the anterior surfaces of the middle and hind tibiae as well as the larger punctures of tergum 1 and larger ridges of the dorsal enclosure of the propodeum.

The male of this species is separated from *kucalumea* by the very long galea and labial palp as described in (14) and (21) below.

MALE. Length, 6.5 mm; forewing length, 5.1 mm; hindwing length, 3.60 mm; clypeal length, 0.56 mm; scutal length, 1.27 mm.

Head. Yellow areas: (1) paraocular area as in *hurdi* but boundary line ending on orbit slightly above level of lower border of facial fovea; (6) mandible basal half. (7) Scape brownish black. (10) As in *hurdi* but larger. (13) Orbital convergence ratio as 1.55:1.16,1.34. (14) Galea finely, distinctly pebbled, relatively shiny, tip narrowly rounded. Galeal gap about fourth of length of galea exposed beyond closed mandibles, 0.17:0.68. (15) Head width to head length as 2.33:1.72,1.38. (17) Eye length, mio, and flagellar length as 1.21:1.16:1.68. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.43:0.46:0.29:0.34. Interocellar less than ocellocular! (19) Ocellolabral greater than clypeal width, 1.41:1.16,1.22. (20) Clypeocellar to outer subantennal sutural as 0.85:0.70,1.22. (21) Basal labial palpomere of paratype 3.2 times length of others combined. (22) Flagellar length about 3.3 times length of scape, 1.68:0.51.

Mesosoma. (24) Scutal and scutellar shorter hairs grayish-white, not hiding scutal surface, longer hairs amberish with tips darkened. (25) Scutal disc with punctures slightly larger than in *hurdi,* deeper, more distinct, contiguous, interspaces shiny but scutum appearing rather dull (20×). (26) Dorsal enclosure of propodeum declivous, intermediate between *hurdi* and *kucalumea;* pattern of ridges as in *hurdi* except finer, closer; median portion, somewhat produced, length about 0.26, or 1.5 mow. (27,28,29) Front, middle, and hind legs colored like those of *pugionis.* (30) Tegula brown with yellow anterior patch. Humeral plate with tiny apical yellow dot. (31) Wing clear, stigma testaceous. (32) Marginal cell 6-9 and 3-4 both greater than 9-wt, 1.07:0.88: 0.78.

Metasoma. (34) As described for female of subgenus. (35) Tergum 1 with punctures of median area subequal to those of scutum, as large as those of *crypta,* but punctures of lateral area smaller than those of *crypta,* 0.5 pwa, interspaces shiny.

TYPE MATERIAL. Holotype male, from Lagos de Moreno, Jalisco, 6400 ft., Aug. 21, 1954 (C. D. Michener and party), is at the Snow Entomological Museum of The University of Kansas, Lawrence, and one male paratype, same data, is in the author's collection.

CALLIOPSIS (CALLIOPSIMA) KUCALUMEA, new species

(Figs. 119-122; Map 7)

The specific name is an acronym formed from Kansas University and California University Mexican Expeditions and is given to this species in recognition of the valuable specimens for this study which have come from several separate expeditions into Mexico made by the two universities.

The species is closest to *hurdi* and is best separated from it by the key characters in couplet 24 for males, and in couplet 32 for females.

FEMALE. Length, 9.0 mm; forewing length, 6.3 mm; hindwing length, 4.35 mm; clypeal length, 0.60 mm; scutal length, 1.68 mm.

Head. Pale yellow areas: (1) as in *hurdi;* (2) clypeus with twin black bars as in *hurdi* (to median portion of clypeus all black except streak of yellow along frontoclypeal suture bordering supraclypeal area); (3,5,6) as in *hurdi.* (7) Flagellomeres 1-2 black ventrally, 3-4 mostly black ventrally with some tan. (8) Hair of vertex fulvous, with brownish tips (all fulvous, or all brownish). (10) Punctures beside lower half of frontal line smaller than those of *hurdi,* deep, 1-2 pwa, interspaces shiny. (13) Orbital convergence ratio as 1.77:1.63,1.08. (14) Galea finely pebbled, slightly shiny. Galeal length much less than in *hurdi,* 0.99:1.39. (15) Head width to head length as 2:72: 1.96,1.39. (17) Eye length, mio, and flagellar length as 1.38:1.63:1.55. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.49:0.54:0.49:0.46. (19) Ocellolabral less than clypeal width, 1:60:1.63,0.98. (20) Clypeocellar to outer subantennal sutural as 1.00:0.88,1.13. (21) Basal labial palpomere about 2.3 times length of others combined. (22) Flagellar length about 2.2 times length of scape, 1.55:0.71.

Mesosoma. (23) As in *hurdi.* (24) Scutal and scutellar longer hairs amberish to brownish. (25) Scutal disc with punctures as in *hurdi,* scutal surface less visible than in *hurdi* because of greater plumosity of scutal shorter hairs. (26) Dorsal enclosure of propodeum slightly shinier than in *hurdi,* ridges fewer, straighter; median portion prolonged posteriorly; posterior border carinate. (27) Foreleg with yellow tibial knee. (28) Spur length more than half of length of middle basitarsus, 0.53:0.97. (30) Tegula brown. Humeral plate brown with apical yellow spot. (31) Wing brownish, clearer than in *hurdi*. Stigma brown. (32) Marginal cell 6-9 greater than, and 3-4 subequal to 9-wt, 1.38:1.17:1.16.

Metasoma. (34) Suberect hairs of disc of tergum 4 fulvous, of disc of tergum 5 mixed white and fulvous. (35) Tergum 1 with punctures of median area smaller than on scutum, deep, mostly less than 1 pwa.

MALE. Length, 7.2 mm; forewing length, 5.4 mm; hindwing length, 3.70 mm; clypeal length, 0.58 mm; scutal length, 1.43 mm.

Head. Yellow areas: (1) paraocular area as in *hurdi;* (5) subantennal plate, a tiny spot (to all yellow except for black subtriangular area around anterior tentorial pit); (6) mandible basal half. (7) Scape as in *quadridentata.* (10) As in *hurdi* but slightly larger, deeper, more distinct. (13) Orbital convergence ratio as 1.68:1.24,1.36. (14) Galea finely pebbled (30×), shiny (to dull), tip narrowly rounded. Galeal gap to length of galea exposed beyond closed mandibles variable, 0.31:0.51(0.39:0.43). (15) Head width to head length as 2.50:1.84,1.36(2.40:1.62,1.48). (17) Eye length, mio, and flagellar length as 1.34:1.24:1.70. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.42:0.48:0.31:0.34. Interocellar less than ocellocular! (19) Ocellolabral greater than clypeal width, 1.48:1.19,1.24. (20) Clypeocellar to outer subantennal sutural as 0.90:0.77,1.18. (21) Flagellar length about 3.3 times length of scape, 1.70:0.56.

Mesosoma. (25) Scutal disc with punctures smaller than in *quadridentata,* larger than in *hurdi,* 0.5 pwa to contiguous, interspaces shiny, but scutum rather dull because of close, deep punctures (20×). (26) Dorsal enclosure of propodeum sharply declivous; pattern of ridges as in *hurdi;* median portion but little produced, length about 0.29, or 1.7 mow. (27) Same note as for *deserticola.* Foreleg colored like that of *pugionis.* (28) Middle leg colored like that of *hurdi;* lengths of tibia, basitarsus, and apicotarsus as 1.07:0.92:0.99, ratios which are almost identical with those of *hurdi.* (29) Hind leg with yellow on basitibial plate, irregular splotching along anterior surfaces of tibia and basitarsus, latter with black border. (30) Tegula brown without yellow patch. Humeral plate brown. (32) Marginal cell 6-9 and 3-4 both greater than 9-wt, 1.24:1.09:0.94.

Metasoma. (35) Tergum 1 with punctures of median area subequal (to slightly smaller) to those of scutum, intermediate in size between those of *kucalumea* and *hurdi,* contiguous, interspaces shiny.

TYPE MATERIAL. Holotype male and allotype female, from Coyotes, Durango, 8300 ft., Aug. 8, 1947 (C. D. Michener, David Rockefeller Expedition), are at the American Museum of Natural History, New York.

In addition four male and six female paratypes are from Mexican localities as follows: Atlacomulco (22 mi. N.), México, 8100 ft., 3 males, Aug. 18, 1954 (C. D. Michener and party); Durango (10 mi. W.), Durango, 1 female, July 12, 1954 (E. I. Schlinger); El Salto (6 mi. N.E.), Durango, 8500 ft., 1 female, Aug. 10, 1947 (M. A. Cazier, David Rockefeller Expedition); Fresnillo (9 mi. S.), Zacatecas, 1 male, Aug. 10, 1954 (E. G. Linsley, J. W. MacSwain, R. F. Smith), 1 female, same locality, Aug. 20, 1954 (J. W. MacSwain), on *Haplopappus gracilis;* Toluca (24.5 mi. N.W.), México, 1 female, July 30, 1962 (Naumann and Marston); Zacatlán (20.7 mi. N.W.), Puebla, 7950 ft., 2 females, Aug. 22, 1962 (University of Kansas Mexican Expeditions). Paratypes are at the University of California, Berkeley; the Snow Entomological Museum of The University of Kansas, Lawrence; the American Museum of Natural History, New York; and in the author's collection.

Subgenus VERBENAPIS Cockerell and Atkins

Verbenapis Cockerell and Atkins, 1902, Ann. Mag. Nat. Hist., (7) 10:44; Michener, 1951, *in* Muesebeck *et al.,* U.S. Dept. Agric., Monogr. No. 2:1103.

Type species. Calliopsis verbenae Cockerell and Porter, 1899, monobasic.

This subgenus is closer to *Calliopsima* than to the others. As discussed under the genus, it has characters in common with *Hypomacrotera* and the South American *Liopoeum* and *Acamptopoeum*. The four species are interrelated, but *verbenae* and *micheneri* are close to each other as are *hirsutifrons* and *nebraskensis*. Depending upon what characteristics are chosen, any one may be thought of as somewhat singular with respect to the other three, a situation which precludes any definitive statement on their phylogeny at present. There are no records from Canada, nor from any southern state east of the Mississippi River. They are apparently oligolectic on *Verbena* flowers, and indeed are particularly adapted to collect pollen from them (see under bionomics of *nebraskensis*).

Verbenapis differs from the other subgenera as follows: propodeum with impunctate, shiny, unsculptured dorsal area bearing a median depression with a longitudinal, low ridge giving the impression of twin pits; posterior dorsal margin of the pronotum without pale maculation; front tarsi of females with rows of long, stout, curled hairs ventrally; male sternum 5 with posterior margin concave medially; sternum 6 with *rounded* lobes instead of pointed projections; areas of the male tergum 7 lateral to pygidial plate dropping sharply downward toward the median sagittal plane of the body and acting as a sheath for the enclosed genitalia.

FEMALE. Length, 6.4-8.8 mm. Integumental background color of head, mesosoma, and metasomal terga black, of metasomal sterna black to brown. Integument almost entirely shiny, non-metallic, rarely some roughening present.

Head. Cream colored areas: (1) paraocular area with a triangular patch in lower ventral corner; (2) clypeus, cream color variable in extent and less than in male; (3) labrum, usually labral plate only, absent on punctate apical portion; (4) absent on supraclypeal area except sometimes a tiny dot; (5) absent on subantennal plate, but indications of potential cream color in some specimens; (6) mandible, basal portion. (7) Scape, pedicel, and flagellomeres 1-4 dark brown to black, upper surface of flagellum dark brown, lower surfaces of flagellomeres 5-10 tan. (8) Hair of vertex, frons, gena, and lateral angles of clypeus white, of disc of clypeus sometimes fulvous. (10) Punctures along ocellocular line medium-sized to very fine, interspaces smooth, moderately shiny; impunctate area lateral to posterior ocellus shiny; punctures of frons near middle of frontal line mixed tiny and large, interspaces smooth, moderately shiny. (11) Frontal line with lower portion a raised, narrow sulcus. (12) Clypeus with lower half of disc flattened or medially concave. Clypeus with a median subapical portion, usually transparent, overhanging the preapical groove from which arise long, amber hairs. (13) Inner orbits slightly convergent below. Facial fovea shallow, shiny, indistinctly sculptured (45×), elongate elliptical, upper limit slightly below level of middle ocellus, lower limit above level of upper rim of antennal socket. (14) Galea long, relatively slender; galeal gap absent or less than mow, length of galea exposed beyond closed mandibles usually extending to or beyond base of prementum. (15) Head width/head length 1.3-1.5. (17) Eye length less than mio, subequal to basal labial palpomere, equal to or less than flagellar length. (18) Interantennal greater than antennocular and more than twice diameter of antennal socket; antennocellar more than twice antennocular. (19) Ocellolabral equal to or greater than mio. (21) Basal labial palpomere 3.0-5.5 times length others combined. (22) Flagellomere 1 equal to or longer than flagellomere 9 (in *hirsutifrons* distinctly shorter). Flagellar length 2.3-2.5 times length of scape.

Mesosoma. (23) Light color absent along posterior dorsal border of pronotum. Some specimens with indistinct yellowish tan dash on medial apical rim of pronotum and similar dash at extreme posterolateral edge of pronotum. (24) Dorsum with hair white to fulvous, white elsewhere. (25) Scutal disc with punctures few, scattered, becoming larger, denser laterad, then abruptly smaller and denser along edges, interspaces shiny. (26) Dorsal enclosure of propodeum impunctate, shiny, unsculptured, bearing a median depression with a low, longitudinal ridge giving the impression of twin pits. (27) Foreleg with cream coloration. Front tarsus with suberect, thick, apically hooked hairs, amber basad, colorless apicad. Front mediotarsus with flattened, expanded tarsomeres each with a posteroventral prolongation. Front distitarsus strikingly different from other distitarsi: base laterally compressed, dorsal surface shiny, hairless, except for a few straight apical hairs. Tibial spurs white. (28) Middle leg with cream coloration; mediotarsus cylindrical. Hind leg dark; mediotarsus cylindrical. (30) Tegula and humeral plate without cream maculation (present in *micheneri*). (31) Wing colorless. Stigma testaceous to brown. (32) Marginal cell 6-9 subequal to longer than, and 3-4 shorter than 9-wt.

Metasoma. (34) Tergal hair bands white, band of tergum 1 often sparse or absent, of terga 2-4 always present. Suberect hair of discs of terga 4-5 long, white, usually moderately abundant. Prepygidial and pygidial fimbriae white, occasionally appearing pale fulvous because of enmeshed pollen or dust particles.

MALE. Length, 5.8-8.8 mm.

Head. Cream colored areas: (1) paraocular area a triangular patch in lower ventral corner; (2) clypeus, mostly to completely, with apical, narrow brown border; (3) labrum, on labral plate to entire impunctate basal portion, absent on punctate apical portion; (4) as in female; (5) absent on subantennal plate; (6) mandible basal fourth to two-thirds. (7) Scape, pedicel and flagellomeres as described for female but lighter. (8) As in female but more intensely fulvous where female has fulvous hair. (10) Punctures as described for female. (11) Frontal line with lower portion a carina with narrow, obsolete sulcus or none. (12) Clypeus as described for female. (13) Eyes bulging, inner orbits moderately to strongly convergent below. (14) Galea as in female. (15) Head width/head length 1.30-1.40. (17) Eye length variable with respect to mio and flagellar length. (20) Clypeocellar greater than outer subantennal sutural except subequal in *micheneri*. (21) Basal labial palpomere as in female. (22) Flagellomere 1 variable with respect to 9. Flagellar length 3.4-4.1 times length of scape.

Mesosoma. (23) As in female. (24) Dorsum with hair as in female. Scutellar and metanotal hair pads absent. (25) Scutal disc with punctures as in female except finer. (26) As in female. (27) Legs with white, cream, or yellowish coloration. Tibial spurs white. Foreleg with cream coloration on femoral apex and stripe along anterior aspect of tibia from knee apicad, interrupted subapically in *nebraskensis* and *micheneri*. (28) Middle leg with cream coloration at least on knee. Middle tibia with dorsoapical projection. (29) Hind leg without light coloration (except in *hirsutifrons*). Hind mediotarsus and distitarsus shorter than those of other legs. (30,31,32) As in female.

Metasoma. (34) As described for female but hair bands sparser. (36,37) Sternum 5 with posterior margin concave medially. Sternum 6 with a bilobed median portion. Sternum 8 with a long, slender, clublike median projection. (38) Sterna and genitalia as illustrated (Figs. 123-143).

CALLIOPSIS (VERBENAPIS) VERBENAE Cockerell and Porter

(Figs. 123-128; Map 8)

Calliopsis verbenae Cockerell and Porter, 1899, Ann. Mag. Nat. Hist., (7)4:412; Cockerell, 1906. Trans. Amer. Ent. Soc., 32:300; Michener, 1951, *in* Muesebeck *et al.,* U.S. Dept. Agric., Monogr. No. 2:1103 (synonym of *hirsutifrons*).

Closest to *nebraskensis* and *micheneri*. The female is distinguished from *nebraskensis* by having the brown color of the basal half of mandible with at most a tiny area of yellow at the extreme base; by the clear oval area on the sclerotized apical portion of sternum 7 being a fourth or more wider than width of median ocellus; by the front basitarsus being about 6 times longer than wide; and by the shape, vestiture, and punctation of metasomal terga 1-2. The male is distinguished from *nebraskensis* by the key characters; by the eye length being less than the clypeal width; by the clypeal length being more than the scape length; and by the sterna and genitalia as illustrated. The male is separated from *micheneri* by the key characters; by a higher ratio of head length to minimum interocular and to intertegular; by the outer subantennal sutural being distinctly less than the clypeocellar; and by the sterna and genitalia, as illustrated.

FEMALE. Length, 8.5 mm; forewing length, 5.7 mm; hindwing length, 3.9 mm; clypeal length, 0.59 mm; scutal length, 1.32 mm.

Head. Cream colored areas: (1) paraocular area a triangular patch in lower corner below line originating at junction of outer subantennal suture and frontoclypeal suture and extending diagonally ending on orbit slightly below level of lower rim of antennal socket; (2) clypeus, apical half or less of median portion with a median dorsal rectangular or concave emargination (usually), cream color extending onto the posteriorly bent sides of clypeus; (3) labral plate; (4) absent on supraclypeal area; (6) mandible a tiny area, often absent, at extreme base. (10) Punctures of ocellar triangle and immediately posteriad, 1 pwa or less. Lower dark paraocular area with punctures distinct, subequal to those of subantennal plate, 1 pwa; of light area few, variable in size. (13) Orbital convergence ratio as 1.67:1.50,1.11. Lower median border of supraclypeal area elevated slightly above level of adjacent clypeus. (14) Galea unsculptured (to finely pebbled at 30×, especially apicad and basad); galeal gap absent, tip of galea in repose extending just beyond base of prementum. (15) Head width to head length as 2.55:1.84,1.39(1.30-1.41). (16) Eye width in profile about 2.5 times protrusion of clypeus beyond it. (17) Eye length, mio, and flagellar length as 1.36:1.50:1.36. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.48:0.53:0.34:0.44. (19) Ocellolabral subequal to clypeal width, 1.51:1.53. (20) Clypeocellar to outer subantennal sutural as 0.92:0.85,1.08. (21) Basal labial palpomere 3.8 (3.3-4.0) times length of others combined. (22) Flagellar length about 2.3 times length of scape, 1.36:0.60.

Mesosoma. (25) Scutal disc with punctures between anterior ends of parapsidal lines of variable size but mostly larger ones, 1-2 pwa. Punctures immediately below episternal scrobe oblong, 1 pwa or less; anterior to scrobe eccentric, less than 1 pwa to contiguous, on a very shiny ground. Punctures of propodeal flats round, very deep, smaller than mesepisternal punctures, larger than scutellar punctures, less than 1 pwa. (27) Legs with cream color the same as on face. Foreleg with cream color on knee. Hooked hairs of front tarsus slenderest of the subgenus. Front basitarsus narrow, length/width from 5.5 to 6.5. Front and middle mediotarsi with lengths subequal and exceeding hind mediotarsi 0.56:0.56:0.53. Front distitarsus fifth shorter than middle distitarsus which is subequal to hind distitarsus. (28) Middle leg with cream color on knee. (30) Tegula transparent dark brown. Humeral plate lighter brown than tegula. (31) Stigma three times as long as wide. (32) Marginal cell 6-9 longer than, and 3-4 shorter than 9-wt, 1.26:1.02:1.14 (1.29:1.11:1.14).

Metasoma. (34) Hair bands of terga 1-3 dense, of tergum 4 sparser. (35) Tergum 1 with punctures of median area subequal to scutal punctures, 1-2 pwa, becoming scattered laterad and posteriad, but dense and regularly spaced anterolaterad, about 1 pwa, interspaces shiny. Declivity of tergum 1 sharply distinct from dorsal portion, shiny, punctures about 15 μ in diameter. Raised dorsal surface at anterior edge of posterior depressed margin of tergum 1 complete from side to side. (36) Tergum 2 with punctures of median area irregularly spaced, about 1 pwa, sparser and larger laterad. Tergum 2 without a median bulge. Pygidial plate with dark brown margin, either light tan or dark brown center, about one-fifth longer than basal width, sides forming about 45° angle, tip narrowly rounded. (37) Sternum 6 with large, oval median clear area in apical sclerotized plate, this area wider than long, 0.26-0.29 by 0.17-0.20, length of area 0.35-0.40 times length of sclerotized plate.

Male. Length, 7.0 mm; forewing length, 5.2 mm; hindwing length, 3.6 mm; clypeal length, 0.51 mm; scutal length, 1.33 mm.

Head. Cream colored areas: (1) paraocular area a triangular patch in lower corner below a line from a point about a third down on inner orbit to about midpoint of outer subantennal suture (or to vicinity of anterior tentorial pit); (2) clypeus except for a brown triangular area in dorsolateral corner below subantennal plate, apical border brown laterally, amber medially; (3) labrum; (4) absent on supraclypeal area; (6) mandible basal half (or more). (10) Punctures similar to female except light portions of paraocular area and clypeus well punctured. (13) Orbital convergence ratio as 1.53:1.24,1.22. (14) Galea with medial portion shiny, basal and apical portions roughened more distinctly than in female; galeal gap absent, tip of galea in repose extending slightly beyond base of prementum. (15) Head width to head length as 2.26:1.72,1.32. (17) Eye length, mio, and flagellar length as 1.21:1.24:1.73. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.43:0.46: 0.27:0.37. (19) Ocellolabral greater than clypeal width, 1.36:1.31,1.04. (20) Clypeocellar to outer subantennal sutural as 0.87:0.75,1.16. (22) Flagellar length about 3.7 times length of scape, 1.73:0.48.

Mesosoma. (25) Punctation as in female except scutal disc with punctures finer, shallower, and less dense than in female or in *nebraskensis,* 2 pwa between anterior ends of parapsidal lines, mesepisternal punctures rounder. (27) Legs with light color in part different from that on face. Foreleg with yellowish stripe on tibia reaching apex; basitarsus and second tarsomere white on anterior surface, others straw color. (28) Middle leg with ventral apical rim of yellow on trochanter; yellow macula on dorsal surface of femoral apex and knee; basitarsus colored like that of foreleg, apicotarsus light tan, darker than that of foreleg; lengths of tibia, basitarsus, and apicotarsus as 1.00:0.68:0.82. (29) Hind leg colored like middle leg but without femoral and tibial light color (basitibial plate may bear indistinct yellow on basal half medially). (30) As in female. (31) Wing 12-13/13-14 about 5. Stigma about 5 times as long as wide. (32) Marginal cell 6-9 longer than, and 3-4 shorter than 9-wt, 1.12:0.97:1.07.

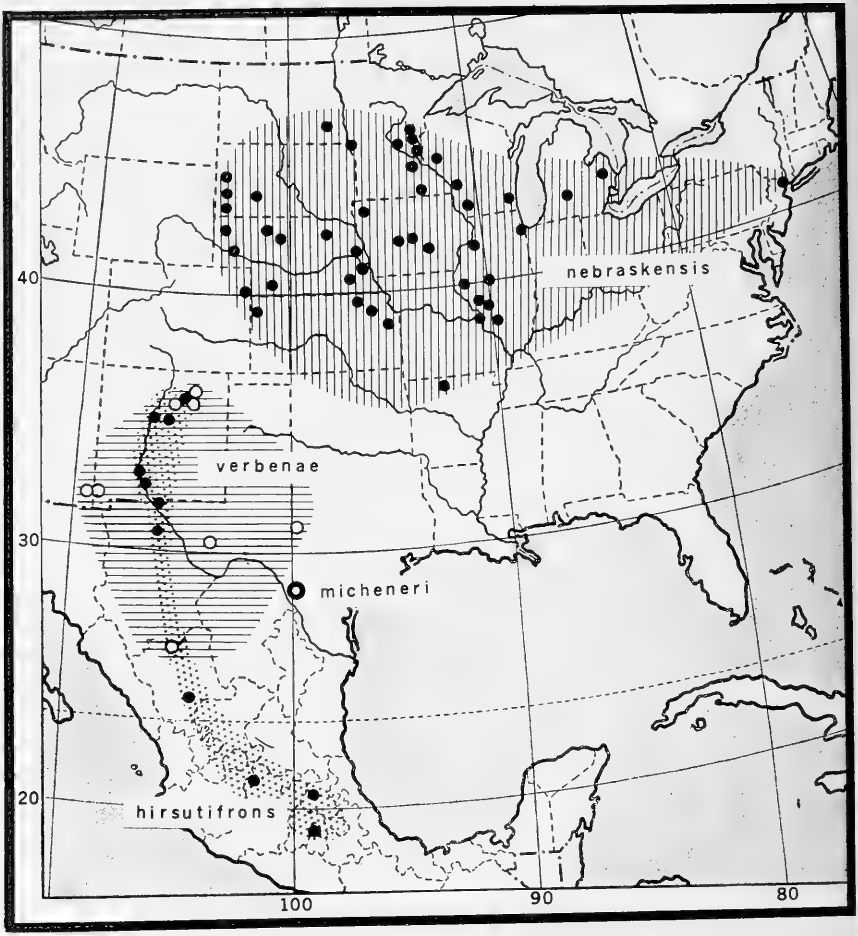
Metasoma. (34) Tergal hair bands as in female but sparser. (35) Tergum 1 with punctures of median area subequal to scutal punctures but deeper, evenly spaced on dorsum, about 1 pwa. Declivity of tergum 1 as in female except at least twice as many punctures, finer than on dorsum. Raised dorsal surface as in female. (36) Tergum 2 with punctures of median area finer than on 1, sparser, but fairly evenly distributed. Pygidial plate with dark brown (to black) flat margin, broadly rounded at tip.

DISCUSSION. Too few specimens of this species are available to make meaningful statements on geographic variation, but the one Mexican female is conspicuously larger than the females from the United States. No data on the bionomics of the species have been published; Robertson's notes on *Verbenapis* actually pertained to *nebraskensis* (q.v.).

TYPE MATERIAL. The holotype female taken at Las Vegas, New Mexico, Aug. 9 (W. Porter), on *Verbena stricta,* has not been located. One male paratype, same collection data, is in the Academy of Natural Sciences of Philadelphia and two male paratypes, same data as above, one in the U. S. National Museum, one in the Museum of Comparative Zoology, Harvard University. The above description of the female is principally based on a specimen from Pecos, New Mexico, July 7 (T. D. A. Cockerell), on *Verbena bipinnatifida,* while that of the male is based on the first paratype listed above.

DISTRIBUTION. Western Texas to southeastern Arizona and south to Durango, Mexico. It has been collected in Texas in April only, but elsewhere from July 7 to September 7.

In addition to the type material, 9 females and 2 males have been examined. The localities below include the type locality: ARIZONA: Portal (5 mi. W.), Chiricahua Mts., Aug. 24, 1958 (P. A. Opler). NEW MEXICO: Ft. Union (2.4 mi. S.), Mora Co., July 9, 1959 (Ray F. Smith); Las Vegas, 3 males, 1 female, Aug. 9 (W. Porter), on *Verbena stricta,* and 1 male, same data, on *Sphaeralcea lobata;* Pecos, 1 female, July 7 (T. D. A. Cockerell), on *Verbena bipinnatifida;* Pecos, 1 male, 1 female, July 19 (Cockerell and Porter), on *Verbena macdougalli;* Rodeo (2.5 mi. N.), Hidalgo Co., Sept. 7, 1959 (D. D. Linsdale). TEXAS: Davis Mts., 1 female, April 17, 1954 (R. H. Beamer), on *Chamaesaracha conloides,* 1 female, same date (L. D. Beamer). DURANGO: El Tascate, 6400 ft., July 28, 1947 (C. D. Michener).



MAP 8. Map showing the known distributions of *Calliopsis (Verbenapis) hirsutifrons* Cockerell, *C. (V.) verbenae* Cockerell and Porter, *C. (V.) micheneri* Shinn, and *C. (V.) nebraskensis* Crawford.

CALLIOPSIS (VERBENAPIS) NEBRASKENSIS Crawford

(Figs. 129-133; Map 8)

Calliopsis verbenae var. *nebraskensis* Crawford, 1902, Canadian Ent., 34:240; Graenicher, 1910, Bull. Pub. Mus. Milwaukee, 1:238.

Calliopsis verbenae nebraskensis; Swenk and Cockerell, 1907, Ent. News, 18:179; Graenicher, 1935, Ann. Ent. Soc. Amer., 28:303.

Verbenapis verbenae; Robertson, 1914, Ent. News, 25:72; 1922, Psyche, 29:171; 1926, Ecology, 7:379; 1929, Flowers and Insects, pp. 10, 216-218; Robertson, Psyche 36:115-116; Pearson, Ecol. Monogr., 3:378. (misidentifications)

Calliopsis nebraskensis; Crawford, 1915, Proc. U.S. National Museum, 48:179; Cockerell, 1916, Ann. Mag. Nat. Hist., (8)17:279; Rau and Rau, 1916, Jour. Anim. Behav., 6:368; Stevens, 1919, Canadian Ent., 51:210; Cockerell, 1921, Amer. Mus. Nov., No. 24:14; Rau, 1922, Trans. Acad. Sci. St. Louis, 24:33; Cockerell, 1928, Univ. Colorado Studies, 16:103; Stevens, 1950, Bull. North Dakota Agric. Exp. Sta., 12:93; Michener, 1951, *in* Muesebeck *et al.,* U.S. Dept. Agric., Monogr. No. 2:1103; Mitchell, 1960, North Carolina Agric. Exp. Sta. Tech. Bull., No. 141, vol. 1:288, 291-294.

Calliopsis sp.; Washburn, 1919, Minnesota Agric. Exp. Sta., Jour. series, Paper No. 156:229 (dorsal view of female).

Females differ from other *Verbenapis* in the shape and punctation of metasomal terga 1 and 2. Females are distinguished from *verbenae* by having the basal third to half of the mandible cream colored; by the clypeal width being subequal to the flagellar length; by the front basitarsus being about four times longer than wide; and by the finer punctation throughout. The male is distinguished from *verbenae* as discussed under that species; from *hirsutifrons,* with which it shows strong affinities based on similarities of facial structure and dimensions, by the key characters, by the lower ratio of head length to intertegular distance, by the flagellar length being subequal to the head length, by the higher value of wing ratio 12-13/13-14, and by the sterna and genitalia, as figured.

FEMALE. Length, 7.5 mm; forewing length, 5.4 mm; hindwing length, 3.7 mm; clypeal length, 0.51 mm; scutal length, 1.33 mm.

Head. Cream colored areas: (1) paraocular area as in *verbenae* (triangular patch frequently truncated dorsally); (2) clypeus as in *verbenae* (upper median emargination of cream colored area may be absent, wedgeshaped, rectangular, evenly concave, or sinuous); (3,4) as in *verbenae;* (6) mandible, basal third. (10) Punctures as in *verbenae* except somewhat finer, less shiny. (13) Orbital convergence ratio as 1.58:1.36,1.16. Lower median border of supraclypeal area slightly below level of adjacent clypeus. (14) Galea unsculptured (30×), narrower and more sharply pointed than in *verbenae;* galeal gap absent, tip of galea in repose just extending to or beyond base of prementum. (15) Head width to head length as 2.43:1.70,1.43(1.36-1.44). (16) Eye width in profile 4.0(3.5-4.0) times protrusion of clypeus beyond it, clypeus more abruptly protuberant than *verbenae.* (17) Eye length, mio, and flagellar length as 1.31:1.36:1.34. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.46:0.46:0.34:0.37. (19) Ocellolabral greater than clypeal width, 1.43:1.36,1.05. (20) Clypeocellar to outer subantennal sutural as 0.92: 0.77,1.20. (21) Basal labial palpomere about 3.5 times length of others combined. (22) Flagellar length about 2.2 times length of scape, 1.34:0.61.

Mesosoma. (25) Scutal disc with punctures as in *verbenae* except finer and shallower. Punctures immediately below episternal scrobe round to ovate, 1 pwa or slightly more; anterior to scrobe as in *verbenae.* Punctures of propodeal flats as in *verbenae* except finer, mostly 1 pwa. (27) Legs with cream color the same as on face. Foreleg with cream color on knee. Front basitarsus broader and shorter than in *verbenae,* length/width from 3.5 to 4.0. Middle mediotarsus fifth its length longer than front mediotarsus, and tenth its length longer than hind mediotarsus. Front distitarsus about fourth shorter than middle distitarsus, which is subequal to hind distitarsus. (28) Middle leg dark. (30) Tegula as in *verbenae*. Humeral plate lighter than tegula and lighter than in *verbenae*. (31) Stigma about 3.5 times as long as wide. (32) Marginal cell 6-9 longer than, and 3-4 shorter than (to subequal to) 9-wt, 1.21:0.97:0.99.

Metasoma. (34) Band of tergum 1 absent, of terga 2-3 present (but much sparser than in *verbenae*), of tergum 4 denser than on 3. (35) Tergum 1 with punctures of median area much finer than scutal punctures, 3-6 pwa, becoming scattered laterad and posteriad. Declivity of tergum 1 not sharply distinct from dorsal portion, shiny, punctures ultra fine, less than 10 μ in diameter. Raised dorsal surface at anterior edge of posterior depressed margin of tergum 1 absent medially, entire median portion sloping anteriorly downward with central portion concave. (36) Tergum 2 with punctures of median area dense, regularly spaced, 1-2 pwa, punctures scattered laterad. Tergum 2 with median area a gently sloping bulge. Pygidial plate similar to *verbenae* but sides forming a smaller angle, about 40°, and tip more narrowly rounded. (37) Sternum 6 with tiny, round median clear area in apical sclerotized plate, diameter 0.09-0.12, length of area about 0.20-0.33 length of sclerotized plate.

MALE. Length, 7.0 mm; forewing length, 5.2 mm; hindwing length, 3.6 mm; clypeal length, 0.48 mm; scutal length, 1.41 mm.

Head. Cream colored areas: (1,2,4) as in *verbenae;* (3) labrum except brown in dorsolateral corners (frequently entire basal half); (6) mandible basal third only. (10) Punctures coarser, more abundant, and more regularly spaced than in female or in *verbenae;* punctures below middle ocellus larger, much denser than in *verbenae,* 1 pwa or less, subequal in size to those of subantennal plate. (13) Orbital convergence ratio as 1.60:1.12,1.42. (14) Galea shiny, unsculptured (30×), but with barely detectable sculpture at 45×; galeal gap absent, tip of galea in repose extending slightly beyond base of prementum. (15) Head width to head length as 2.33:1.72,1.36. (17) Eye length, mio, and flagellar length as 1.22:1.12:1.80. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.43:0.46:0.26:0.32. (19) Ocellolabral greater than clypeal width, 1.36:1.19,1.14. (20) Clypeocellar to outer subantennal sutural as 0.88:0.71,1.24. (22) Flagellar length about 3.5 times length of scape, 1.80:0.51.

Mesosoma. (25) Punctation as in female except scutal disc with punctures larger, denser than in either female or *verbenae,* 1 pwa or less between anterior ends of parapsidal lines, punctures immediately below episternal scrobe about 2 pwa. Punctures of propodeal flats finer than in *verbenae,* 1 pwa or more. (27) Legs with light color in part different from that on face. Foreleg with yellow stripe on tibia interrupted preapically; basitarsus pale whitish on anterior aspect, apicotarsus straw color. (28) Middle leg with only faint indication of yellow on dorsal surface of femoral apex and with (or without) light color on knee; basitarsus pale amber to light brown, apicotarsus light brown; lengths of tibia, basitarsus and apicotarsus as 0.94:0.73:0.75. (29) Hind leg entirely light brown. (30) As in female. (31) Wing 12-13/13-14 about 10. Stigma about 4 times as long as wide. (32) Marginal cell 6-9 and 3-4 longer than 9-wt, 1.16:0.99:0.94.

Metasoma. (34) Hair bands of terga 1 and 4 obsolete, of terga 2-3 very sparse. Suberect hair of disc of tergum 5 shorter than in *verbenae*. (35) Tergum 1 with punctures of median area extremely fine, about third of diameter of scutal punctures, evenly spaced on dorsum, 3 pwa. Declivity of tergum 1 similar to female. (36) Tergum 2 with punctures of median area larger than on tergum 1. Pygidial plate with black upturned margin, narrowly rounded at tip. (38) Penis longer in comparison to penis valve than in *verbenae*.

TYPE MATERIAL. Holotype female, U. S. N. M. No. 5237, from Lincoln, Nebraska, July 7, 1901 (J. C. Crawford, No. 427), on *Verbena*, one female paratype, same data except Aug. 4, 1901 (No. 527) and two male paratypes, same data as holotype but Crawford No. 425 on one, no Crawford No. on the other, are at the U. S. National Museum. One male paratype, same data as holotype except Crawford No. 420, is at the Academy of Natural Sciences of Philadelphia, and one male paratype, same data as holotype except Crawford No. 423, is at the University of California, Riverside. Description of the female is principally based on the female paratype specimen listed above, while that of the male is based on the Crawford paratype No. 420.

DISTRIBUTION. North Dakota south to Colorado and Kansas, east to Arkansas and northeast following the Prairie Peninsula and Great Lake states (if the range is continuous) all the way to northern New Jersey.

In addition to the type material, 150 males and 65 females were examined from the following localities which include the type: ARKANSAS: Marion Co. COLORADO: Wray, 3700 ft. ILLINOIS: Adams Co.; Carlinville; Chicago; Grafton; Havana; Havana, Devil's Hole; Meredosia (Sand Pit); Moline. IOWA: Ames; Boone (13 mi. N.W.); Gilbert (4 mi. E).; Iowa Co.; Johnson Co.; Sioux City. KANSAS: Baldwin; Douglas Co.; Lawrence; Linn; Washington Co.; Riley Co.; Sherman Co. MICHIGAN: Ionia Co.; Lapeer Co. MINNESOTA: Browns Valley; Fridley Sand Dunes, Anoka Co.; Hennepin Co.; Princeton; Sargents Bluff; Sucker Lake, Ramsey Co. MISSOURI: St. Louis. NEBRASKA: Halsey; Hamlet; Lincoln; Louisville; Monroe Canon, Sioux Co.; Neligh; Northport (2 mi. E.); Omaha; Valentine (27 mi. S.), Cherry Co. NEW JERSEY: Closter, Bergen Co. NORTH DAKOTA: Valley City. SOUTH DAKOTA: Hot Springs; Philip; Rapid Canyon; Whitewood. WISCONSIN: Genoa, Vernon Co.; Maiden Rock, Pierce Co.; Milwaukee Co.; Prescott, Pierce Co.; Rutledge, Grant Co.; Waukesha Co.; Wyalusing, Grant Co.

REMARKS. The specimens at hand are homogeneous for obvious external characters. Although specimens from North Dakota and Minnesota are larger than those from more southern localities, the difference is not statistically significant. The easternmost specimens, from northeastern New Jersey, differ from others in the combination of piceous integument and darker colors in all areas; more deeply fulvous hair of vertex, thoracic dorsum and abdominal bands; and smaller head length and abdominal width despite an average length hindwing. The affinities of *nebraskensis* seem to be mostly with *verbenae,* yet the striking similarity in facial dimensions and ratios which groups *nebraskensis* with *hirsutifrons* and *verbenae* with *micheneri* suggests that *nebraskensis* is not a lineal descendant from either *verbenae* or *hirsutifrons,* and that its ancestor is some extinct or uncollected form.

BIONOMICS. Most of the flower records are for *Verbena* species; one each for *Ambrosia* and *Asclepias* are probably accidental. I have seen mixed pollen loads which incorporated pollen of Verbenaceae and Leguminosae. Robertson regarded this species as oligolectic on *Verbena* spp. and (1914) described the action of the females in obtaining pollen of *Verbena:* "Anthers of *Verbena* are included in a slender tube and above them is a circle of hairs. . . . Ordinary bees can only collect pollen which adheres to their tongues. *Verbenapis verbenae* [misidentification for *nebraskensis*] has its front tarsi provided with curled bristles. When collecting pollen the bee thrusts both front legs into the tube of the corolla and drags out the pollen with its front tarsi." Examination of specimens supports this observation, for pollen was often found packed between the curled hairs of the front tarsi. Robertson (1929) records the species at Carlinville, Illinois, as active from June 28 to September 11 which gives the flight period of the bee as 75 days, or well within the period of anthesis of *Verbena* from May 22 to October 5. Both sexes were taken by Robertson (1922) on *Verbena hastata, V. stricta,* and *V. urticifolia* (*in copulo* on the last two).

Robertson *(op. cit.)* found *Calliopsis (Calliopsis) andreniformis* visiting *Verbenaceae,* too: *Lippia lanceolata* and *Verbena bracteosa,* neither of which were visited by *nebraskensis.* At Lawrence, Kansas, *C. andreniformis* males visit *Verbena* sp., and at Nacogdoches, Texas, *Verbena tenuisecta,* but I have not seen females at *Verbena* at either locality.

Rau and Rau (1916) and Rau (1922) give notes on the nesting of *nebraskensis* at St. Louis, Missouri; it is similar to that of *andreniformis.* Hard-packed bare soil is selected for nest construction, e.g., a baseball diamond! A burrow is dug with a single or double entrance, in the latter case, the openings about two inches apart, and kept covered by a mound of "fine dust." Mating was quietly effected on the ground and copulation lasted perhaps five minutes. The same sort of buzzing, tumbling, and whirling in small circles by pairs on the dusty ground was seen for *nebraskensis* as I have seen with pairs of male *andreniformis.* Cockerell has observed similar behavior by males of *Nomadopsis zebrata* and mating pairs of *Calliopsis coloratipes,* and Rozen (1958) has noted it for *Nomadopsis a. anthidius* and *N. micheneri.* In the last instance, Rozen found mating pairs rather than males alone. The Raus state that this tumbling did not immediately precede or follow mating, but they were not able to catch pairs to determine sexes. *Sphecodes* spp. enter the burrows freely and are suspect, but unproven, parasites. *Schecodes* *brachycephalus* Mitchell and *Sphecodes* sp. are discussed as possible parasites of *Calliopsis andreniformis* in the section on the biology of that species.

FLOWER RECORDS. Literature and label records include *Ambrosia* and *Asclepias,* both of which are probably accidental, *Medicago sativa, Verbena hastata, V. stricta, V. urticifolia, Vernonia.*

CALLIOPSIS (VERBENAPIS) HIRSUTIFRONS Cockerell

(Figs. 134-138; Map 8)

Calliopsis hirsutifrons Cockerell, 1896, Canad. Ent., 28:158; 1897, Bull. Univ. New Mexico, 24:19; Michener, 1951, *in* Muesebeck *et al.,* U.S. Dept. Agric., Monogr. No. 2:1103.

Readily distinguished from other *Verbenapis* by the small size. It is closest to *nebraskensis* on the basis of numerous head dimensions and ratios as well as the nature of the clear, median disc of the metasomal sternum 6 of the female.

It has a punctation pattern similar to that of *verbenae* and *micheneri,* and the shape of the metasomal terga is closer to them than to *nebraskensis.* The concave nature of the medial basal margin of metasomal sternum 8 distinguishes the male from other *Verbenapis.* In the female the first labial palpomere is a fourth to a third shorter than the flagellar length, but in the other species it is subequal to or up to a third longer than the flagellar length. The female differs from *nebraskensis* in having the base of the middle tibia yellow, and from *verbenae* in the more extensive cream colored area on the mandible, and from both in the shape of the clypeal cream colored area as described in (2) below.

FEMALE. Length, 6.5 mm; forewing length, 4.5 mm; hindwing length, 3.1 mm; clypeal length, 0.44 mm; scutal length, 1.19 mm.

Head. Cream colored areas: (1) paraocular area similar to *verbenae* and *nebraskensis* but dorsal apex of triangular patch ends at or above level of lower rim of antennal socket (may reach to level of lower border of facial fovea); (2) clypeus, the median portion of cream colored area produced dorsally to within half mow of frontoclypeal suture, the lateral portion extended to within less than 1 mow of anterior articulation of mandible; (3) labrum entirely or labral plate only; (4) absent on supraclypeal area (small dot may occur in impunctate lower median part adjacent to frontoclypeal suture); (6) mandible basal fourth. (10) Punctures of ocellar triangle fine, distinct, 1 pwa or more; punctures immediately posteriad larger, less than 1 pwa. (13) Orbital convergence ratio as 1.39:1.22,1.14. Lower median border of supraclypeal area at same level as adjacent clypeus. (14) Galea unsculptured; galeal gap subequal to mow. (15) Head width to head length as 2.14: 1.53,1.40(1.39-1.45). (16) Eye width in profile about 6.5 times protrusion of clypeus beyond it. (17) Eye length, mio, and flagellar length as 1.14:1.22:1.24.

(18) Interocellar, ocellocular, antennocular, and interantennal as 0.41:0.39:0.32:0.36. (19) Ocellolabral greater than clypeal width, 1.29:1.19,1.08. (20) Clypeocellar to outer subantennal sutural as 0.85:0.65,1.31. (21) Basal labial palpomere about 3.2 times length of others combined. (22) Flagellar length about 2.4 times length of scape, 1.24:0.51.

Mesosoma. (25) Scutal disc with punctures between anterior ends of parapsidal lines distinct, mostly large, about 1 pwa. Punctures immediately below episternal scrobe deep, round, 1 pwa; anterior to scrobe, round, less than 1 pwa. Punctures of propodeal flats as in *verbenae* but finer, less than 1 pwa. (27) Legs with cream color the same as on face. Foreleg with cream color on knee. Front basitarsus long, narrow, length/width about 8.0 to 9.4. Front, middle, and hind mediotarsi as in *nebraskensis*. Front distitarsus third shorter than middle distitarsus which is subequal to hind distitarsus. (28,30) As in *verbenae*. (31) Stigma about 3 times as long as wide. (32) Marginal cell 6-9 longer than, and 3-4 shorter than 9-wt, 1.02:0.82:0.87.

Metasoma. (34) Bands of terga 1-4 quite dense, least so on tergum 1. (35,36) Tergal punctures finer than in *verbenae*, tergum 1 with punctures of median area more scattered, but punctation pattern similar. Pygidial plate similar to *nebraskensis*. (37) Sternum 6 with round, median clear area in apical sclerotized plate, diameter of area less than mow (about 0.15:0.17), and about third of length of sclerotized plate.

MALE. Length, 6.0 mm; forewing length, 4.3 mm; hindwing length, 2.9 mm; clypeal length, 0.41 mm; scutal length, 1.10 mm.

Head. Cream colored areas: (1,3) As in *verbenae;* (2) clypeus except for narrow dark strip below subantennal plate; (4) supraclypeal area, a medial round spot touching frontoclypeal suture; (6) mandible basal third. (10) Punctures similar to those of female but different in manner described for male *verbenae*. (13) Orbital convergence ratio as 1.36:0.97,1.40. (14) As in female. (15) Head width to head length as 1.99:1.43,1.40. (17) Eye length, mio, and flagellar length as 1.02:0.97:1.72. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.36:0.41:0.20:0.32. (19) Ocellolabral greater than clypeal width, 1.17:0.97,1.21. (20) Clypeocellar to outer subantennal sutural as 0.77:0.61,1.25. (22) Flagellar length about 4.0 times length of scape, 1.72:0.43.

Mesosoma. (25) Punctation as in female. (27) Legs with light color in part different from that on face. Foreleg as in *verbenae*. (28) Middle leg colored like *verbenae* but tip of tibia cream colored, and apicotarsus dark brown. (29) Hind leg as in *verbenae* except apicotarsus dark brown. (30) As in female. (31) Wing 12-13/13-14 about 8.5. Stigma about 3.5 times as long as wide. (32) Marginal cell 6-9 and 3-4 longer than 9-wt, 0.94:0.85:0.80.

Metasoma. (34) Hair bands of terga 1-3 distinct, sparse medially, of tergum 4 obsolete. Suberect hair of disc of tergum 5 shorter than in *verbenae*.

(35) Tergum 1 with punctures of median area larger and deeper than scutal punctures, evenly spaced on dorsum, 1-2 pwa. Declivity of tergum 1 similar to female. (36) Tergum 2 with punctures of median area as in *verbenae*. Pygidial plate usually darker peripherally with an irregular submarginal line of coarse, oblong punctures.

TYPE MATERIAL. Holotype male, U. S. N. M. No. 5821, from Albuquerque, New Mexico, middle Aug., 1895 (T. D. A. Cockerell, No. 4527), is at the U. S. National Museum. The description of the female is principally based on a specimen from Garfield, New Mexico, July 16, 1952 (R. H. and L. D. Beamer, W. E. La Berge, and Cheng Liang), while that of the male is based on a specimen from Hot Springs, New Mexico, July 22, 1950 (R. H. Beamer).

DISTRIBUTION. North central New Mexico, east of the Rio Grande River, to El Paso, Texas, south across the Mexican desert to the state of México.

In addition to the type material, 24 males and 9 females have been examined from the localities listed below which include the type: NEW MEXICO: Albuquerque, middle Aug.; Garfield, July 16; Hot Springs, July 22; Moriarty, June 24; Radium Springs, July 16. TEXAS: El Paso, July 11. CHIHUAHUA: Villa Ahumada, 5700 ft., July 28. DURANGO: San Juan del Rio, 5200 ft., July 30. GUANAJUATO: León (1 mi. N.W.), Aug. 9. HIDALGO: Ixmiquilpan, 5200 ft., July 29; Lagunilla, June 14. MEXICO: Tepexpán, 6500 ft., Aug. 12.

REMARKS. A female specimen from León, Guanajuato, has clypeus with only a lateral cream spot, labrum and mandible completely brown. A male specimen from San Juan del Rio, Durango, is the largest specimen and exhibits other differences in structure that may indicate a population worthy of subspecific recognition. Unfortunately the sterna and genitalia are not in good enough condition to make positive statements. The genital capsule is flatter, penis valve rather broader distally, volsella more sharply pointed, and penis slightly shorter in comparison to the penis valve than in other specimens. No biological data are available for the species.

CALLIOPSIS (VERBENAPIS) MICHENERI, new species

(Figs. 139-143; Map 8)

This large, distinctive species is named in honor of Dr. Charles D. Michener who discovered it and who has done much to aid in the present understanding of this genus. The species is distinguished from others of the subgenus by the occurrence of a triangular area of opaque cream coloration on the outer apical half of the tegula and by the high ratio of the first labial palpomere to the length of the others combined, usually about 5. The female is separated from *verbenae* by having finer punctures with wider interspaces, and by the basal outer half of the mandible being cream colored. The male is readily known by the large size and the pointed, narrow pygidial plate.

FEMALE. Length, 8.3 mm; forewing length, 6.0 mm; hindwing length, 4.1 mm; clypeal length, 0.53 mm; scutal length, 1.44 mm.

Head. Cream colored areas: (1) paraocular area as in *hirsutifrons* but triangle less extensive, ending dorsally at (or slightly above) level of upper portion of frontoclypeal suture, well below level of lower rim of antennal socket; (2) clypeus as in *hirsutifrons* except lateral cream color extends to within half (or more) mow of anterior articulation of mandible; (3,4) as in *hirsutifrons;* (6) mandible basal half (to third). (10) Punctation similar to *verbenae* but finer. Lower dark paraocular area with punctures distinct, finer than those of subantennal plate, 2-3 pwa. (13) Orbital convergence ratio as 1.60:1.41,1.13. Lower median border of supraclypeal area below level of adjacent clypeus. (14) Galea finely, distinctly pebbled on entire anterior surface (30×); galeal gap absent, tip of galea in repose extending slightly beyond base of prementum. (15) Head width to head length as 2.47:1.80,1.37(1.34-1.37). (16) Eye width in profile about 2.5 times protrusion of clypeus beyond it. (17) Eye length, mio, and flagellar length as 1.34:1.44:1.33. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.44:0.46:0.32:0.44. (19) Ocellolabral less than clypeal width, 1.46:1.53,0.96. (20) Clypeocellar to outer subantennal sutural as 0.94:0.82,1.14. (21) Basal labial palpomere 3.5 (3.5-5.5) times length of others combined. (22) Flagellar length about 2.3 times length of scape, 1.33:0.58.

Mesosoma. (25) Scutal disc with punctures between anterior ends of parapsidal lines uniform, fine, 2 pwa. Punctures immediately below episternal scrobe round, 1.5-2.5 pwa; anterior to scrobe round, 1 pwa. Punctures of propodeal flats round, finer than in others of the subgenus, subequal in size to scutal punctures, about 2 pwa. (27) Legs with light color the same as on face. Foreleg colored as in *hirsutifrons.* Front, middle, and hind mediotarsi and distitarsi as in *verbenae.* (28) As in *verbenae.* (30) Tegula transparent smoky tan with anterior patch of opaque cream coloration; humeral plate with anterior half cream colored, posterior half brown. (31) Stigma about 4 times as long as wide. (32) Marginal cell 6-9 longer than, and 3-4 shorter than 9-wt, 1.22:0.94:1.19.

Metasoma. (34) About as in *verbenae.* (35) Tergum 1 with punctures of median area almost as fine as in *hirsutifrons,* diameter subequal to scutellar punctures, tergum generously covered including posterolateral areas, punctures 1-3 pwa. (36) Tergum 2 with punctures of median area as in *verbenae* but 1-2 pwa anteromedially. Pygidial plate similar to *hirsutifrons* but more slender. (37) Sternum 6 with oval, median clear area in apical sclerotized plate, this area wider than mow, wider than long, about 0.24:0.19, and about third of length of sclerotized plate.

MALE. Length, 8.8 mm; forewing length, 6.1 mm; hindwing length, 4.1 mm; clypeal length, 0.60 mm; scutal length, 1.59 mm.

Head. Cream colored areas: (1,2,3,4) as in *hirsutifrons;* (6) mandible as in *nebraskensis.* (10) Punctures similar to those of female but different in the manner as described for *verbenae.* (13) Orbital convergence ratio as 1.77:1.48, 1.19. (14) Galea lightly, distinctly roughened as in female; galeal gap absent, tip of galea in repose extending beyond base of prementum by length of second labial palpomere (or more). (15) Head width to head length as 2.70: 2.01,1.35. (17) Eye length, mio, and flagellar length as 1.45:1.48:1.87. (18) Interocellar, ocellocular, antennocular, and interantennal as 0.49:0.49:0.32:0.48. (19) Ocellolabral less than clypeal width, 1.36:1.58,0.86. (20) Clypeocellar subequal to outer subantennal sutural, 0.94:0.95. (22) Flagellar length about 3.6 times length of scape, 1.87:0.53.

Mesosoma. (25) Punctation as in female. (27) Legs with light color the same as on face except tibial stripe yellowish. Foreleg with color as in *nebraskensis* except trochanter as in *verbenae,* knee cream colored, tarsus brown. (28) Middle leg with trochanter as in *verbenae,* knee cream colored, tarsus brown. (29) In a few specimens, hind leg with medial portion of basitibial plate whitish with black (to dark brown) border. (30) As in female. (31) Wing 12-13/13-14 about 5.5. Stigma about 5 times as long as wide. (32) Marginal cell 6-9 longer than, and 3-4 shorter than 9-wt, 1.26:1.00:1.17.

Metasoma. (34) Hairiest of the subgenus. Hair bands of terga 1-4 distinct, sparse. Suberect hair of disc of tergum 5 denser and much longer than other species in the subgenus. (35) Tergum 1 with punctures of median area subequal to scutal punctures, deeper and finer than in *hirsutifrons* or *verbenae,* 1-2 pwa. Declivity of tergum 1 similar to female. (36) Tergum 2 with punctures of median area as described for *verbenae.* Pygidial plate twice as long as broad at base with extremely narrow, black, slightly upturned border; sides forming 25° (to 30°) angle, tip very narrowly rounded. (37) Medial lobes of sternum 6 separated by a deep cleft, depth about twice (or more) width of one lobe. (38) Penis valve rounded at apex with distinct subapical pointed protuberance.

TYPE MATERIAL. Holotype male and allotype female from Carrizo Springs, Dimmit Co., Texas, April 14, 1949 (C. D. Michener and R. H. Beamer), on *Verbena cloveri,* are in the Snow Entomological Museum of The University of Kansas, Lawrence. Two female and 25 male paratypes bear the same collection data; two male paratypes, same locality, were taken March 28, 1946, by C. D. Michener who informs me that they were visiting the same species of *Verbena.*

REMARKS. Known only from the type locality in Texas. Its host flower is endemic to Texas.

NOMEN NUDUM IN CALLIOPSIS

CALLIOPSIS BRIDWELLI Bridwell

Calliopsis bridwelli Bridwell, 1899, Trans. Kansas Acad. Sci., 16:210.

This name was published in a list of insects of Kansas and must represent a misidentification of a common species.

NOMEN DUBIUM IN CALLIOPSIS

CALLIOPSIS FLAVIFRONS Smith

Calliopsis flavifrons Smith, 1853, Catalogue of Hymenoptera in the British Museum, 1:129, male; Cresson, 1887, Trans. Amer. Ent. Soc. Suppl. :245; Cockerell, 1897, Bull. Univ. New Mexico, 24:26; 1898, Trans. Amer. Ent. Soc., 25:197; 1905, Trans. Amer. Ent. Soc., 31:321, female; Sandhouse, 1943, Proc. U.S. Nat. Mus., 92:531 (=*Camptopoeum prinii* Holmberg, 1884) (misidentification); Michener, 1951, *in* Muesebeck *et al.*, U.S. Dept. Agric., Monogr. No. 2:1103; Mitchell, 1960, North Carolina Agric. Exp. Sta. Tech. Bull. No. 141:293.

Smith's description of the male is given below.

"MALE. Length 4 lines [=8.47 mm]. Black, the face, *scape of the antennae in front**, labrum and mandibles yellow, the latter have a black line on their inferior margin and are ferruginous at the tips; the flagellum pale testaceous beneath. Thorax, the disk thinly covered** with pale ochraceous pubescence; the anterior and intermediate tibiae in front yellow; all the tibiae and tarsi have a pale glittering pubescence; the apical joints of the tarsi ferruginous; wings subhyaline, iridescent, nervures fuscous, the tegulae testaceous. Abdomen short and somewhat globose, delicately punctured, the margins of the segments have on each side a short fascia of white pubescence.

"Obs. The fascia on the abdomen probably in very recently disclosed specimens would be entire. Hab. East Florida. Coll. of F. Smith. [Collector E. Doubleday, Esq.]"

Cockerell (1905) described a female in the British museum collection bearing the *flavifrons* type label. The specimen he described was undoubtedly *C. andreniformis* Smith. The difference in sex shows that he did not have *flavifrons* before him.

At least three thoroughly competent bee specialists (Cockerell, Mitchell, and Moure) have failed to find the type of this species in the British Museum or among the Smith types at the Hope Museum in Oxford.

The original description is inadequate to determine the species, and *flavifrons* must remain a *nomen dubium*.

SPECIES ERRONEOUSLY ASSIGNED TO CALLIOPSIS

Perhaps a score of species occurring outside the United States and Canada have been described as *Calliopsis*. All but two have subsequently been transferred to other genera, mostly to related panurgine genera. The following two species are here asisgned their proper genera.

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* When compared to Smith's description of *Calliopsis flavipes* this character is a clue that Smith described either the form of *C. coloradensis* Cresson from the southeastern United States, or an exceptional specimen of *Acamptopoeum* accidently introduced to Florida by man. Italics mine.

** The disc of the thorax is *thinly* covered with pale ochreous pubescence in the specimens of *C. coloradensis* from the southeastern United States but all known species of *Acamptopoeum* have the disc of the thorax densely covered.

I am indebted to Padre J. S. Moure, as mentioned elsewhere, for his notes and measurements on the first species, and also for advising me of the correct placement of the second species based on his examination of the type specimen.

ACAMPTOPOEUM MACULATUM (Smith) new combination

(Map 1)

Calliopsis maculatus Smith, 1853, Catalogue of Hymenoptera in the British Museum, 1:129, male; Cockerell, 1889, Trans. Amer. Ent. Soc., 25:196; Cockerell, 1901, Ann. Mag. Nat. Hist., (7)7:129 (transferred to *Spinoliella*); Cockerell, 1905, Trans. Amer. Ent. Soc., 31:321, female; Michener, 1951, *in* Muesebeck *et al.*, U.S. Dept. Agric., Monogr. No. 2:1103; Mitchell, 1960, North Carolina Agric. Exp. Sta. Tech. Bull. No. 141:293.

The description of the female type by Smith is given below.

"FEMALE. Length 4 lines [=8.47 mm.]. Black, the sides of the clypeus, a coronet-shaped spot above, on each side of it a minute lunate spot, and another at the base of the mandibles, yellow; the flagellum fulvo-testaceous beneath. Thorax, the disk has a fulvous pubescence, on the metathorax and beneath it is a griseous; the wings hyaline, iridescent, their apical margins having a slight fuscous cloud, the tegulae testaceous; the tibiae and tarsi above have a glittering pale yellow pubescence, on the tarsi beneath it is bright fulvous, the claw-joints ferruginous; the calcariae [tibial spurs] ferruginous, the extreme base of the anterior and intermediate tibiae yellow. Abdomen ovate, the margins of the segments narrowly testaceous, and having a marginal fascia of pale ochraceous pubescence, on the two basal segments usually nearly obliterated. Hab. East Florida. Coll. of F. Smith." [Collected by Edward Doubleday, Esq., in 1838.]

Supplementary description and measurements by Professors Padre J. S. Moure, T. B. Mitchell (1960), and Charles D. Michener (1965) are given below.

FEMALE. Length, 9.2 mm; forewing length, 7.4 mm; clypeal length, 0.65 mm.

Head. Yellow areas: (1) paraocular area a very small mark in lowermost corner and short, very narrow stripe adjacent to frontoclypeal suture running ventrolaterad from anterior tentorial pit; (2) clypeus on each side laterad from labral notch, dividing it about equally into thirds, middle third black; (3) absent on labrum; (4) supraclypeal area a spot; (5) subantennal plate a small spot; (6) mandible a basal spot. (7) Scape and pedicel black; flagellomere 1 with a vague yellowish mark on ventral (frontal) surface. (10) Punctures of frons and gena exceedingly minute, barely visible (30×), interspaces shiny; (11) Frontal line with lower portion a sharp raised carina. (12a)

Clypeus with punctures of disc deep, distinct, close, interspaces shiny. (12b)* Labrum with area basad from high premarginal carina punctate, area apicad to carina smooth, shiny, impunctate. (13a)* Inner orbits only slightly convergent below, orbital convergence ratio as 2.02:1.97,1.03. (13b) Facial fovea shallow, broad medially, narrowed almost to acute angle above and below. (15) Head width to head length as 3.20:2.18,1.47; abdominal width 3.25. (17)* Eye length, mio, and flagellar length as 1.60:1.97:1.76. (18) Interocellar, ocellocular, antennocular, interantennal, and antennocellar as 0.51:0.61:0.54: 0.44:0.71. Antennocular subequal to width of eye in frontal view. (19)* Ocellolabral shorter than clypeal width, 1.73:1.98,0.87. (20) Clypeocellar to outer subantennal sutural as 1.09:0.44,2.46. Outer subantennal sutural:inner subantennal sutural:width of subantennal plate as 0.44:0.22:0:31. Clypeal length 0.65. (22) Lengths of flagellomeres 1-4 and 10 as 0.20:0.14:0.16:0.16: 0.31. Flagellar width less than mow, 0.20:0.22. *Flagellar length about 2.1 times length of scape, 1.76:0.84.

Mesosoma. (23) Light areas absent. (24) Hair of dorsum abundant, rather short, and whitish. (25) Scutal and scutellar punctures very fine, close, deep and distinct, interspaces shiny. (26) Dorsal enclosure of propodeum slightly longer than mow, 0.26:0.22, surface unsculptured, not excavated, highly polished. (27) Foreleg with yellow spot on distal end of femur and base of tibia. (28) Middle leg with two yellow spots on femur and one at base of tibia. Lengths of tibia, basitarsus, and spur as 1.43:1.12:1.12 (spur as long as basitarsus!). Spur with several coarse teeth on apical two-thirds. (29) Hind leg dark. (31) Stigma 4.33 times as long as broad (includes costal vein), 0.88:0.20. (32) Marginal cell 6-9 4 times as long as broad, 1.73:0.43, and greatly exceeding 9-wt, 1.31. Prestigmal length 5-2,0.34. Wing 10-11/11-14 as 1.00:1.14; 11-12/13-14 as 0.22:0.14. Hindwing with 11 hamuli.

Metasoma. (34) Suberect hair of disc of tergum 5 dark in part. (35,36) Terga 1 and 2 with punctures of median area minute, close, interspaces shiny.

TYPE MATERIAL. Holotype female, No. 17.a.1800, from East Florida, collected by E. Doubleday in 1838, is in the British Museum (Natural History).

DISTRIBUTION. If this specimen was really captured in East Florida, it is presumably because it had been recently introduced there by man's activities. No other specimens of *Acamptopoeum* have ever been taken north of Colombia, South America.

DISCUSSION. The specimen is unquestionably a panurgine bee closely related to *Calliopsis,* and the list below summarizes certain key characteristics found in *maculatum* as to their occurrence in species of the listed genera and constitutes the evidence for my transfer of *maculatum* to the genus *Acamptopoeum*. The numbers refer to characters indicated in the description above;

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* Measurements kindly made by Prof. Charles D. Michener, July 1965.

+ means that the character of *maculatum* occurs in the genus; — means that the character does not occur in the genus.

Number	*Calliopsis*	*Acamptopoeum*	*Hypomacrotera*	*Liopoeum*
1	—	+	+	—
2	+	+	—	—
10	—	+	+	—
11	—	+	—	—
12b	—	+	—	—
13b	—	+	—	—
24	—	+	—	—
28	—	+	—	—

Items 12b and 28 seem absolutely diagnostic for *Acamptopoeum*. Item 28 shows a mesotibial spur as long as the middle basitarsus and coarsely toothed on the apical two-thirds. In *Calliopsis* only *squamifera* has a spur almost as long as the basitarsus, and it is completely bare (30×).

BICOLLETES SPEGAZZINI (Jorgensen) new combination

Calliopsis spegazzini Jörgensen, 1912, Zool. Jahrb., Syst., 32:121.

Padre J. S. Moure has determined the correct generic assignment from an examination of the type specimen.

BIOLOGY AND ECOLOGY OF *CALLIOPSIS ANDRENIFORMIS*

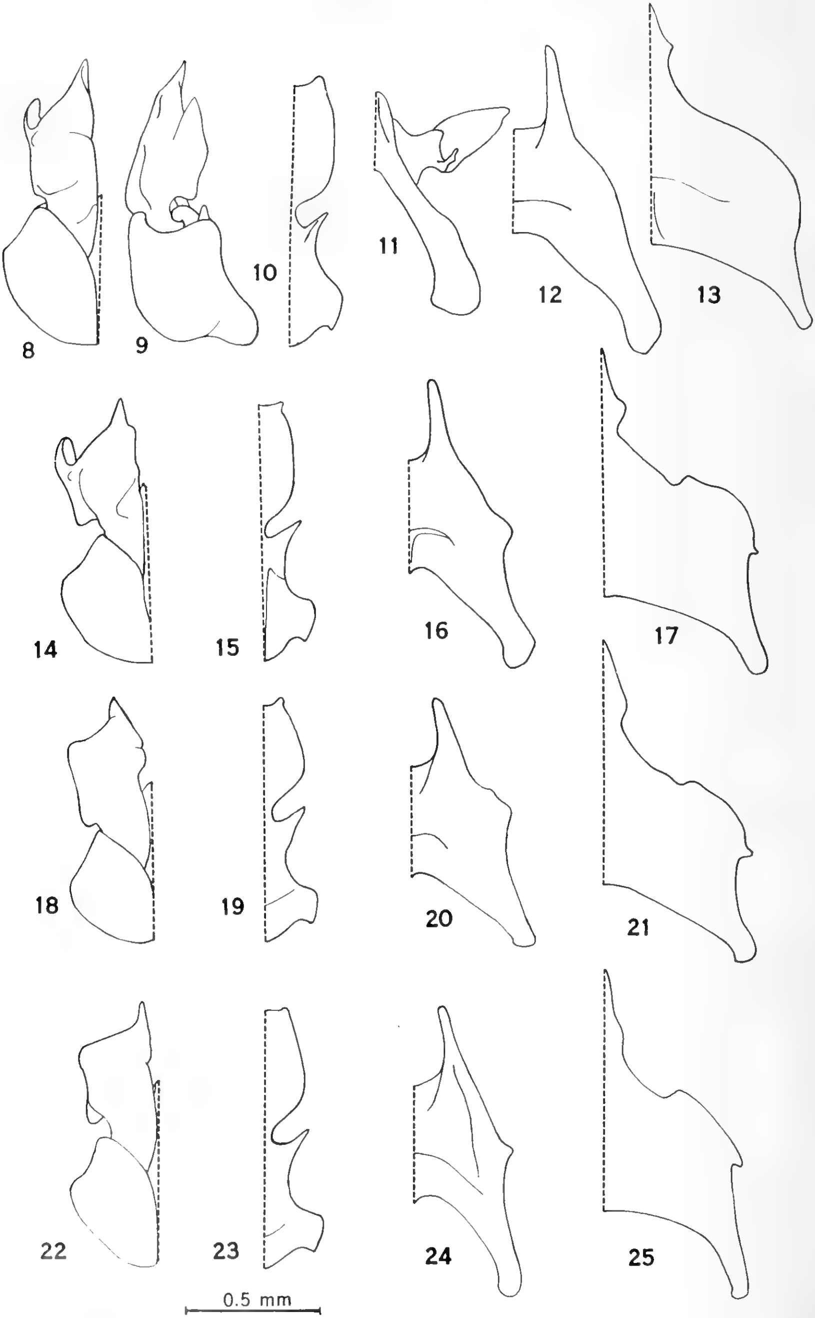
INTRODUCTION. This work on *Calliopsis andreniformis* Smith is meant to furnish a frame of reference for comparative studies in the biology and ecology of other species of *Calliopsis* and other burrowing bees. This is the most widespread and commonest member of the genus in the United States and Canada and is an apparently effective pollinator of many wild plants as well as alfalfa and various cultivated clovers.

Most of the observations were made on the campus of The University of Kansas at Lawrence, Kansas, with additional ones on the campuses of the public schools and of Stephen F. Austin State College at Nacogdoches, Texas; at Hancocks Bridge, New Jersey; and at Knoxville, Tennessee.

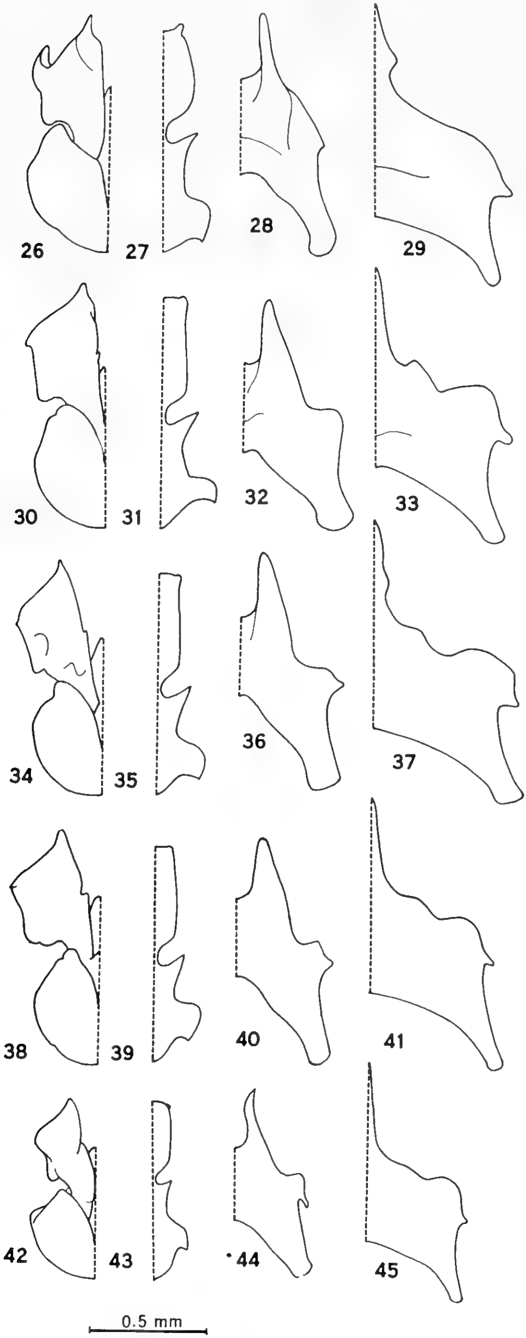
The Campus Bee has been proposed in the generic revision as the common name for this species because of its ubiquity on campuses of colleges and schools. Its closest relatives are *C. teucrii* and *C. hondurasica,* whose nest burrows are shown with those of *C. andreniformis* in Figs. 148-153.

Specimens documenting this study will be deposited in the Snow Entomological Museum of The University of Kansas, Lawrence, Kansas.

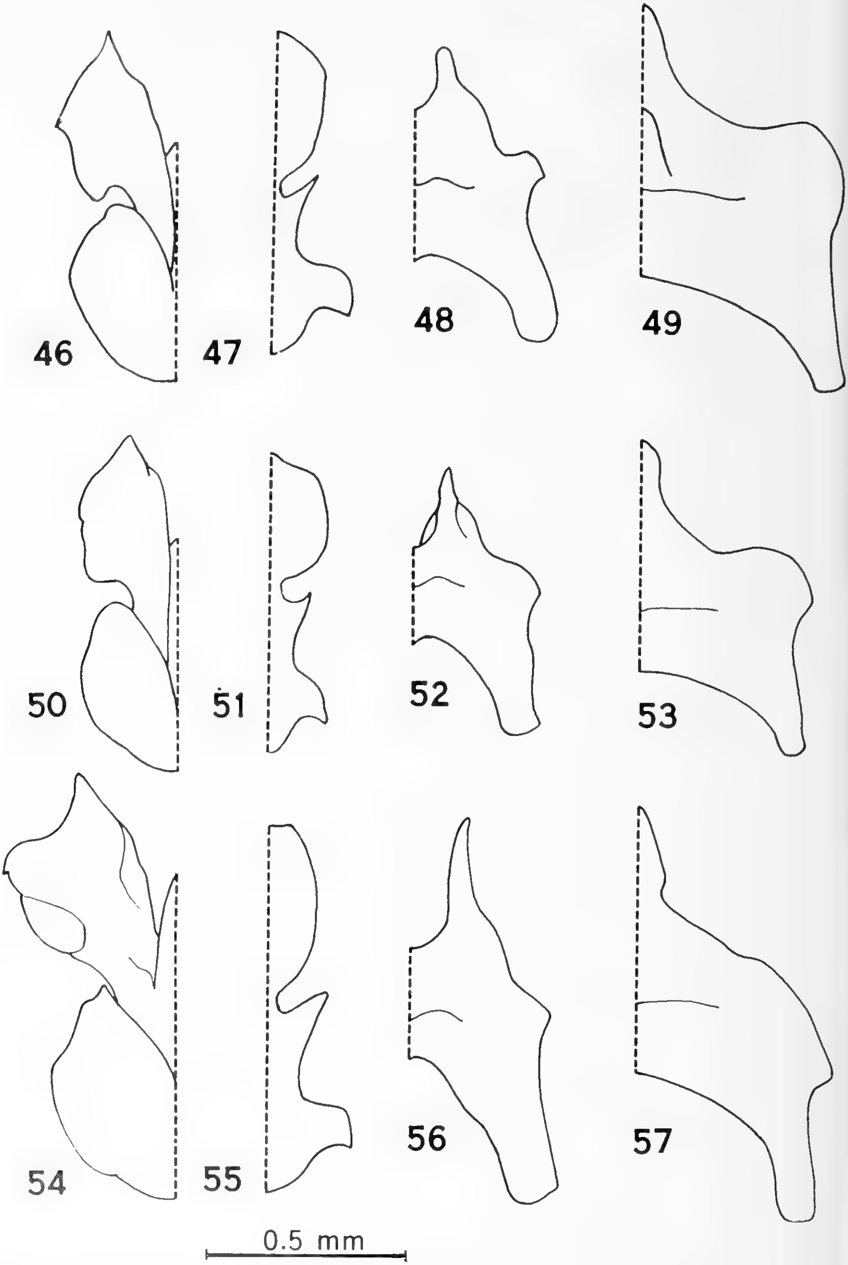
Techniques used in the study were in part obtained from Michener, Cross, Daly, Rettenmeyer, and Wille (1955). Weston dial thermometers were used



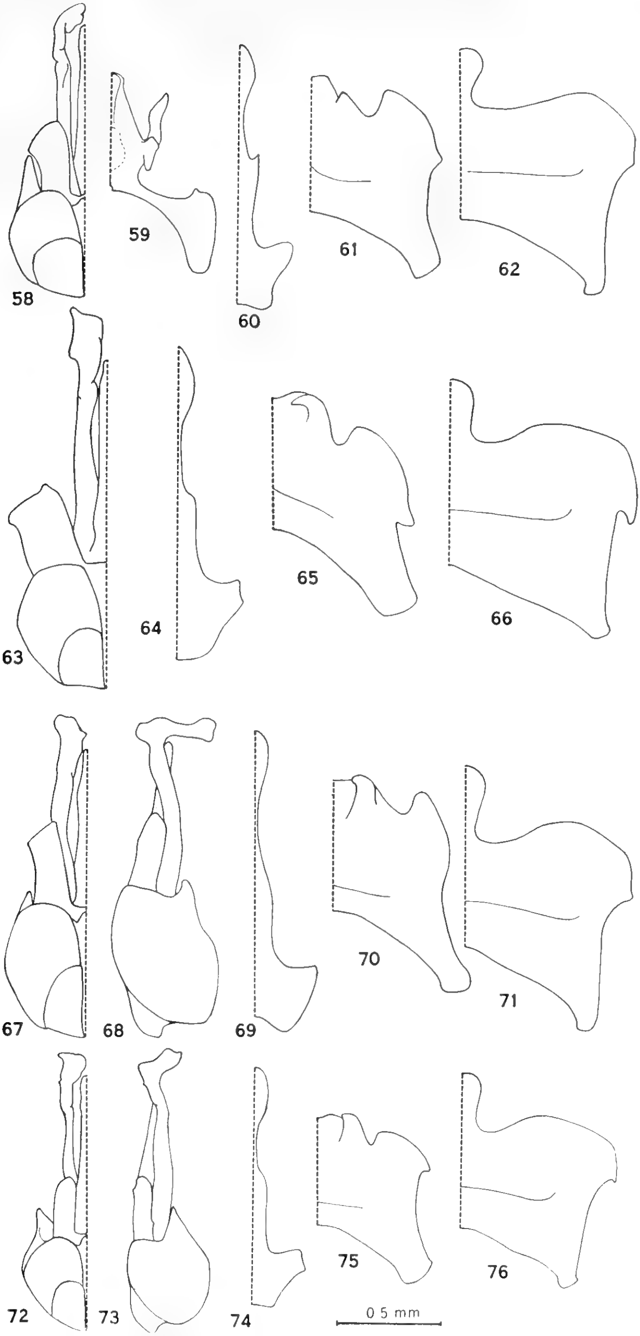
FIGS. 8-25. Male terminalia. Subgenus *Calliopsis*. Dorsal view of genital capsule (also lateral for *andreniformis*), ventral view of sterna 8, 6, and 5 (also 7 for *andreniformis*). 8-13. *C. andreniformis*. 14-17. *C. teucrii*. 18-21. *C. granti*. 22-25. *C. rhodophila*.



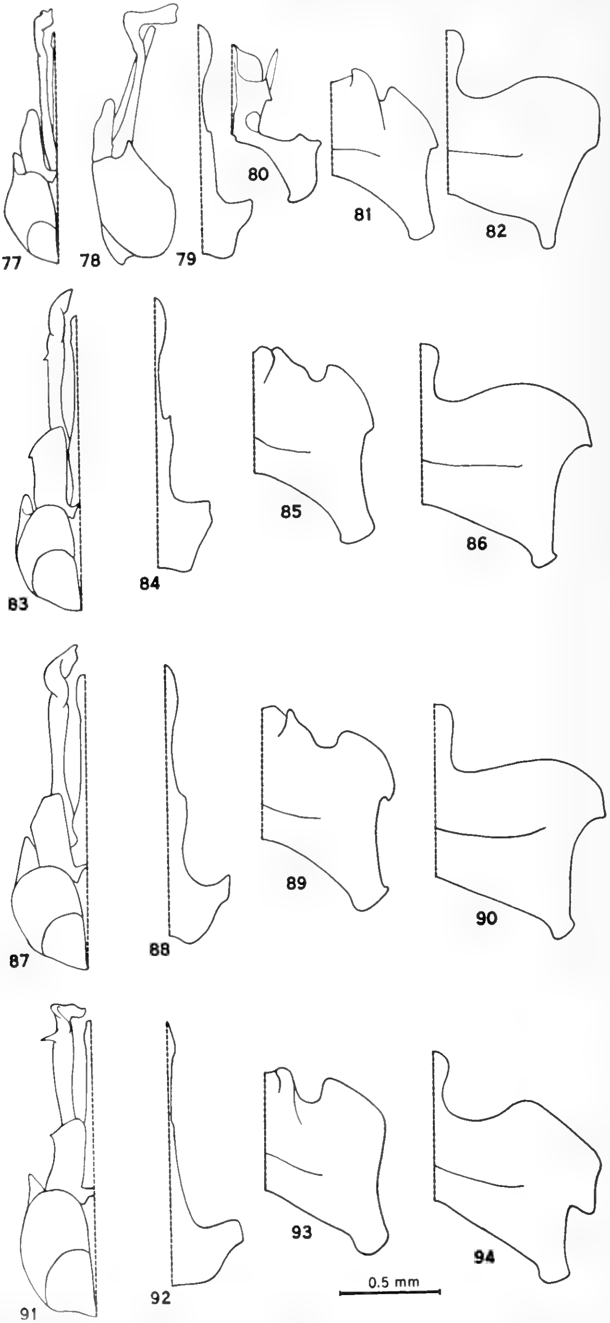
Figs. 26-45. Male terminalia. Subgenus *Calliopsis*. Dorsal view of genital capsule and ventral view of sterna 8, 6, and 5. 26-29. *C. mourei*. 30-33. *C. hondurasica*. 34-37. *C. sonora*. 38-41. *C. empelia*. 42-45. *C. squamifera*.



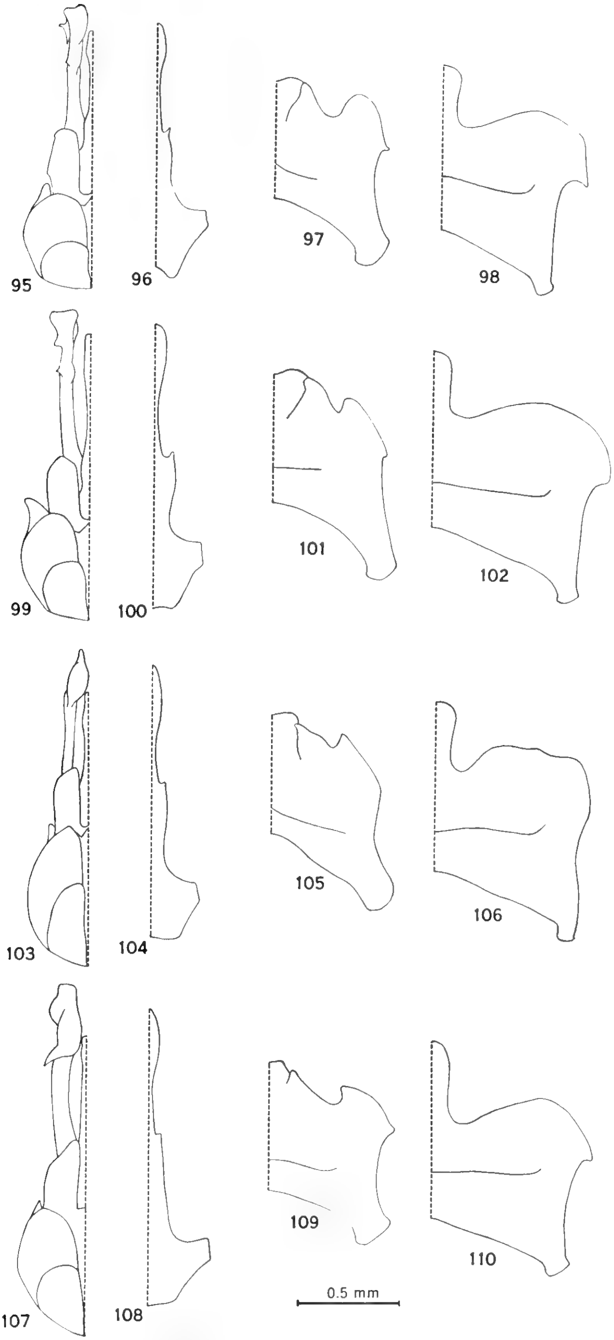
FIGS. 46-57. Male terminalia. Subgenus *Perissander*. Dorsal view of genital capsule and ventral view of sterna 8, 6, and 5. 46-49. *C. anomoptera*. 50-53. *C. rogeri*. 54-57. *C. gilva*.



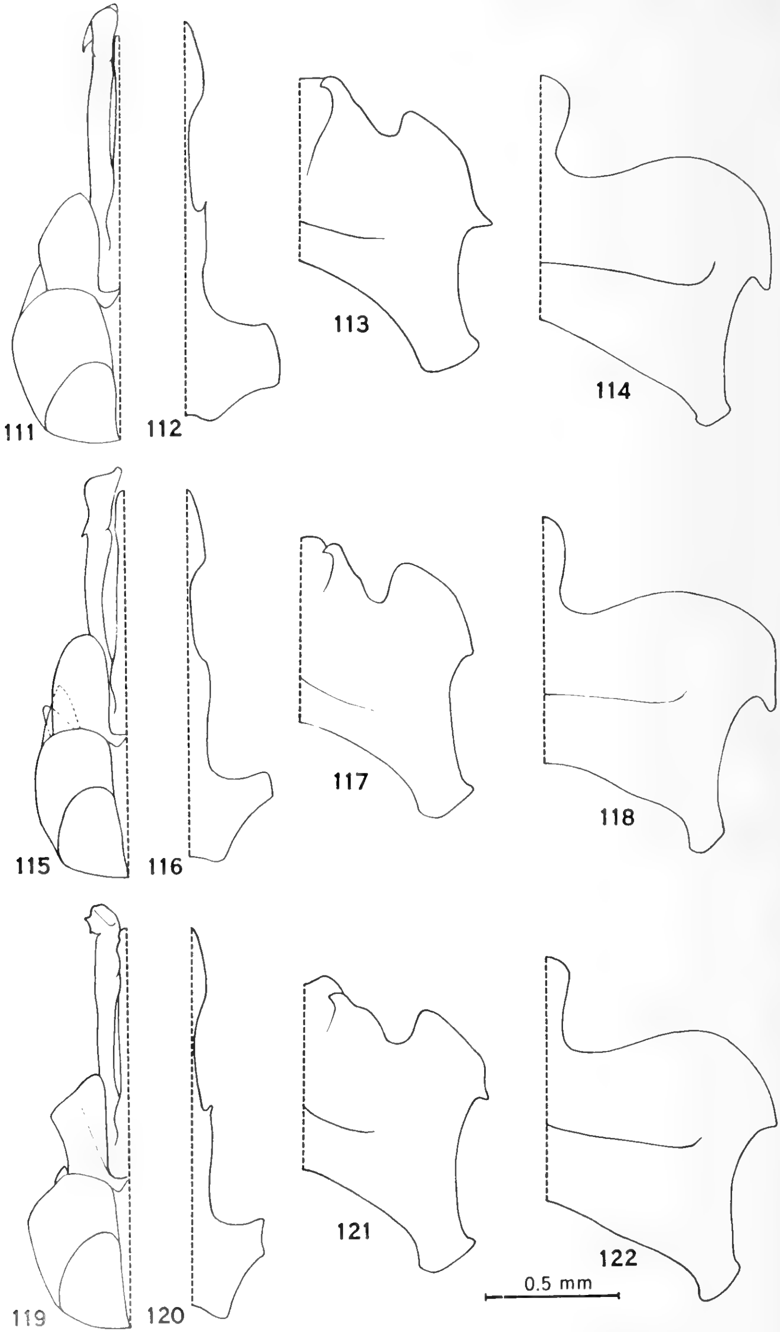
FIGS. 58-76. Male terminalia. Subgenus *Calliopsima*. Ventral view of genital capsule (also lateral view for *pectidis* and *timberlakei*) and ventral view of sterna 8, 6, and 5 (also 7 *rozeni*). 58-62. *C. rozeni*. 63-66. *C. coloradensis*. 67-71. *C. pectidis*. 72-76. *C. timberlakei*.



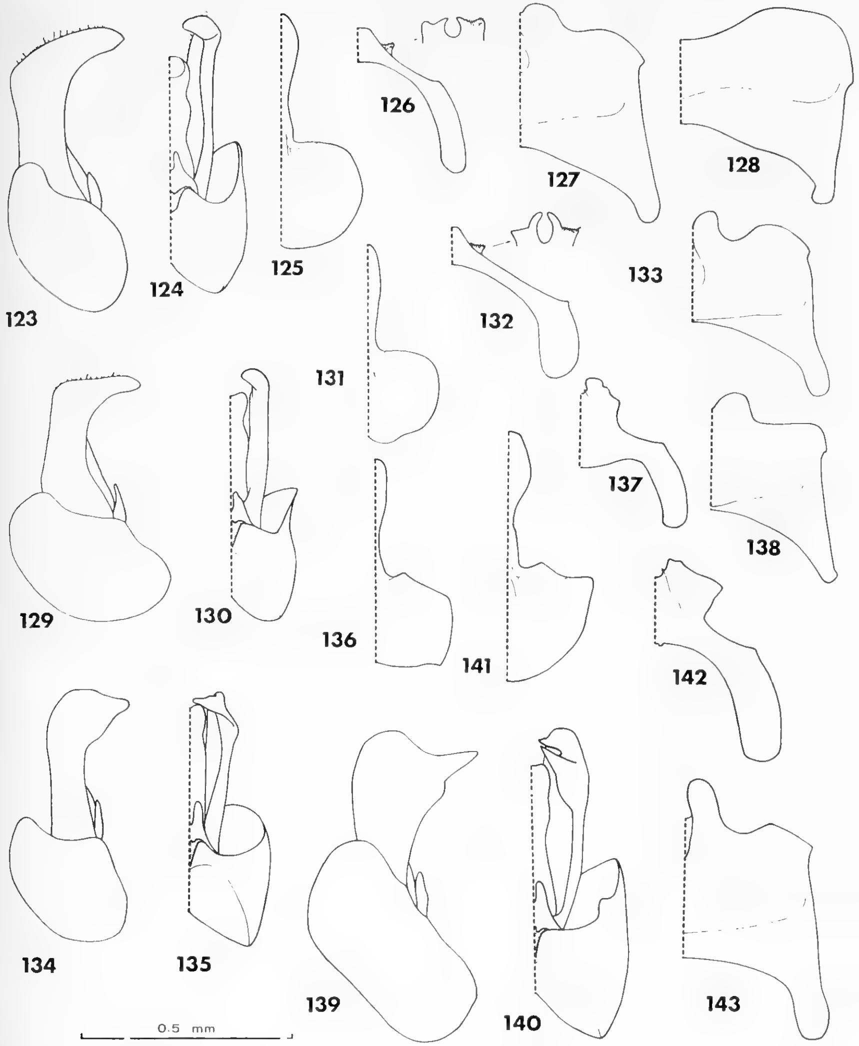
FIGS. 77-94. Male terminalia. Subgenus *Calliopsima*. Ventral view of genital capsule (also lateral view for *bernardinensis*) and ventral view of sterna 8, 6, and 5 (also 7 for *bernardinensis*). 77-82. *C. bernardinensis*. 83-86. *C. unca*. 87-90. *C. crypta*. 91-94. *C. azteca*.



FIGS. 95-110. Male terminalia. Subgenus *Calliopsima.* Ventral view of genital capsule and ventral view of sterna 8, 6, and 5. 95-98. *C. chlorops.* 99-102. *C. coloratipes.* 103-106. *C. deserticola.* 107-110. *C. pugionis.*



FIGS. 111-122. Male terminalia. Subgenus *Calliopsima*. Ventral view of genital capsule and ventral view of sterna 8, 6, and 5. 111-114. *C. hurdi*. 115-118. *C. quadridentata*. 119-122. *C. kucalumea*.



FIGS. 123-143. Male terminalia. Subgenus *Verbenapis*. Lateral and ventral views of genital capsule and ventral view of sterna 8, 7, and 6 (also 5 for *verbenae* only). 123-128. *V. verbenae.* 129-133. *C. nebraskensis.* 134-138. *C. hirsutifrons.* 139-143. *C. micheneri.*

for taking soil temperatures; fine copper screen cones were used for retaining bees as they came out of their burrows. Quick-drying acetate paints were used for marking individual bees, and roofing nails with yellow-painted heads bearing red numbers marked the locations of nest entrances. A string grid was fixed permanently in place for use in mapping the location of burrows. Excavations of nests were usually made by carving away the clayey soil with a sharp blade.

Because of its efficiency in pollinating legumes as well as a wide variety of other plants (see Table 8), *Calliopsis andreniformis* doubtless has an important ecological role in the maintenance of native flora. No quantitative assessment of this role has ever been made. Nonetheless, Crandell and Tate (1947) report that H. M. Tysdal observed (Unpublished, 1942) that the species was primarily responsible for very good seed set in alfalfa at Lincoln, Nebraska, over several seasons. They note, however, that *C. andreniformis* visits alfalfa flowers at a slower rate than *Megachile* and must be present in large numbers to effect a good seed set. Moreover, adults are present for a relatively short time, late June and July, and this limits their effectiveness. Their utilization in pollination would necessitate regulation of the flowering time of alfalfa or other plants involved to coincide with the period of adult activity. The same authors point out that this was not difficult at their nurseries in Lincoln, Nebraska, since the alfalfa blooms over a relatively long period.

My observations suggest that *andreniformis* would be a valuable pollinator of *Trifolium repens* and *Trifolium procumbens,* as well as alfalfa. Further discussion on the anthecology of the species appears under Flower Relationships.

The principal nesting habitat for *andreniformis* is bare, clayey soil, fully exposed to the sun, with leguminous plants of the clover group nearby. The farthest from a clover supply that any nesting site was located was about 59 m. In a tangled growth of virgin prairie on the campus of The University of Kansas, nests were made at the bases of the tall grasses and legumes in loamy soil. Even here preference was given to those small areas where the plants gave the thinnest cover, and the sun penetrated to the surface at least four hours daily. I have often found nests of the species in city ball parks or on school grounds, and these are the first places to look when in a new locality to see if the species occurs there in any numbers. Although the nesting sites usually have a slight slope, some very large aggregations have been found in flat fields, newly sown in clover and grass, e.g., football practice fields at The University of Kansas and at Stephen F. Austin State College, Nacogdoches, Texas.

The extremes of the flight period for the species are from early April to late September in the southern states, with peak activity in June and July; in the more northerly states it is from early June to early October, with peak activity in July and August.

A summary of the life history is as follows. The species over-winters as prepupae in closed, wax-lined cells in the ground. In spring the bees metamorphose and emerge as the active adults of the overwintering generation. Aggregations of males and females segregate by sex in digging their individual overnight burrows. In about a week mating is observed and females begin nest construction by, 1) making a cell at the bottom of the overnight burrow; 2) beginning a new shaft near the mid-point of the overnight burrow; or, 3) abandoning the overnight burrow and digging a new one. Females typically construct two nests of three or four cells each, provisioning each cell with a spherical ball of leguminous pollen and laying one egg atop it. In about two weeks these eggs have given rise to the adults of the first summer generation. This generation in turn constructs nests and lays eggs, some of which give rise to the second generation and some of which enter diapause to overwinter as prepupae. Apparently most of the eggs laid by the second generation produce young which enter diapause, for the adult population drops drastically by the end of July. Individual females, however, lay about the same number of eggs, seven, as the females of the overwintering generation. A few adults provision nests as late as September. The last of the adults dies by early autumn.

Relatively few data are available on the continuity of nesting sites of *C. andreniformis.* Ainslie (1937) followed the progress of an "exceedingly active colony . . . in hard trodden ground in front of a grocery store at Sioux City, Iowa . . . three years under observation and study, then for unknown reasons colonies could not be found where they formerly were populous." Crandall and Tate (1947) had an aggregation under study for two consecutive years. Michener and Rettenmeyer (1956) mention a nesting site for *andreniformis* at Lawrence, Kansas, which apparently persisted from 1949-1953, and had not returned by 1959. My observations in Kansas and Texas indicate that *andreniformis* will stay at least three years in the same nesting site if flowers are available for pollen.

STUDY SITES. Sites used in the study are listed and briefly described below. Major nesting sites for *C. andreniformis* on The University of Kansas campus were designated Horseshoe, Sunnyside Field, Athletic Field, Gym Area (West Stake, East Stake, Gym Path), Prairie Acre, Curb, Corner, Malott Path, and Smoke Stack; major sites at Nacogdoches, Texas, on the campus of Stephen F. Austin State College and vicinity, were designated Stadium, Raguet School, and High School.

Horseshoe is the only locality found by me that sloped northward. It was about 91 m from Michener and Rettenmeyer's (1956) site, which also sloped northward. The soil at Horseshoe is clayey, probably a clay loam, and is covered by fine stones and pebbles to a depth of about five mm. The top 2.5 cm of soil are black with tan soil below. The area surrounding it is somewhat woodsy with considerable shade, but Horseshoe is in the sun from 10:30 a.m. till about 5 p.m. After rains, Horseshoe takes longer to dry out than any other locality where I have found *andreniformis.* Moreover, the dried soil splits and cracks more than at any other locality. Much *Trifolium repens* and *T. pratense* were there along with lesser amounts of *T. procumbens. C. andreni-*

formis was first taken one week later than at the localities on south-facing slopes. *Halictus, Agapostemon,* and *Lasioglossum* are also common on flowers here.

Sunnyside Field, Athletic Field, Gym Area, Malott Path, and *Smoke Stack* are sites with clayey soil, less dense than at Horseshoe, and in general resemble neglected lawns where the grass is relatively sparse and considerable *Trifolium repens* grows. *Halictus, Lasioglossum, Augochlora,* and *Apis* were common.

Prairie Acre is a remnant of the original prairie of the region, with abundant wild flower cover and native grasses. *Psoralea tenuiflora* was common along with *Asclepias tuberosa* and other milkweeds. The nesting sites were at the bases of grasses and flowers where the growth was slightly sparser than elsewhere. *Megachile, Lasioglossum,* and *Apis* were the commonest bees.

Curb and *Corner* were bare, with many small and large stones that interfere with burrowing. *Lasioglossum* was the only other bee there.

The Texan localities, *Stadium, Raguet School,* and *High School,* were very similar, and much like the description above for Sunnyside Field *et al.*

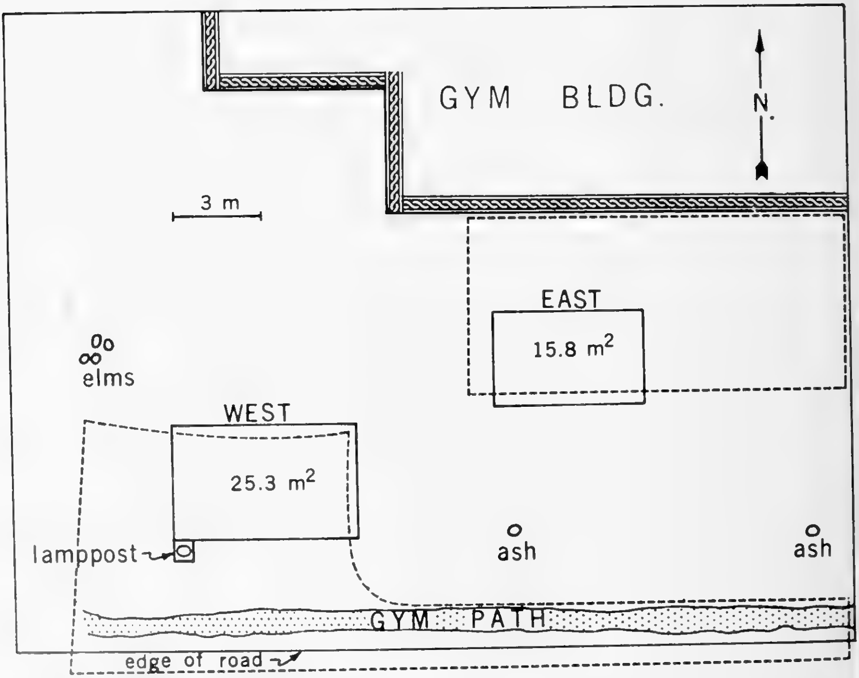


FIG. 144. Diagram of the East and West Stake plots at the Gym Area. The dashed lines enclose areas continuously exposed to sunlight from 10 a.m. to 3 p.m., whereas the remainder of the area was intermittently shaded by the leaves of the trees whose positions are shown on the diagram.

Panurginus polytrichous and *Lasioglossum* were the commonest bees at the *Calliopsis* nesting sites.

In order to study the seasonal development of nesting sites, two plots were chosen for intensive study during the summer of 1957 and 1958 in Kansas. Both were subdivisions of the Gym Area, called West Stake and East Stake (Figs. 144, 145, 146). A grid of squares 30 cm on a side was laid out on both areas with cord within about 3 days of the start of nesting activity on June 28, 1957. Arrangements were made to prevent cutting of grass by mowers in the area, and disturbance was otherwise minimized. The areas were close enough together that I could check activity on East Stake with binoculars while attending to other matters at West Stake. No emergence holes were present; the bees had just started this as a new area of aggregation and the full progression could be followed.

The soil at *andreniformis* nesting sites was of the loam, clay loam, or clay textural classes. At the Gym Area the soil became so hard upon drying that a scalpel was necessary to whittle it away in excavating burrows. The pH of the soil at the West and East Stakes was 7.43 to 8.79. Values for all other sites fell within these limits.

Distribution of Nests. Fig. 145 shows the distribution of nests in the West Stake plot, and a tabulation is made of them in Table 4. The density of nests varied with the barrenness of the soil. Bare soil, area 4, had about 6 times as many nests per unit of surface as the grassy areas 1 or 2, the vegetation of

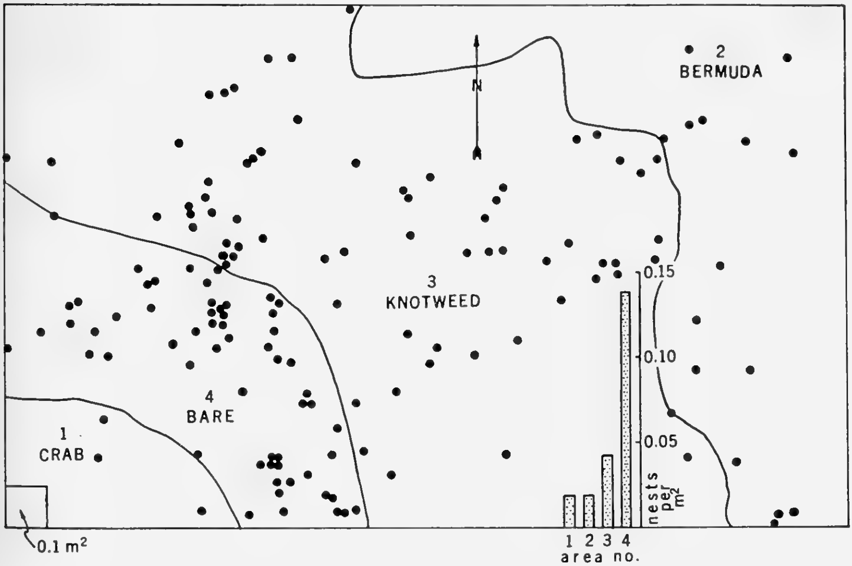


Fig. 145. Distribution of nests among different types of vegetational cover in the West Stake plot. The principal vegetation for zones 1 to 4 is indicated.

which covered a relatively large area of the soil. The density of nests in area 3 was about twice that in areas 1 or 2, and the vegetation of area 3 covered considerably less of the soil than that of areas 1 or 2. The density of nests was significantly different among the areas of the West Stake (Chi square equals 70.8, $P<0.001$).

TABLE 4. Distribution of Nests of *Calliopsis andreniformis* in the West Stake Plot (See Fig. 145)

AREA No.	AREA Dominant plant	Area in m^2	Number of Nests	No. of Nests per m^2
1	*Digitaria decumbens*	1.36	3	2.21
2	*Cynodon dactylon*	6.65	15	2.26
3	*Polygonum buxiforme*	13.39	66	4.93
4	Bare	3.92	56	14.29
	TOTALS	25.32	140	

$X^2 = 70.8, P < 0.001.$

Calliopsis andreniformis will persist in a nesting site until the site becomes more than 80% covered with vegetation, provided that its pollen source remains available. The nesting sites at Lawrence held good populations of the species despite grass-sowing. When the normally preferred, hard-packed clayey soil sites acquired a cover of grass and clover, the bees accepted sites with surface layers of coarse sand 25 mm deep, and dug down through it to reach suitably firm soil. In observations at Lawrence from 1957-1959, and at Nacogdoches from 1960-1962, there was no evidence of appreciable fluctuation in numbers of nests or of social parasites where the physical state of the nesting site remained relatively unchanged. Where grass cover left less than about one-fifth bare area and had little or no admixture of *Trifolium repens, C. andreniformis* clearly migrated elsewhere. This occurred at the Texan nesting sites, Raguet School and High School, and at the Kansan sites, Horseshoe, Sunnyside Field, Malott Path, and the East Stake plot, all of which had previously held good populations of the species. Males remained at Prairie Acre despite the high density of herbage.

The most spectacular effect upon populations of *C. andreniformis* was brought about by man's activities. The following locations are close together on the south side of the campus at Lawrence. A football practice field at Lawrence having approximately one nest with five larvae per 3.7 m^2 was plowed to 15 cm depth, reconditioned, and sown with grass in May. 1958. In the summer of 1958 only ten nests were found in this field which carried at least 4500 bees prior to the reconditioning. Beside a curbing more than 200 nests were dug up in placing an electrical conduit, with a loss of about 1000 bees. When the West Stake plot was run over by a truck approximately 600

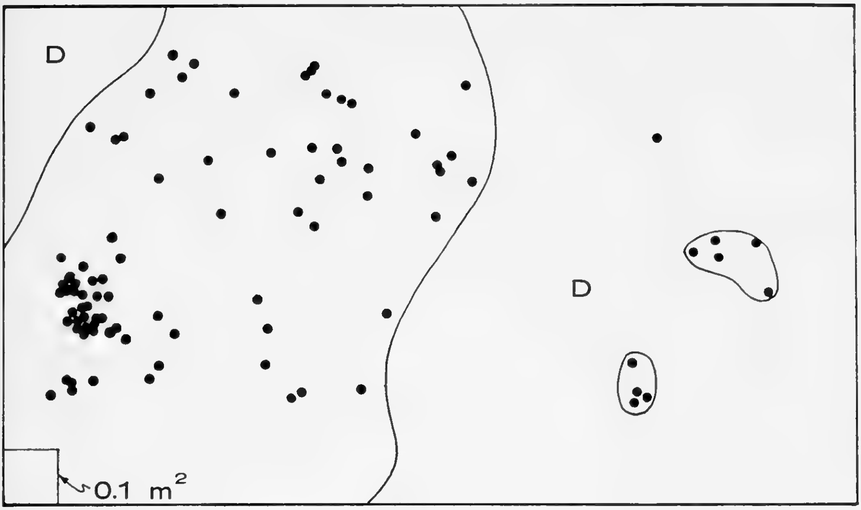


FIG. 146. Distribution of nests in the East Stake plot of the Gym Area. The letter D signifies a relatively dense growth of *Cynodon dactylon*.

bees were killed. Razing of buildings in the vicinity of the West Stake plot destroyed several thousand more. Thus between 7,000 and 10,000 *C. andreniformis* bees were destroyed in one season, the overwintering generation of 1957-1958, and the species was scarce in this locality in the summer of 1958.

Where *C. andreniformis* depends largely on *Trifolium repens,* it suffers when this clover is cut and its nectar and pollen become unavailable. This delays the time sequence of nest construction. On the other hand, cutting makes the clover season longer, and if the clover is not all cut at one time, the net effect is to extend the total length of the bee's active season.

A study of the changing pattern of sunlight and shade revealed that every nest burrow was located so as to receive continuous sunlight for 5 hours between 8:30 a.m. and 4:30 p.m. Especially striking was the absence of nests in bare ground along the southern strip of the East Stake. This seemed to be ideal nesting territory but *andreniformis* did not nest there, presumably because two ash trees cast a strip of shade there as the day progressed. I watched females come down to the shady area and investigate it for digging. Each often returned several times but eventually went a few inches north into the East Stake area and burrowed there (Fig. 146).

The bees are active up to 54°C soil surface temperature. At this temperature, however, they plunge quickly into their burrows and seldom loiter about on the hot surface. They fly, or attempt to fly, in winds up to 32 km per hour, but gusty winds of 48 km per hour discourage them and they spend much time in their burrows. Air temperatures between 27°C to 40°C characterized their most active flying periods with diminishing activity as temperatures fell to 21°C at which most flying ceased. In the soil they are sluggish at such temperatures. The area receiving continuous sunlight from 10 a.m. to 3 p.m. is shown in Fig. 144. Many suitable nesting sites were available for *andreniformis*, and numerous small aggregations of nests were scattered around the campus, mostly on the southward slopes. Other nesting sites were found within the city of Lawrence, but human activities usually ruined them for study.

Although nests of *andreniformis* characteristically are aggregated, there are always some that are rather isolated from others. Although it does not seem to hide its burrow entrances deliberately, it does succeed in doing so very effectively on occasions. About 10% sink their shafts against and under a twig or a leaf that is fairly well anchored in the ground. If large enough, such an object covers the tumulus. I have seen nests under prostrate dandelion leaves, aluminum chewing gum wrappers washed into the soil, and stones about 2 cm in diameter. Rozen (1958) has described a similar tendency in *Nomadopsis*.

At Horseshoe I initially netted *andreniformis* females but could not locate their tumuli. Since the resting burrows of males were readily located, the female burrows were expected nearby. I found them at the bottom of soil cracks as large as 150 mm deep by 13 mm wide. This location would have serious disadvantages when the next rain came, and likely would wipe out many of them as the cracks closed.

SEQUENCE OF NESTING IN RELATION TO PHYSICAL FACTORS. The sequence of nesting activity at the Gym Area in the East and West Stake plots, including the air and soil temperatures and rainfall is given in Fig. 147. The first nest burrows appeared after a rainfall of 1.6 cm which followed a dry period of 12 days during which less than 2.1 cm of rain fell. It seems likely that this sudden, drenching rain, which fell mostly between 8 and 11 a.m., triggered the nest-building activity at the Gym Area.

The first burrows appeared on June 29th and all activity ceased after August 13th, a span of 47 days. The bees which arrived to nest were doubtless the first generation (offspring of the overwintering generation). Emergence of the first summer generation is between four and six weeks after emergence of the overwintering generation. Most likely these bees emerged from a revegetated area which was bare the year before and migrated to the bare Gym Area.

The rainfall of their first four days in the area made burrowing easy, and the total number of active nests rose rapidly to a peak on the sixth day. As the soil dried and soil temperatures rose, burrowing activity dropped to a minimum until the next soaking rain on the 13th and 14th days, June 9th and 10th. Again the total number of active nests rose to a maximum on the sixth day following the rain. The second peak of activity is much broader than the first and represents the emergence of the second spring generation plus further burrowing of the first spring generation. Most burrowing activity had died down by the 27th day, July 24.

I decided to wet the plots using a garden hose; enough water was sprayed to moisten the soil to a depth of six to seven cm, that is, to the level of the first to third cells below the ground. I believe the third, weak peak of burrowing activity is attributable to this watering, but I had no control test for it. Fifty-five dormant nests were reactivated.

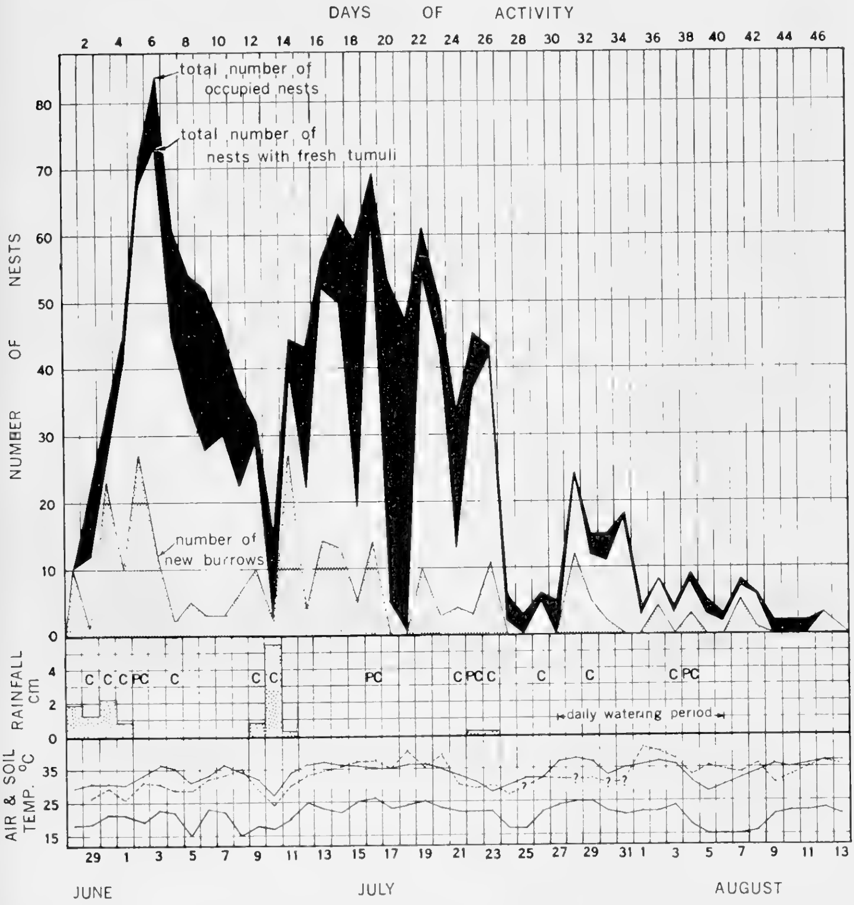


Fig. 147. Graph of nesting activity at the Gym Area. The solid black area gives a measure of the nests which are not abandoned, but are inactive for a particular day. The white area includes nests previously begun and currently active, while the stippled area shows the number of active nests on a particular day which are new burrows. In the rainfall diagram, C means cloudy, PC means partly cloudy, and days without a symbol were clear. The daily maximum and minimum air temperatures are connected by solid lines; the dashed line connects values for maximum soil temperatures at a depth of 12 cm. The question marks signify that no value was recorded for that date.

SPRING EMERGENCE. The nest burrow fills up completely with soil during the winter months of rain and snow, freezing and thawing. The adult emerges by crawling through the soil plug in the neck of the cell; it does not break through the waxed wall. Apparently it displaces dirt behind it into the cell as it digs its way out. Emergence holes are close to the original burrow entrance. Males and females appear almost simultaneously, but more males appear to emerge than females.

The factors which influence emergence of the overwintering brood are soil temperature, in turn influenced by slope, exposure, and rainfall. As mentioned previously, bees nesting on a south slope are out a week earlier than those on a north slope.

The emergence of the overwintering brood was best correlated with the flowering of *Trifolium repens* (White Dutch Clover, the common lawn clover) at Lawrence, Kansas; Nacogdoches, Texas; and Knoxville, Tennessee. The species usually emerged about a week after the first flowering of *T. repens*. At Lawrence, *T. procumbens, Melilotus officinalis,* and *Verbena bracteata* flowered within a week of first emergence of *C. andreniformis* in 1957-1959. This close synchrony did not hold true for *T. procumbens* and *M. officinalis* in Texas, 1960-1962, or in Tennessee, 1963-1964, and the last species was not found in the Texas or Tennessee study areas.

PRENESTING ACTIVITY AND RESTING BURROWS. The prenesting activity lasted 7-12 days at different sites. Females and males flew about the area from which they emerged, resting on the ground or on sticks, twigs, and light-colored objects. Females were especially attracted to the painted yellow heads of the roofing nails used to mark burrows.

Although some 40 marked female bees which emerged from an established aggregation in the Gym Area dug burrows there, some bees possibly migrated out of their original area either by intent or because they did not know the landmarks well enough to return. I lost 10 out of 20 marked males and females at Smoke Stack in 1958 within 10 days after their emergence (death or predation could, of course, have caused the loss).

At night the females rest in vertical or slightly slanting, closed burrows which they dig about 50 mm deep. The males do not rest in burrows with the females but make their own, which are usually about 25 mm deep. When the nesting site is established, males rarely have overnight burrows among those of the females, or even on the fringe of the site. They usually are as much as 6 m from the nearest female's nest.

At Prairie Acre 12 tumuli of males were crowded into an area of 0.046 m^2, some within 25 mm of each other, with a 10 mm depth. Many more tumuli were scattered around the edges of a patch of *Psoralea tenuiflora*. The burrows were initiated between tangled roots. The ground stayed damp because of the density of the vegetation. I trampled down some of the grass so that sun would shine to the ground, and many more tumuli appeared in this spot than in the less accessible and damper areas.

Two males at *Horseshoe* were timed from the start of digging of their burrows until the last movement was seen in the tumulus covering the burrow. A large male began at 3.25 p.m. and finished 34.5 minutes later. The resultant conical tumulus was 15 mm wide and 9 mm high at the center. A smaller male began at 4:28 p.m., same date, and finished 36.5 minutes later at a depth of 25 mm. Both males and females return to their same burrows night after night. The female usually deepens her burrow into a nest but may dig a new burrow or make another tunnel down from the original entrance.

Both sexes dig with their mandibles and their front feet, passing the dirt along under them and giving it an expeditious kick out of the burrow. As dirt accumulates and begins to drop into the burrow, the bees apparently pass the dirt upward as before and then press it upward with the tip of the abdomen.

Night burrows of male and female can be distinguished because the tumulus of the female is much the larger of the two. The average dimensions of 104 tumuli cast up by females by 7 p.m. of the first night's digging of a burrow were 23.3 mm wide by 6.1 mm high. The comparable figures for 9 males were 11.4 mm wide by 4.5 mm high. The largest tumulus of a male was 13 x 18 x 4 mm high at the center. The smallest tumulus of an overnight burrow of a female was 20 x 12 x 4 mm high, with nearly all others being larger than 20 mm diameter by 7 mm high at the center. The periphery of the tumulus of *andreniformis* is not always round; a slightly compressed circular outline or very broad oval frequently results from the way the soil is pushed out of the burrow.

MATING AND MALE PATROLING. Mating takes place on clovers (rarely) or other flowers or at the nesting site. Stevens (1950) took mating pairs in North Dakota on *Lactuca pulchella* (Blue Lettuce) in early July. Mating attempts at clovers usually are met with evasive action or resistance by the female. At the nesting site a male advances from behind, mounts the female, usually biting at her wings. Copulation lasts 2 minutes or less. Sometimes the two fly away *in copulo*. I have only a single record of a female which was mated more than once during the brief time I kept her in sight, and she did not resist a second mating. Often the first male on the female is pulled off as a succession of males try to mate with her. Females with huge pollen loads mate in the nest area.

The males patrol fairly well prescribed routes which they seem to consider their own property. They choose a favorite spot in this route—a twig, stone, or leaf—and set forth in a definite flight pattern, then return and alight repeatedly at the same place. If another male intrudes upon this flyway, an aerial "dog-fight" occurs. The two rise vertically, tumbling over each other in aerial acrobatics. If one catches hold of the other they fall to the ground, kicking up dust and biting each other. The intruder soon leaves, as I know from four marked males that became involved in such fights. This seems to be a clear instance of territorial behavior. The flyway is from 2 to 5 m long, and is not necessarily straight. Two males may have adjacent flyways with one loop of one overlapping that of the other; if they chance to meet a fight is sure to ensue. Males captured and marked with paint return to their flyways as if nothing had occurred. Two records of different males give some idea of the amount of time spent in a flyway versus that spent flying over nearby clover. One male spent three minutes in the flyway, one and a half minutes over clover, then ten minutes back in the flyway. During the ten minutes in the flyway it rested on the ground for periods of 11, 8, 3, 6, and 6 seconds respectively. A second male alternated between flyway and clover as follows: 5, 2, 6, 5, and 3 minutes respectively.

I have never seen a male try to copulate with any insect or object other than a female *Calliopsis*. An apparently non-receptive female is sometimes pursued from flower to flower by a number of males.

NEST STRUCTURE AND CONSTRUCTION. In beginning her burrow, *andreniformis* shows a characteristic pattern which I have not seen in other bees. She bites the soil into a sloping arc to make her entranceway, then digs the shaft more or less perpendicular to the ground level. The female may begin several entrances, some clockwise and some counterclockwise, before proceeding with the sinking of the shaft. Females with full pollen loads dig burrows with front legs and mandibles. Wille and Michener (1951) give a female's progress as 44 mm in 30 minutes digging. The rate of progress depends upon soil moisture. They do not carry water but wait until the soil is moist enough to work. Hence, immediately after a rain, numerous tumuli appear. Many are made by bees that have not dug previously, but some are made by females that have provisioned three or four cells (evidence from four marked females). They may start a new nest rather than sink the first one deeper. This seems a waste of energy, for the average depth to the top of the first cell is 54 mm, whereas later (lower) cells are made with an average vertical distance between them of only 7 mm, usually at different compass bearings from the main shaft.

The tumulus thrown up seems always somewhat moist, and it may be that it is at this time that the female imparts an odor to the tumulus, possibly by adding secretions to the soil to soften it. The tumulus is always a closed mound, the entrance of the burrow being filled by the loose soil. Wind or rain will eventually obliterate the tumulus, but the upper 25 mm or more of the burrow remains filled with loose dirt. The female may chew out some of the upper wall of the burrow to keep an adequate dirt fill in the shaft.

Pickles (1940) reported that the tumulus of *Andrena armata* is more alkaline than the ordinary soil from which it is dug. His published data, however, are not statistically significant for the soil of the mounds, although the central core is decidedly more alkaline than the ordinary soil or the soil of the rest of the mound. Twenty-six paired samples of soil dug from burrow walls and the tumuli from the same nests from several localities were tested for differences in pH. A glass electrode pH meter and soil:water ratios from 1.10 to 1:17.5 were used for the tests. The mean and standard error of the pH of the soil of the burrow walls was 8.169±0.0590 and that of the tumuli was 8.198±0.0666; the difference is not statistically significant. The range in pH of the samples was between 7.4 and 8.6.

Diagrams of the nests of *C. andreniformis, C. hondurasica,* and *C. teucrii* are shown in Figs. 148-153, and Table 5 gives dimensions for nests of *C. andreniformis.* The diameter of the main shaft of *andreniformis* is sometimes slightly constricted at ground level by 0.5 to 1.0 mm, and this applies to the only nest of *teucrii* found. Professor Alvaro Wille of the University of

TABLE 5. Dimensions of Burrows of *Calliopsis andreniformis*

(All dimensions are in mm)	*N*	*Mean*	*Standard Error*
Diameter of burrow, 25 mm below ground level	18	3.688	0.1291
Same, male burrow, 10 mm below ground level	4	2	NA
Length of plug at entrance	14	32.0	3.04
Depth to top of first cell	70	55.16	1.416
Depth to top of second cell	49	62.90	1.426
Depth to top of third cell	31	72.68	2.087
Depth to top of fourth cell	22	80.32	2.365
Depth to top of fifth cell	16	83.81	2.261
Depth to top of sixth cell	9	86.80	2.351
Depth to top of seventh cell	9	83.22	0.707
Depth to top of eighth cell	9	90.89	1.871
Depth to top of ninth cell	9	97.66	2.483
Depth to top of tenth cell	3	106.00	1.155
Minimum depth to top of first cell	1	34	NA
Maximum depth to bottom of last cell	1	162	NA
Weighted mean number of cells per nest	70	3.375	NA
Depth of female overnight burrow	15	51.20	2.590
Depth of male overnight burrow	26	26.00	1.277
Length of lateral burrow	16	8.00	0.713
Diameter of cell	17	3.871	0.0757
Length of cell	19	7.842	0.2356
Diameter of first night's tumulus, female	20	22.90	0.894
Diameter of first night's tumulus, male	9	11.56	1.291
Maximum height of first night's tumulus, female	20	6.75	0.673
Maximum height of first night's tumulus, male	9	4.56	1.232

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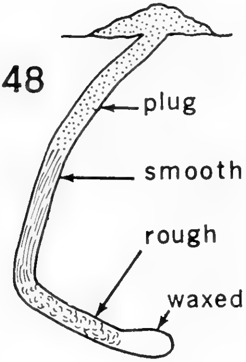

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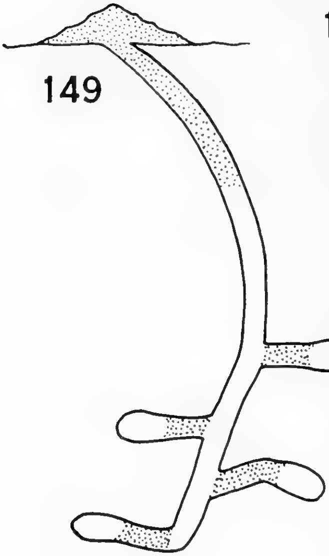

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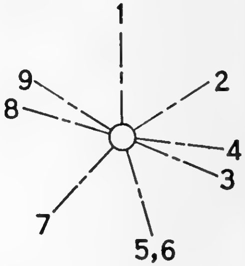

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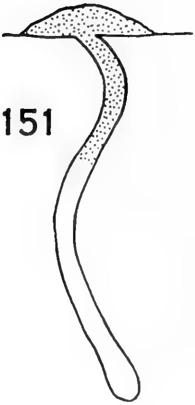

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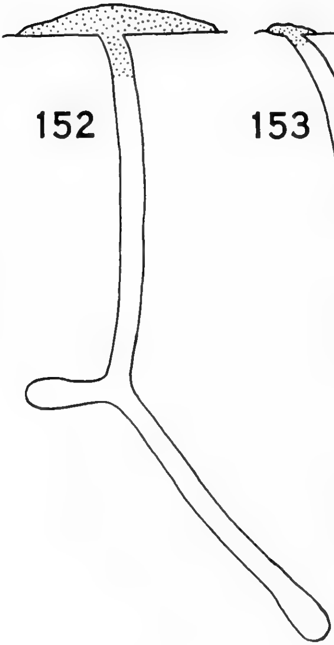

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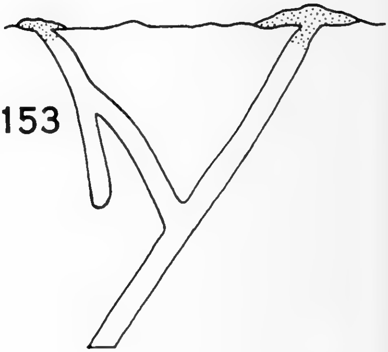

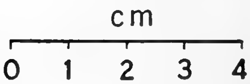

Costa Rica drew the nest diagrams of *hondurasica* based on excavations he made in a little used road at Playa del Coco, Guanacaste Province, Costa Rica. The only dimensions he recorded were the depths of cells. The architecture of all three species is closely similar so far as is known. No data are available on the cells of the nests of *teucrii*, but the diameter of the burrow is 4 mm, which falls within the range for that of *andreniformis*.

After the entrance has been made the nest may be continued vertically downward or may slope; in the latter case it may be irregularly helical. If helical, the burrow usually follows the direction of the arc set at the entrance hole. Only one cell is placed at the end of each relatively short, lateral burrow. If the main burrow is a helix, the cells may be built off from it regularly clockwise or counterclockwise as the helix goes deeper, but some cells show regressions (Fig. 150, cell 4), and others are built one directly below another.

Only two nests of *andreniformis* with a double entrance were discovered in the course of the study. Several nests had a single opening with a slanting, blind burrow of about 50 mm depth to one side slightly below the entrance. Probably these were cases where females dug new burrows rather than deepening their night burrows of the prenesting period. The only nest positively identified as that of *C. teucrii* had both a double entrance and a blind burrow (Fig. 153).

One nest was provisioned by two different females at the same time. Unfortunately this was one of the casualties when a truck ran over the West Stake site and I do not know the architecture of the nest. Two instances were found, in August 1957, of females taking over abandoned, provisioned nests. The second females added 3 and 4 cells respectively to nests of 5 cells and 3 cells. This was determined by dusting bees and tumuli with metallic red powder when they first took over the nests, and then observing which cells of the excavated nests showed the metallic powder.

The cells for the developing young are short, oval, and the short lateral burrows to which they are attached often slant *up* from the main shaft. The cell slants slightly downward toward its apex. The neck is closed with soil, packed tightly and filling the lateral burrow (Fig. 149). The interior of the cell is beautifully smoothed and coated with a wax-like substance which is insoluble in cold carbon tetrachloride, cold 95% ethyl alcohol, and cold water, but dissolves instantly in ethyl ether. The thin, pliable coating of the spherical pollen ball in the cell is demonstrated by placing the ball in glacial

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FIGS. 148-153. Diagrams of nests of three species of *Calliopsis*. FIG. 148. *C. andreniformis*, showing regions in a burrow. FIG. 149. *C. andreniformis*, a typical nest for the species. FIG. 150. *C. andreniformis*, top view showing disposition of cells about the central burrow; cell 1 is uppermost and this nest is a "clockwise" nest except for cell 4. FIGS. 151, 152. *C. hondurasica*, as interpreted from field sketches from Prof. Alvaro Wille. FIG. 153. *C. teucrii*, Coaldale, Colorado.

acetic acid and slicing it with a sharp blade. The internal pollen mass retracts from the coating and is easily seen.

Cells are made and provisioned from the upper level downward. The time required to complete a nest varies with the kind of weather, and, on The University of Kansas campus, with the frequency and thoroughness of mowing the grass and clover mixed with it. Infrequent mowing allowed the bees to have clover supplies for relatively long periods of time between drastic drops in their major pollen source.

A female of *andreniformis* customarily makes two nests. The average number of cells per nest is about 3.4. This figure is derived from excavations of burrows where activity had ceased, and may be biased by accidental death of the maker (see Table 5). It is my impression that nests made later in the season when the ground is hard and dry are more frequently deeper with more cells per nest, but I lack adequate data to substantiate this impression. The largest number of cells found in a single nest was ten, in a nest dug in Malott Path, August 1957.

Other than the chasing of *Holcopasites* out of the nesting area by the male *andreniformis,* I have seen nothing which would be construed as a protective tactic. The female did not even try to re-establish the tumulus over her burrow when I pushed it aside, but the tumulus did not seem to discourage social parasites anyway, with the possible exception of *Parabombylius,* which only flips eggs into burrows without tumuli.

IMMATURE STAGES. Table 6 gives sizes and weights of eggs and pollen balls. The eggs are slightly arcuate upward when in position on the pollen ball, have rounded ends and their middle portions may contact the pollen ball (Fig. 154) or may be raised above it. At a temperature of 30°C six eggs

TABLE 6. Physical Data on Adults, Eggs, and Provisioning of Nests of *C. andreniformis*

	N	*Mean*	*Standard Error*
Weight of female, mg	23	12.35	0.367
Weight of male, mg	5	6.440	0.1311
Length of egg, mm	6	1.295	0.1213
Width of egg, mm	6	0.3666	0.02646
Length of pollen-collecting trips, minutes	13	70.5	9.97
Time spent in nest between pollen-collecting trips, minutes	15	7.33	2.964
Pollen load (both legs), mg	7	1.529	0.1460
Pollen ball, mg	7	10.86	0.407
Pollen ball, diameter, mm	11	2.475	0.1567
Calculated number of trips for one pollen ball	7	7.10	0.71

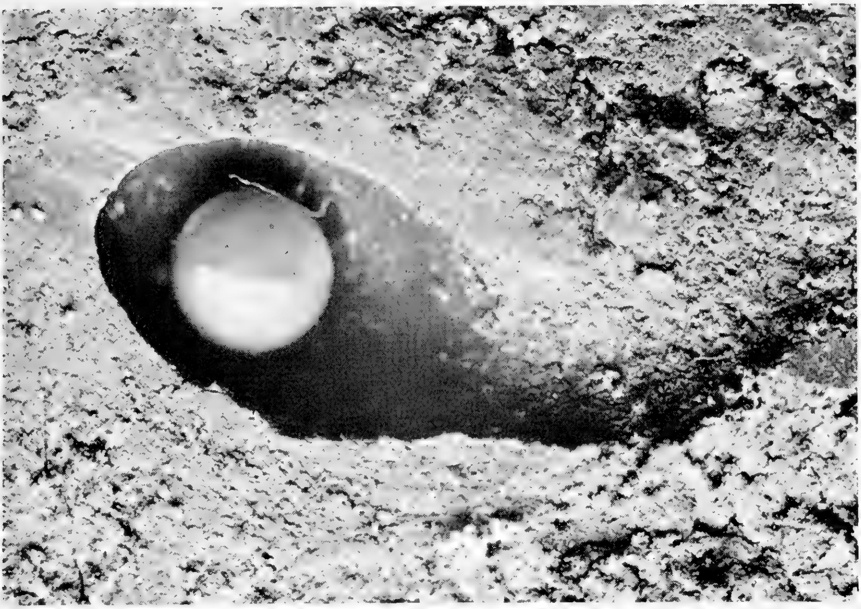

FIG. 154. Top view of the wax-lined cell made by *Calliopsis andreniformis* showing the pollen ball and egg in place. Note the mandibular markings in the wall of the lateral near its junction with the neck of the cell. The broader end of the egg is the anterior end and faces the opening of the cell.

hatched in between 24 and 48 hours. The exact time of hatching is difficult to determine because the chorionic membrance is not visibly shed, but rather seems to be absorbed.

The egg is oriented with the broader, head end toward the entrance, or plug, of the cell (Fig. 154). The posterior end is somewhat tapered. When the egg becomes a first instar larva, the larva seems to spread a secretion on the pollen ball surface, then uses its mandibles to break into the pollen ball. Perhaps it is a combination of a secretion and the action of the mandibles that opens up the enveloping coat of the ball and allows the larva to begin feeding. As the larva continues to feed, it eats downward on the pollen ball so that it eventually rests on its back, rear toward the entrance of the cell, a vestige of the pollen ball on its venter, and head toward the apex of the cell. Wille and Michener (1951:56,59) made similar observations.

After the larva has fully fed it reorients with its head toward the cell entrance and rests for 2-4 days. Defecation then begins, with the excrement being plastered on the distal, upper end of the cell wall (Fig. 149) by the lateral and circular movements of the posterior end of the larva. Several fully fed larvae were placed in gelatin capsules which approximated the curvatures of their cells. They performed the above process visibly within the capsules.

Larvae do not have to have a wall against which to void excrement. They will do so lying on their backs in the small plaster rearing cells described under laboratory rearing methods. In the latter case the excrement is voided as a stringlike mass which coils itself under the larva. Under such conditions the excrement often is like a string of toad eggs, each segment somewhat flattened and about 0.33 mm long. This long golden length is followed by pasty, gray matter which is smeared uniformly over the other excrement on the cell wall.

Molting larvae presumably eat their shed skins as none are found in the cell. It takes the developing larva 6-8 days to consume the pollen ball at a temperature of 27°C. After defecation the larva can either become quiescent for 3-5 days and then pupate, or it may go into diapause. Fig. 155 shows a lateral view of two overwintering prepupae, and Michener (1953a) described and figured the prepupal head, mandible, spiracle, and full lateral view. The pupal stage lasts about 10 days in the summer. After the pupal skin is shed, the adult remains quiescent, and in about 36-48 hours a gray liquid suspension is voided. The adult usually remains inactive for a day or so under laboratory conditions; after that it becomes active.

An attempt was made to differentiate male and female prepupae on morphological or morphometric bases. No significant external morphological difference was found between the sexes. There was so much overlap of prepupal weight, width of head capsule, width of body, length of body, and intertubercular distance that these measurements were impractical to use for separation of sexes.

LABORATORY REARING. Immature specimens of *C. andreniformis* from egg to prepupal stage were taken from cells and placed in various containers at different relative humidities and temperatures in order to rear them to adulthood. No eggs or young larvae were reared through to adults. The earliest stage which was reared to an adult was one in which the pollen ball was about two-thirds consumed.

The most convenient rearing container for a large number of specimens was a cigar box coated with paraffin and with its top replaced by a piece of glass for observation of the specimens. The cigar box can be made airtight with putty. It may be important to isolate specimens from each other if mold spore contamination is widespread. In order to handle individuals easily, small rectangular blocks 18 x 25 x 9 mm deep were made of plaster of Paris and a depression 8 x 12 x 5 mm deep of the approximate shape of the lower half of a bee cell was excavated in it by means of a hand-held grinding tool. The depression of the block was coated with paraffin. The upper surfaces surrounding the depression would take pencilled identification symbols. With this system individuals could be easily shifted from container to microscope stage with the least disturbance.

Obtaining specimens for laboratory work was an exasperating undertaking. Excavation was not difficult, but opening the cell containing the developing bees without getting grains of dirt on the pollen ball, egg, early developing larva, or, worst of all, in the moisture condensate often found in

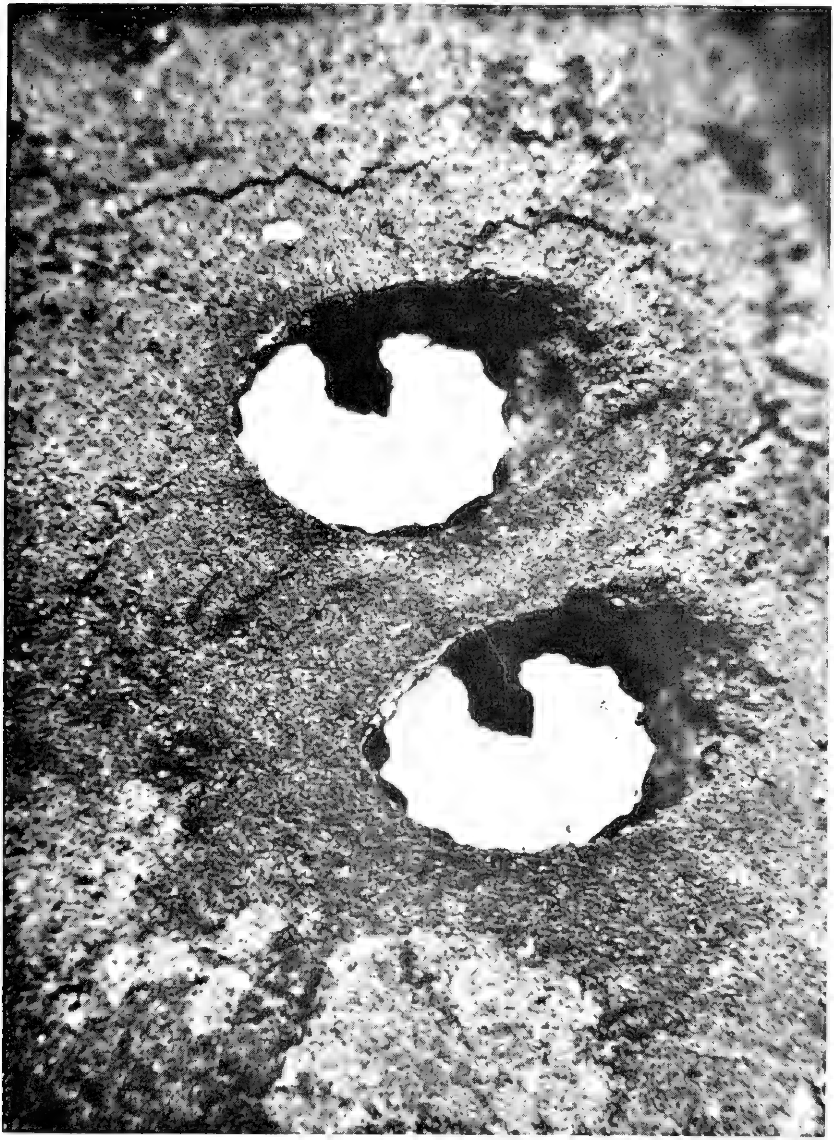

FIG. 155. Vertical section through two cells of a nest of *Calliopsis andreniformis* showing the overwintering prepupae in place. Note that their heads are towards the openings of the cells. The larval feces are seen near their posterior ends on the upper distal surfaces of the cells.

the cell around the bottom of the pollen ball, required painstaking precautions and luck! If a small piece of dirt lodged on the egg it could often be removed with very fine jewelers forceps. If it fell on the first stage larva a watery "blister" appeared and the larva died; if on the pollen ball, it was usually quickly dispersed on the wet surface and mold invariably grew there, killing the immature form; and, if in the cell condensate, mold usually resulted, but even if not, the larva ceased to feed when it came in contact with the dirt-contaminated pollen. If the pollen ball dried a little too much, the larva refused to feed and died. If the spherical pollen ball was deformed in being removed from the cell, the same thing occurred. It should not be surprising that I have the impression that *C. andreniformis* is a sensitive, fastidious species.

To cope with these difficulties, the following techniques were used successfully. A petri dish was designed to serve as a receiving vessel for immature specimens in the field. The lower half of a standard petri dish was half-filled with melted beeswax (paraffin did not give sufficient friction for this surface). A flat piece of galvanized sheet metal was cut to form a V-point, the angle of the V such that a pollen ball resting in the conical cut made in the wax by this tool would be supported at or below its middle. The V-point was simply pressed lightly into the solidified beeswax and slowly turned to give the necessary conical excavation. Other cone-shaped depressions were sunk deeper to receive water which maintained the pollen balls at their proper moisture during their time in the field. It was necessary to shade the petri collection dish for otherwise the temperature would have risen high enough to kill the specimens.

A device was made to remove pollen balls with no resulting distortion of shape. A circular loop 1.5 mm in diameter was formed at the end of each of two number one stainless steel insect pins whose heads were removed. These were cemented to the tips of a pair of fine forceps with the planes of the loops parallel to each other and to the sides of the forceps. This afforded such steady handling that moisture condensate could be blotted with ease from the bottom of the pollen ball with lens tissue during transfer from nest cell to petri collection dish. Once set in the conical depression, the pollen ball did not shift in orientation. Larvae suddenly exhumed from complete darkness into full sunlight continued to consume pollen normally.

Pollen balls kept in a closed container of 93% relative humidity (saturated solution of $NH_4H_2PO_4$), with daytime temperature 30°C, dropping to 18°C nightly, shrunk in diameter from 2.83 mm to 2.50 mm in 48 hours. The feeding larva contracted, became motionless, and mold growth began in 24 more hours.

Pollen balls with eggs or early larvae kept in a closed container at 100% relative humidity (distilled water) and 30°C did well until a sudden drop in room temperature precipitated moisture on them. This invariably resulted in cessation of feeding and mold formation shortly thereafter. Mold formation followed cessation of feeding in so many instances that I am led to speculate that there may be a cause and effect relationship. Why should moisture condensate in the laboratory disrupt feeding when obviously moisture condensate in the cell in the field does not do so? The answer may lie in the kind of container I used: a flat-topped one. The plane surface allowed coalescence of condensate and several *large* drops fell on top of the pollen ball and larva. In the rounded, waxed cell, moisture condensate rolled down the rounded sides of the cell and collected around the bottom of the pollen ball; neither pollen ball above nor specimen were wetted. Had I copied nature in making a waxed, domed roof for my rearing chamber at high humidity I would perhaps have been successful in carrying through these early stages which require such high humidity, yet apparently cannot stand moisture condensing directly on them. Gaseous mold inhibitors, or possibly a fine film of a liquid one applied to the pollen ball, would probably defeat the mold problem.

DAILY ACTIVITY. Daily activity was dependent primarily on soil moisture, soil temperature, and air temperature. If the ground was soaked, the bees stayed in their burrows even though the weather was very good. Obviously they could not struggle through the mud. Although the greatest number of *andreniformis* were on the wing when the weather was clear and bright, many of them collected pollen on days when the light level was down to 860 milliphots in contrast to 8600 to 12,900 milliphots on the best days. Cloudy weather, even complete overcast (30 milliphots), did not make them cease activity altogether. Possibly they could sense a real storm coming, for I never saw any of them working just prior to a downpour. Both males and females spend much time at the nesting site, flying about and landing here and there. Their antennae are held straight and move side-to-side in tandem, or to and fro when they settle in the area. The female ventures only a short distance from her burrow on the day after digging it. This seems strange because she has apparently gotten thoroughly acquainted with the area around it by actually walking over it time and time again before deciding just exactly what spot suits her. She is often seen to push her head and part of her thorax out through the tumulus and remain there moving her antenna. She eventually emerges but may do nothing more than walk around the tumulus scratching about like a cat. She may come out and immediately go back in. After the first day following burrow construction, the female may fly out of the area, presumably on foraging flights. A common action was noticed by Ainslie (1937), and anyone studying females at the nest will soon see it again and again; females often fly immediately above the ground surface if it is bare, and they create little whirlwinds of dust with their rapidly vibrating wings. Upon leaving their nests they may hover a few mm above the tumulus in the manner of hover flies, pivoting slowly about the tumuli, then fly one or two somewhat circular patterns over the tumuli and fly out of the area.

The female's orientation flight upon first leaving the nest in the morning is very short. She bursts quickly through the tumulus, circles a few times at rapidly increasing distances from the nest and is gone. I was never able to follow her closely enough to sketch the motions, but the orientation flight is not intricate.

On returning, she may fly straight to the tumulus or, more usually, she flies back with her pollen load to the general vicinity of the nest and alights here and there. Eventually she goes into her nest. I never saw a female mistaking another female's nest for her own. Related bees such as *Andrena* and *Perdita* may have considerable trouble finding their own nests (Michener and Rettenmeyer, 1956; Michener and Ordway, 1963) and may make errors in entering another's nest before finding their own. Individual female *Calliopsis* nests may have distinctive odors that prevent such errors.

Odor of Calliopsis and Orientation about the Nests. A distinctive odor resembling that of oil of lemongrass (Guenther, 1950) was first noticed when a female *andreniformis* on her first emergence was captured at 9 a.m., July 24, 1957; she secreted a large drop of clear fluid from her mouthparts onto my fingers. Rough handling elicits this odor from females but gentle handling does not do so. Specimens captured with an aerial net impart their lemony scent to the net. I have tried to provoke its release in males but have noticed only the faintest odor from one specimen, a fresh male dug out of its overnight burrow at 6 p.m., May 26, 1958. Dr. J. G. Rozen, Jr., has informed me (1963) that both *C. crypta* and *C. rozeni* give off a lemony odor; they are members of a different subgenus.

The odors of non-*Apis* bees have been a neglected facet of bee biology. G. E. Bohart has told me that his field experience indicates that most genera of solitary bees have distinctive odors. Bees with which a lemon-like odor has been associated are listed in Table 7.

Malyshev (1913) found that Russian *Ceratina* with atrophied stings defend themselves and their nests by secreting "a yellow saliva, vigorously scenting of lemon. If a *Ceratina* is seized across the body with a forceps, it hastily strives to place its fragrant secretion upon the instrument by means of its fore and then middle legs. When the *Ceratina* are expelling earwigs from their nests this odour of lemon . . . is sometimes perceptible."

Moure (1958) described Warwick Kerr's discovery that the meliponid bee *Lestrimelitta limao* uses its scent glands to give off a strong odor of lemon which is used to invade and rob the nests of the meliponine bees, *Trigona emerina, remota,* and *testaceicornis.* The strong lemony odor "overpowered the normal odor of the nest. . . . Once the robbed colony has lost control of

TABLE 7. Bees Which Produce a Lemon-like Odor

Author	Odor	Locality	Bee
Shuckard (1866)	Citron	England	*Prosopis* (=*Hylaeus*)
Ferton (1901)	Vervain = lemony	France	*Colletes* *Prosopis* (=*Hylaeus*) *Andrena* *Panurgus*
Malyshev (1913)	Lemon	Russia	*Ceratina*
Schwarz (1948)	Lemon-like	Central & South America	*Trigona testaceicornis* *Lestrimelitta limao*
Shinn	Oil of Lemongrass; Citral	Colorado	*Calliopsis teucrii*
		Kansas	*C. andreniformis*
		Tennessee	*C. andreniformis*
		Texas	*C. andreniformis*
	Rank Oil of Lemongrass	Colorado	*Nomadopsis scitula scitula*
Moure (1958)	Lemon	Brazil	*Lestrimelitta limao*
Kullenberg (1953)	Lemon scent: citronellol-geraniol-citral	Sweden	*Prosopis* (=*Hylaeus*) *Halictus* *Heriades* *Megachile* *Andrena* *Nomada* *Apis mellifera* (Italian)
Rozen (1963)	Lemon	Arizona	*Calliopsis crypta* *Calliopsis rozeni*
Rozen (1965a)	Lemon	Switzerland	*Melitturga clavicornis*
Weaver, Weaver, and Law (1964)	Geraniol-Citral	Texas	*Apis mellifera*

the odor, the *Lestrimelitta* workers can enter and leave freely. . . . (the lemony odor) seems to be the important factor in orienting the arrival of the robbers, guiding them to the correct entrance, even if other nest entrances are close by. . . ."

The above references then give three functions for the lemony odor: defense; offense; guidance towards location of others of their group. The first function is likely in *andreniformis* as indicated above, and I suspect the presence of the last. The tumuli of the females have this odor, and it may be a factor which influences the bees to build their nests in aggregations. Most females have no trouble finding their own nests, even though several other entrances may be only an inch or so away. A female may plunge straight into her tumulus, dig furiously downward, and disappear in a few seconds.

To test whether she detected her individual scent spectrum at close quarters to the tumulus, I performed the following experiments. Each individual of a number of pairs of bees which nested very close together in the East Stake plot was differentially marked. A period was chosen when two bees of a pair having tumuli of similar size left their nests. Then the tumuli were exchanged and arranged approximately as found. When a female returned to the nest, she exhibited one of five actions:

(1) Flew directly to her nest with neighbor's tumulus, dug down and deposited pollen in the nest as though undisturbed by the exchange of tumuli: 5 individuals.

(2) Flew directly to her nest with neighbor's tumulus, but was disturbed, buzzed around tumulus and adjacent tumuli, and dug into her true tumulus over neighbor's nest, but came right up again. Found her own nest after flying around, deposited pollen load in nest: 4 individuals.

(3) Same as (2), except dug into several tumuli including her own, taking more than 10 minutes to find her own nest: 1 individual.

(4) Came into area, settled nearby (usually about a foot distant from her nest), made several sorties over tumuli including her own, then landed on hers. Dug right in, but came up again. Flew away, returned to her nest with neighbor's tumulus over it, dug down, deposited pollen: 4 individuals.

(5) Came into area without pollen, investigated several tumuli, left area; back in the proper nest the next morning (1 individual never returned): 3 individuals.

To the five individuals of (1), and the one of (3) a scented tumulus was unimportant in finding their true burrows. To the four specimens of (2), and the four specimens of (4) odor apparently played a part in the decision as to which tumulus was theirs, but the real test was whether the burrow itself was theirs or not. If not, they did not deposit pollen in it. Unfortunately, exactly the right conditions for this experiment were rarely encountered, and more trials will be necessary to draw definite conclusions.

Apparently landmarks are important to *andreniformis* in finding its own burrow, but it also seems likely from these trials that scent sometimes plays a role when the bee alights on the tumulus. I think it possible that some bees depend more upon physical-object orientation at close range, while others pay more heed to the scent of the tumulus. The males return to their same burrows night after night in some cases, and their tumulus is apparently unscented. It is possible that odor may also function as a sex attractant, but I have no evidence for such a role.

Newly emerged females in the laboratory give off the scent; males do not. If it were directly from their pollen ball or nectar, the males would be expected to furnish the scent, too. The one male that gave a very faint scent may have been scented by a female.

C. andreniformis uses the nectar of *Verbena,* which possesses the lemon-odored citral in its pollen and leaves (Guenther, 1952), but the clovers used for pollen and nectar lack terpenes whose odors resemble citral. The odor of *C. andreniformis* is also reminiscent of citronellol and citronellal. The last two compounds are not widespread among plants, but it is not impossible that any of the three compounds could result from the bee's metabolic breakdown of products present in clover. Citronellol in crocodile musk has been attributed to the breakdown of cholesterol.

Although the terpenes above are powerful scents which diffuse quickly, female tumuli at the West Stake plot continued to give the odor for more than two weeks (not tested after that length of time). A cat and dog repellent, Chaperone(R), whose principal active ingredient is oil of lemongrass, persists this long on soil or longer when applied to garbage cans which are left out in the sun and rain.

FLOWER RELATIONSHIPS. Robertson (1929) listed 51 species of flowers visited by *Calliopsis andreniformis* at Carlinville, Illinois. It has been taken on flowers of 98 species in all. It is certain, however, that a fair number of the records from the literature and specimen labels are for flowers that play little or no role in the ecology of the bee.

In general, *andreniformis* gathers pollen and sucks nectar primarily from species of Leguminosae, Compositae, Verbenaceae, Oxalidaceae, and Malvaceae, in descending order of frequency of use according to my observations. The last family is especially favored in the salt marsh areas of southern New Jersey where both *Malva rotundifolia* and *M. neglecta* are abundant.

In visiting flowers of *Trifolium, Lespedeza, Psoralea,* and *Melilotus,* the bee holds onto the wings of the legume blossom with its feet, slides the frons down against the standard, and thrusts the proboscis into the flower to get the nectar. Pollen is carried by the females on the hind tibiae exclusively; I have not observed the method of collecting the pollen. Flight ranges are usually short because the bee picks the closest suitable nesting site to its flower. They will fly at least 45 m from their nest in search of pollen, and they probably fly farther if their source of pollen is destroyed.

Flowers used by *andreniformis* as determined by direct observation or by examination of pollen loads or pollen balls are listed in Table 8 and include Robertson's (1929) records as well as any others where the nature of the visit to the flower is stated. The composition of the loads of pollen was examined for only 17 specimens—too few for generalization. These 17 pollen loads were of all Leguminosae, all Malvaceae, or mixed Malvaceae-Compositae.

Both male and female bees feed on pollen. Taniguchi (1956) records this habit for Japanese *Andrena,* and Michener and Rettenmeyer (1956) state that the females of *A. erythronii* regularly eat pollen. The species was never seen to suck up dew, and their water requirement is probably met by nectar collection.

Table 8. Known Pollen Sources of Female *Calliopsis andreniformis*

FAMILY	SPECIES
COMPOSITAE*	*Aster ericoides villosus*
	Erigeron canadensis
	Verbesina helianthoides
CONVOLVULACEAE	*Convolvulus sp.*
LABIATAE	*Lycopus sinuatus*
	Pycnanthemum pilosum
LEGUMINOSAE*	*Desmodium marilandicum*
	Desmodium paniculatum
	Melitotus alba
	Melitotus officinalis
	Psoralea onybrychis
	Trifolium procumbens
	Trifolium repens
	Trifolium pratense
LYTHRACEAE	*Lythrum alatum*
MALVACEAE*	*Malva neglecta*
	M. rotundifolia
OXALIDACEAE	*Oxalis stricta*
POLYGALACEAE	*Polygala sanguinea*
POLYGONACEAE	*Polygonum buxiforme*
RUBIACEAE	*Hedyotis purpurea*
SCROPHULARIACEAE	*Gerardia tenuifolia*
VERBENACEAE*	*Lippia lanceolata*
	Verbena bracteata
	Verbena hastata
	Verbena urticifolia

* These families are the most important pollen sources.

The emerging overwintering generation depends largely on *Trifolium repens*, *T. procumbens*, *Melilotus officinalis*, and *Verbena bracteata* for its foraging. These plants begin blooming in early May. By about the first week in June *Psoralea*, *Polygonum*, *Erigeron*, and *Convolvulus* are in use for pollen and nectar. By the middle of June *Melilotus alba* and *Oxalis stricta* are flowering and are used for pollen and nectar. The second generation visits mostly *Trifolium repens* and *Melilotus alba*, as do any third generation bees which may emerge (rare). I never saw *andreniformis* make any visits to the numerous flowers of *Taraxacum officinalis* which bloomed in the vicinity of every nest site I observed.

Social Parasites. The social parasites most in evidence at all localities where nest sites were located were bees of the genus *Holcopasites*. These ubiquitous parasites have been reported by Ainslie (1937) to parasitize *C. andreniformis*. *Holcopasites calliopsidis* parasitizes *andreniformis* at Lawrence, Kansas; Nacogdoches, Texas; Knoxville, Tennessee; and apparently in

Iowa and Illinois. Here recorded for the first time is the fact that *Holcopasites illinoiensis* (determination by P. D. Hurd, Jr.) parasitizes *C. andreniformis* during the same period as *H. calliopsidis* does, at Nacogdoches, Texas.

Since there are only three species of *Calliopsis* in the eastern United States, and there are as many as 13 species of *Holcopasites* (Muesebeck, Krombein, and Townes, 1951), it seems likely that some of the species will be found to parasitize other panurgine bees closely related to *Calliopsis*. Linsley, MacSwain, and Smith (1956) reported the association of *H. arizonicus* with a *Pseudopanurgus* in Mexico; I reported (Shinn, 1965) P. D. Hurd's record of the association of this species with *Calliopsis pectidis* in Arizona; and Rozen (1965b) reported the strong likelihood that this species parasitizes *Pseudopanurgus* in Arizona. He also reported finding larvae of *H. knulli* in nests of *C. crypta* and suggested that it also attacks *C. rozeni*.

Despite excavations of nests of *C. andreniformis* which had been repeatedly visited by *H. calliopsidis,* I failed to find the eggs of the parasite. Rozen (1965b) found the eggs of *H. knulli* inserted at an angle under a U-shaped flap of the cell wall in the cells of *C. crypta* and *Pseudopanurgus aethiops*. Most of the eggs were positioned in the roof or side of the cell.

At some of the nesting sites *H. calliopsidis* emerged at the same time as the first *andreniformis* males, but at others it emerged 7-10 days later. Males and females appeared virtually simultaneously. The species disappeared from nesting sites about the time that the bulk of female *andreniformis* disappeared. I have seen no individuals persist as late as some of the female host bees, which may live well into September. Possibly *calliopsidis* never has more than two generations, whereas *andreniformis* may have a weak third or fourth generation, depending upon latitude.

H. calliopsidis spends much time walking around the *andreniformis* nest sites. It walks in a singular fashion; *Holcopasites* is the only known bee which tucks its wings between metasoma and legs and drags them in the dust as it busily examines the ground. I believe this is the first notice of this unusual habit. Rozen (1965b) described *H. arizonicus, H. insoletus,* and *H. knulli* as flying slowly over the nesting sites, stopping frequently on tumuli or at the edges of stones under which there might be burrow entrances. This difference in behavior from that of *H. calliopsidis* may be a species difference or possibly a function of the density of nests.

H. calliopsidis flew over the nest sites with seemingly little regard for the presence of *andreniformis* females. It would occasionally arrive at a tumulus simultaneously with a female *andreniformis*. No conflict was observed, but *andreniformis* preceded *calliopsidis* into the burrow. The male *andreniformis* does not tolerate the presence of *calliopsidis*. It chases the latter out of its area.

The female *calliopsidis* burrows down through the host's tumulus and may spend as much as half an hour inside. On several occasions (at least 5), the female *andreniformis* returned and entered the nest during this time, but there was no indication of combat. The pollen-laden *andreniformis* spent the necessary time unloading pollen, emerged for another pollen-collecting trip, and the *calliopsidis* subsequently emerged.

In the light of Rozen's (1965b) observations that *Holcopasites* lays its eggs before *Calliopsis* provisions its cells, it would be interesting to determine if adult females of *Holcopasites* eat pollen from partially provisioned cells of *Calliopsis.* This might explain some of the long underground stays I recorded for *H. calliopsidis.*

The developmental time for *calliopsidis* may be shorter than that of *andreniformis* because in two nests the shallower cells contained fully fed larvae of *Calliopsis* which had not yet defecated while three deeper cells contained prepupae of *Holcopasites.*

H. calliopsidis has much longer diurnal flight activity than *andreniformis.* It flies from 8 a.m. to 6:30 p.m., whereas *andreniformis* is on the wing from about 8:30 a.m. to 4:00 p.m. Part of this difference in time is spent by the females of *andreniformis* in digging their burrows. The total active hours of *andreniformis* are greater than *calliopsidis,* because the former often continues digging until 8 p.m.

At least 30% of the nest burrows in the West Stake plot (Fig. 146) were visited by *calliopsidis,* but less than 4% of all the dug cells of *andreniformis* contained *calliopsidis* larvae (Table 10). Apparently many visits are made before *calliopsidis* finds a cell suitable for laying her egg. A single female may briefly visit several nests repeatedly—a few seconds each—before remaining underground in one of them for a longer time of a minute or more.

Frequent mating of *Holcopasites* took place at the *Calliopsis* nesting sites. I never saw mating attempts on flowers. The male calmly mounted the female, which did not struggle to escape, and copulation lasted 1-2 minutes on the ground, the female not attempting to fly. At each nesting site the parasites were readily netted and were marked with quick-drying colored airplane dope. They returned repeatedly to the same site, but ten of twenty marked at the Gym Area disappeared within a week's time. Possibly they disperse to other nesting sites.

Dr. Howell V. Daly found a few *calliopsidis* asleep at 6 p.m., July 14, 1957, on the acuminate tips of the grass, *Setaria glauca* (det. R. N. McGregor) on The University of Kansas campus. They slept holding by their mandibles alone, their wings tucked between the metasomal sternum and hind legs (Fig. 156). Rozen (1965b) described the same sleeping position for *H. insoletus* and *knulli.* The depth of sleep in *calliopsidis* was such as to permit the grass plant on which it was sleeping to be dug up and transported 1 km by foot to a laboratory for photographing without disturbing the bee. More

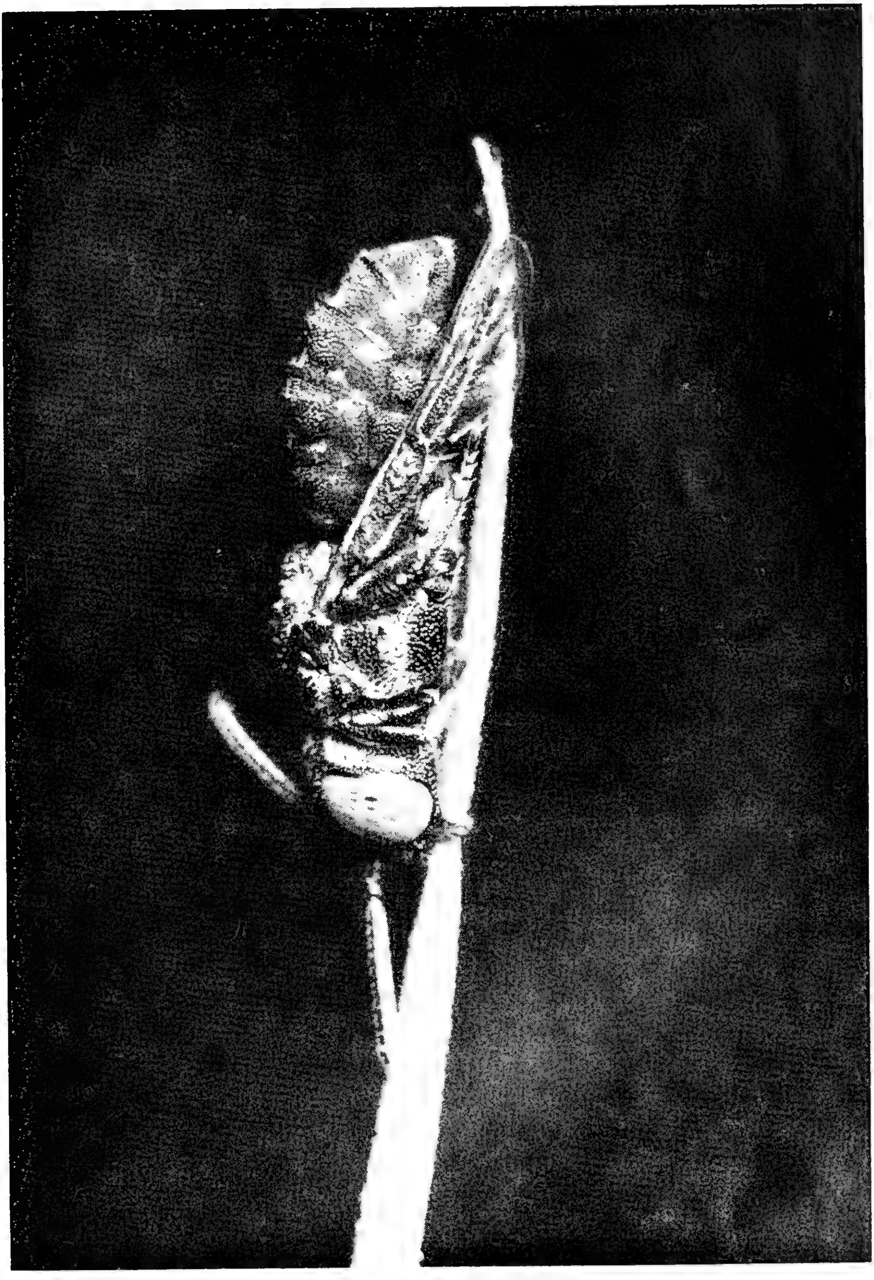

Fig. 156. Photograph of *Holcopasites calliopsidis* asleep on the upright, acuminate tip of a blade of the grass *Setaria glauca*. Note the characteristic position of the wing which lies between the hind leg and the metasomal sternum.

than a dozen *calliopsidis* bees which I marked with colored paints returned to sleep in the same vicinity, sometimes on the same blade of grass.

Sphecodes bees were found at every nesting site I studied. They were much scarcer than *Holcopasites,* but I made no quantitative comparisons. They investigated the *andreniformis* burrows and entered them, staying as long as ten minutes (14 timings, mean 4.86±1.015). I found no larval *Sphecodes* in any *andreniformis* cell; however, the larva from a cell of *andreniformis* described as that of *Holcopasites* by Michener (1953a) is totally unlike that of other pasitine bees, and Dr. J. G. Rozen, Jr., *(in litt.)* considers it to be a *Sphecodes.* There is therefore little doubt that *Sphecodes* does parasitize *Calliopsis.*

At the Stake nest plots two sizes of *Sphecodes* were present and were presumably two species. Both visited the *Calliopsis* burrows, although the smaller one made most of its visits to *Lasioglossum* nests in the area. Mitchell (1956) suspected that *Sphecodes brachycephalus* is a probable parasite of *C. andreniformis.* He also writes (1960) that his personal observations in nesting areas suggest both *Calliopsis* and *Perdita* as hosts for *Sphecodes.* Ainslie (1937) observed *Sphecodes* flying around and active in nest sites of *C. andreniformis* at Sioux City, Iowa. Rau and Rau (1916) found *Sphecodes* sp. in constant attendance at the nest sites of *Calliopsis nebraskensis* near St. Louis, Missouri, and considered them as visitors to the nests.

Villa sinuosa and *Parabombylius ater* were the only bee flies whose actions suggested that they were parasites of *C. andreniformis.* The former was rare, but the latter was a frequent visitor at the Kansas nesting sites and was very abundant at the Texas nesting sites. Several bombyliid larvae were excavated from *andreniformis* cells, but none pupated.

Several counts of *P. ater* were made. On July 4 and July 16, 1957, five and seven individuals were simultaneously active in the West Stake nest plot, or one per 5.1 m^2 and one per 3.6 m^2, respectively. At the Stadium nesting site in Texas on May 10, 15, and 17, 1962, there were 12, 16, and 20 individuals simultaneously active in an area of comparable size, or one per 18.6, 14.8, and 12.0 m^2, respectively. The bee flies hover about 25 mm from a nest whose tumulus has been removed, and they flick tiny white eggs into the exposed burrow entrance. Presumably the larva burrows down through the dirt-filled upper portion of the nest entrance, enters a cell and eats pollen and *Calliopsis* larva, for cells containing bee fly larvae have no traces of anything else in them. *Parabombylius ater* appears about the same time as *C. andreniformis;* its peak of abundance is about coincident with mid-season for its host, and its population appears to drop sharply after this. I interpret this to mean that it has only one generation in Kansas. The fact that several larval specimens dug up in early June did not metamorphose, whereas prepupal *Calliopsis* did, tends to support this interpretation.

Other Associates. The pyemotid mite, *Trochometridium tribulatum* (Cross, 1965) was discovered in two cells of one nest on The University of Kansas campus. Both fungus and pollen were present in these cells. No traces of the bee larvae were found. Krombein (1961) points out that several families of mites contain species that are parasites of solitary wasps and bees, and that several species of *Pyemotes* kill and feed on the more or less helpless immature stages of many insects. This may be the case with *Trochometridium*.

The mites were collected July 22, 1957, from cells 73 and 90 mm below ground level from a block of soil which had been recently brought to the laboratory. Several hundred mites were in the two cells taken together. A huge gravid female was in one cell and almost all the mites were in the egg stage. The mites were transferred to a covered Syracuse dish for observation at room temperature (29.5°C). On July 23, most of the mites were in a ball, but four walking specimens had appeared. On July 24, twelve walking females were present, and on July 25 two males appeared. Females were distinguished from males by a straight white line on the dorsum, by their smooth contour in lateral view, by their more elongate form, and their smoother locomotion. The male bore a broader white line on the dorsum with several strong constrictions along its border, exhibited a posterodorsal tubercle in lateral view, was broadly oval in outline, and moved slowly and clumsily. Its locomotion was mostly by means of the middle two pairs of legs, for the front and hind pairs were borne aloft. By July 27 most eggs had hatched, but mold was forming on the unhatched eggs. Only a few males had appeared, the bulk of the specimens being females. Inasmuch as Dr. Earle A. Cross had recognized them as a new genus and species, the specimens were preserved on July 27. Ainslie (1937) found larvae of *C. andreniformis* infested with mites of the genus *Pygmephorus* (=*Pigmeophorus* Banks, 1904) as determined by H. E. Ewing. He gave no estimate of the extent of the infestation, but I infer it was relatively minor. Crandall and Tate (1947) state that late in the season of *C. andreniformis* at Lincoln, Nebraska, ". . . many of the cells containing larvae were infested with mites. . . ." They listed the mites as: *Pediculoides americanus* (Banks) and *Tyrophagus* sp., both determined by E. W. Baker, and *Lohmannia* sp., determined by H. E. Ewing.

Three species of fungi were identified from prepupal *C. andreniformis: Penicillium cyclopium, Aspergillus flavipes,* and *A. sydowi.* Dr. Robert Lichtwardt kindly determined the molds. The molds came from specimens in the soil block discussed above, from the West Stake plot, and from specimens reared in the laboratory. Only bees in the rearing boxes kept at 88% relative humidity (maintained by $BaCl_2$ solution) and above developed mold

TABLE 9. Contents of *Calliopsis andreniformis* Cells Dug During Summer and Early Autumn

	Number	*Percentage*
C. andreniformis, live, immature	192	77.4
C. *andreniformis*, dead, moldy, immature	22	8.9
Empty, waxed cells	12	4.8
Holcopasites or *Sphecodes*, prepupae	10	4.0
Beeflies, larvae	8	3.2
Mites, *Trochometridium tribulatum*	4	1.6
Totals	248	99.9

growth. Two bee fly larvae, surrounded by moldy bee prepupae, did not support a mold growth.

Penicillium cyclopium is worldwide and found on many different substrates, for example, rotting bulbs of Liliaceae, mildewing tentage, soil and decaying vegetation, and in bee hives (Raper and Thom, 1949). Both *Aspergillus* species are cosmopolitan. *A. flavipes* is particularly common in soil and decomposing organic materials, and *A. sydowi* is known from soil of several eastern states and from beehives in Michigan (Thom and Raper, 1945).

A small asilid fly was present at three nest sites at Lawrence, Kansas. It looked remarkably like a female of *C. andreniformis* and acted and flew like the female as well. Its only known prey were two male *andreniformis,* which tempts speculation that it may be aided in obtaining its prey by its superficial resemblance to the female.

Although the bee-predator wasps of the genus *Philanthus* were seen about the West Stake nesting plot as well as several others, they were never seen to take *andreniformis,* or for that matter, any prey. Reinhard (1924) records *Philanthus gibbosus* as using *andreniformis* for prey: *Philanthus* cells yielded 1 female and 5 males of *andreniformis* and 325 specimens of halictid bees. It seems that *andreniformis,* representing only 1.8% of the prey of *Philanthus,* could well be considered as accidental prey. *Philanthus* captures its prey on flowers, and a list of flowers given by Reinhard as used by *P. gibbosus* includes some flowers used by *andreniformis: Achillea millefolium, Erigeron,* and *Polygonum*. These flowers are rarely used by *andreniformis,* but much by Halictidae. This, too, lends support to my supposition that *andreniformis* is an exceptional prey for *P. gibbosus* rather than one that is customarily used at a low percentage.

A *Nysson* wasp was much in evidence about *andreniformis* nests at the West Stake plot, often entering nests, but never emerging with any plundered prey or external evidence of pollen. Rau (1922) recorded the entrance of

Nysson raui into the burrow of *C. (Verbenapis) nebraskensis.* I have no other observations about the wasps' action in connection with *andreniformis* nests.

White podurid collembolans were sometimes found in nests. A clamydid beetle larva which encases itself in a mud cocoon occasionally spent the night in burrows whose upper portions were free of loose, excavated dirt.

Table 9 lists the contents of cells from apparently completed nests which were dug during summer and autumn.

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THE UNIVERSITY OF KANSAS
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THE CULICOIDES OF NEW MEXICO (DIPTERA: CERATOPOGONIDAE)

(Diptera: Ceratopogonidae)

By

William R. Atchley

Vol. XLVI Pages 937-1022 March 3, 1967 No. 22

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THE UNIVERSITY OF KANSAS
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The Culicoides of New Mexico (Diptera: Ceratopogonidae)[1]

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ABSTRACT

A taxonomic review is provided for the biting midges of the genus *Culicoides* (Diptera: Ceratopogonidae) occurring in New Mexico. The descriptions of females and males, if known, of 23 species are given of which 4, *Culicoides (Drymodesmyia) byersi, C. (Oecacta) doeringae, C. (O.) novamexicanus* and *C. (O.) sublettei* are described as new to science. *Culicoides pampoikilus* Macfie, previously reported from Central America, is recorded from New Mexico and constitutes a new United States record. Biological as well as morphological evidence is presented to support the relegation of *C. variipennis australis* Wirth and Jones to synonomy. *Culicoides tenuilobus* Wirth and Blanton is elevated from synonomy.

INTRODUCTION

The genus *Culicoides,* an almost worldwide group of minute hematophagous gnats, is a conspicuous part of most environments. The anthropophilic behavior of these flies makes them readily perceivable to even the most unobserving "naturalist."

It has only been in the last 40 years or so that students of the Ceratopogonidae have devoted their energies to the taxonomy of these small flies. The Palearctic fauna has been well studied through the efforts of the following workers: Goetghebuer (1920, 1933-1934) first monographed the Belgian species and later more extensively studied the Palearctic fauna, while Kieffer (1925) and Edwards (1926, 1939) treated the French and British

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[1] Contribution No. 1333 from the Department of Entomology, University of Kansas.

species. Such workers as Callot and Kremer are continuing the studies of the French fauna, while Kettle and Lawson are among the more recent contributors of the studies relating to the British species. The revision by Campbell and Pelham-Clinton (1960) represents the most up-to-date treatment of the British fauna. Among the more notable Russian contributors to the taxonomy of the Palearctic *Culicoides* have been Gutsevich and Dzhafarov.

Carter, Ingram and Macfie (1920), DeMeillon (1936-1961) and Fiedler (1951) have contributed to our knowledge of *Culicoides* in the Ethiopian Region, although Macfie's later contributions were by no means restricted to this area.

The Australian species have been recently monographed by Lee and Reye (1953). The Oriental Region has long been ignored by ceratopogonid workers and, with the exception of a reference by Causey (1938) to species occurring in Siam, little is known of the *Culicoides* of this region. Tokunaga (1932 to date) and Arnaud (1956) have conducted extensive taxonomic studies on the species in Japan and surrounding areas, and, in addition, Tokunaga has recently presented excellent studies of the Micronesian and Papuan fauna.

Valuable contributions have been made to the taxonomy of the Neotropical species by Barbosa (1943-1952), Fox (1942-1955), Lane (1944-1961), Lutz (1912-1914), Macfie (1937-1948), Ortiz (1949-1954), and Vargas (1944-1960). The excellent monograph of the Panamanian species by Wirth and Blanton (1959) provides a valuable addition to our knowledge of the Neotropical species.

Within the boundaries of the continental United States the *Culicoides* of California, Florida, Wisconsin, Oklahoma and New York have recently been the subjects of rather extensive taxonomic studies. A perusal of the literature pertaining to the *Culicoides* of the United States, however, reveals a conspicuous void regarding the culicoid fauna of the southwestern states.

Information regarding the *Culicoides* of the southwestern United States can be found in the works of James (1941, northern Colorado), Fox (1946, Utah), Wirth (1952, California), and Khalaf (1952, 1957, Oklahoma), and Wirth (1955), Wirth and Bottimer (1956), and Jones and Wirth (1958) have studied the Texas species. Occasional records of southwestern species are given by Foote and Pratt (1954) in their treatment of the *Culicoides* of the eastern United States. Wirth and Hubert's (1960) study of the *copiosus* group of *Culicoides* includes distribution records for species occurring in California, Arizona and Texas, as well as some Mexican records.

The Catalog of North American Diptera, North of Mexico (1965) lists 21 species occurring in Texas, and Khalaf (1957) lists 22 valid species in Oklahoma. This compares quite unfavorably with 9 species recorded in the literature as occurring in New Mexico. New Mexico, the point of fusion of four physiographic regions, i.e., Southern Rocky Mountains, Great Plains Province, Colorado Plateau and the Basin and Range Province (Fenneman, 1931), presents a diverse ecological situation. Because of this diversity, one would expect a varied and interesting fauna of *Culicoides.*

The primary objective of this study is the presentation of a taxonomic treatment of the *Culicoides* of New Mexico. It is hoped that this endeavor, when added to the works of Wirth (1952) and Khalaf (1957), will form the basis for a future extensive taxonomic investigation of the *Culicoides* of the western United States. Such a study is of paramount importance if serious investigations involving the public health significance of this group in the western United States are to be continued.

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In conclusion, I would like to express my deep obligation to my wife, Wilinda, for her encouragement and assistance throughout the duration of this study.

HISTORICAL REVIEW

One of the first accounts of *Culicoides* was given as early as 1713 by Derham (Edwards, 1939) in his excellent description of a small gnat referred to as *Culex minimus nigricans maculatus sanguisuga.* Concerning this small gnat, Derham states, "It is spotted with blackish spots, especially on the wings, which extend a little beyond the body. It comes from a little slender Eel-like Worm, of a dirty white Colour, swimming in stagnating Waters by a wrigling Motion.

"Its *Aurelia* (pupa) is small, with a black Head, little short Horns, a spotted, slender rough Belly. It lies quietly on the top of the Water, now and then gently wagging itself this way, and that.

These Gnats are Greedy Blood-suckers, and very troublesome where numerous . . . ."

In spite of this early beginning the Ceratopogonidae were shunned by early workers because of their small size and the consequent difficulties imposed by their taxonomy. Only one species of *Culicoides,* then called *Culex pilicarius,* was known to Linneaus. Winnertz's (1852) monograph of the European species represented the first major attempt at the classification of the Ceratopogonidae. Both Winnertz and Coquillett, who first studied the North American fauna, included all the known species in the genus *Ceratopogon.*

It was Kieffer who first began to define generic limits in the Ceratopogonidae and in 1906 resurrected the generic name *Culicoides* Latreille (1809). Following the work of Kieffer, Malloch (1917) proposed the recognition of the Ceratopogonidae as a distinct family from the Chironomidae.

Hoffman (1925) reviewed the North American species of *Culicoides,* described several new species and included a key for females. The 1937 revision of the North American *Culicoides* by Root and Hoffman included additional new species and distribution records, keys for female characters and male genitalia and illustrations of male genitalia of most of the known species.

With the exception of a few isolated descriptions of new species or species lists of very limited geographical areas, the next taxonomic works were those of Johannsen (1943, 1952) and Wirth (1952). Johannsen's (1943) generic synopsis and list of the North American species of Ceratopogonidae filled a long neglected taxonomic gap. The monograph on the Ceratopogonidae (=Heleidae) of California by Wirth (1952), with its excellent species descriptions, keys and overall systematics, stands as the outstanding North American treatment of this family.

Foote and Pratt (1954) treated the species occurring in the eastern United States; however, the usefulness of this paper is somewhat limited, due to the inadequacy of the species descriptions. These authors were among the first to attempt classification of females on the basis of structural characters, instead of relying completely on the traditional wing and mesonotal patterns.

Khalaf (1952, 1957), studying the seasonal incidence of the *Culicoides* of Oklahoma, described the relative abundance and distribution of these flies and provided descriptions of new species and keys to the Oklahoma *Culicoides.* As in the case of Foote and Pratt, Khalaf supplemented his 1957 key to external characters and male genitalia with a key to slide-mounted females. This is of significance to the problem at hand, since many of the species found in Oklahoma also occur in New Mexico.

The catalogue of the bloodsucking midges of the Americas by Fox (1955) includes a compilation of the known species, together with keys and a geographical index; however, more up-to-date information regarding distribution records, classification and synonymies is now available in the Catalog of North American Diptera (Stone *et al.,* 1965).

Considerable emphasis has recently been placed on the taxonomy of species groups, resulting in revisions of the *copiosus* group by Wirth and Hubert (1960), the eastern species of the *piliferus* group by Wirth and Hubert (1962), and the *obsoletus* group of eastern U.S. by Jamnback and Wirth (1960). Although these studies represent a strong beginning, there exists a great need for studies involving the western species of the *piliferus* and *obsoletus* groups, as well as the *crepuscularis* group, or the subgenus *Selfia,* to name only a few pressing taxonomic problems.

The study of the immature stages of *Culicoides* in the United States has recently been given a needed stimulus through studies by Jones and Williams, although our knowledge still lags behind that of the British, who have amassed considerable literature relating to immature stages of various Palearctic species through the excellent works of such entomologists as Kettle, Lawson and Parker.

ECONOMIC IMPORTANCE

The bloodsucking behavior of *Culicoides* (and two related genera of Ceratopogonidae) has gained them considerable notoriety. When these small gnats (commonly known as punkies, moose-flies, no-see-ums or sand-flies, although the last name has been applied also to *Phlebotomus*) occur in large numbers, their hematophagous habits result in great annoyance both to man and his animals. To many people the mention of "biting gnats" brings to mind painful, vicious, invisible and insatiable bloodsuckers. As Reye (1964) has so ably stated, "the abrupt fall in morale and the strong desire to be elsewhere which they *(Culicoides)* engender, are difficult to convey to those who have not experienced them." The irritation resulting from the bites of these small flies has been described as worse than that of mosquitoes, and the reaction by some people to the saliva of *Culicoides* may be quite severe. Their small size enables them to pass through netting or screens which would normally restrain a mosquito. Several authors have cited evidence of depressed development and property value in coastal and resort areas where high infestations of these gnats occur. In some areas outdoor work is made impossible due to the severity of attack of *Culicoides*. It was probably these conditions which prompted Kettle (1962) to comment that while "one midge is an entomological curiosity, a thousand can be hell!"

It was Sharp (1928) who made the first definite association between pathogen transmission and *Culicoides* when he reported the development of the microfilariae *Acanthocheilonema perstans* in *Culicoides austeni* and *C. grahami* in Cameroon, West Africa. This was later confirmed by Hopkins and Nicholas (1952); however, Henrard and Peel (1949) and Chardome and Peel (1949) doubted the validity of Sharp's conclusions when they demonstrated *C. grahami* to be an intermediate host of *Dipetalonema streptocerca* in the Belgian Congo. Duke (1954) confirmed the earlier experiments on the development of *D. streptocerca* in wild *C. grahami* but, in addition, showed the flies will take up, at the same time, fully representative numbers of *A. perstans* microfilariae when the host is infected with both parasites.

Steward (1933) demonstrated the transmission of *Onchocerca reticulata* (as *O. cervicalis*), the principle causitive agent of fistulous withers in horses, by *C. nubeculosus* in England. This was followed by a report by Dampf (1936) of the development of *O. cervicalis* and *O. volvulus* in *Culicoides* in Mexico; however, later experimentation by Gibson and Ascoli (1952) failed to show *Culicoides* as a vector of *O. volvulus*. Buckley (1938) has shown *Onchocerca gibsoni*, occurring in cattle in Malaya, to be transmitted by the bite of *Culicoides*.

Culicoides was demonstrated by Buckley (1934) to be an intermediate host of *Mansonella ozzardi*, a common human filarial blood parasite in the British West Indies. Robinson (1961) reported the early development of an avian filarial worm in *C. crepuscularis*, which had fed on an infected starling. Allergic dermatitis, Queensland itch, of horses in Australia has been shown by Riek (1954) to be caused by hypersensitivity to bites of *Culicoides brevitarsis*.

More recently Fallis and Wood (1957) have established that *Culicoides downesi* is an intermediate host of the protozoan *Haemoproteus nettionis* occurring in ducks in Canada, and Fallis and Bennett (1960) have demonstrated sporogony of *H. canachites* in *Culicoides sphagnumensis*. Akiba (1960) has incriminated *C. arakawae* in the transmission of *Leucocytozoon caulleryi* to chickens in Japan, and Garnham et al. (1961) have shown *Culicoides* to be involved in the transmission of *Hepatocystis kochi* in monkeys in Africa.

The transmission of fowlpox virus by *Culicoides* has been suggested by Tokunaga (1937), and bluetongue virus has been shown to be transmitted to sheep by the bite of *Culicoides* by du Toit (1944), Price and Hardy (1954) and Foster, Jones and McCrary (1963). The virus of eastern encephalitis has been isolated from an unknown species in *Culicoides* in southern Georgia by Karstad *et al.* (1957). Levi-Castillo has described the isolation of Venezuelan encephalitis from *Culicoides* in Ecuador (cf. Karstad *et al.* 1957).

The beneficial aspect of ceratopogonids has been greatly overshadowed by their bloodsucking habits. Recent authors (Macfie, 1944; Posnette, 1944; Warmke, 1951, 1952; Saunders, 1959; Wirth, 1956) have shown ceratopogonids to be involved in the pollination of cacao and para rubber trees in tropical America. Wirth (1956) has shown that two species of culicoid flies, *C. jamaicensis* and *C. diabolicus,* are involved in rubber tree pollination in Brazil and Guatemala.

As of this time there have been no published reports involving the economic significance of this group in New Mexico. I have accumulated definite man-biting records for two species, *C. reevesi* Wirth and *C. obsoletus* (Meigen), and have taken engorged females of *C. stellifer* (Coquillett) on two occasions from light traps located in horse and cattle pens. H. T. Miller, Vector Control Section of the New Mexico Department of Public Health, informs me that *Culicoides* constitute a considerable annoyance in the lower Rio Grande Valley of southern New Mexico.

METHODS AND MATERIALS

Most of the material used in this study was collected at light, either by New Jersey light traps, or by illuminating a white, vertically oriented bedsheet with a 15-watt fluorescent tube. The remainder was obtained by sweep-net collection and rearing of immature stages. Some discussion of the relative merits of the two methods of collection at light might be worthwhile.

By operating the 15-watt light tube from the battery of a vehicle, the collector is relatively mobile and may sample isolated areas where collection with a standard light trap is impossible. The collector is also able to discriminate in his collecting, i.e., he can aspirate relatively pure samples of small flies from the sheet, thus excluding the beetles, moths, etc., common in collections made by light trap, which may damage ceratopogonids. One limitation in the use of the light tube is the endurance of the collector.

It was discovered that the collecting of gnats from the sheet by aspiration could be supplemented by sweeping with a fine mesh insect net at various levels over the light tube. Examination of segregated catches made at the same locality, for example, on the Jemez River, Sandoval County, showed that only one species, *Culicoides hieroglyphicus* Malloch, was collected by aspiration from the sheet; however, by sweeping at various levels over the light tube, small numbers of *C. crepuscularis* Malloch, *C. haematopotus* Malloch, *C. palmerae* James, *C. sitiens* Wirth and Hubert, *C. variipennis sonorensis* Wirth and Jones and *C.* n. sp. nr. *villosipennis* were obtained.

After collection the material was stored in 70% ethyl alcohol. For study purposes alcoholic material is greatly preferred over pinned specimens. The loss of the color pattern of the mesonotal disc is over-compensated by the clarity of structures and the ease with which alcoholic material can be manipulated. Dried specimens are very difficult to handle due to their extreme fragility, and palps, antennae and legs are easily broken and lost during handling. With many of the more common species, identification can often be made on the basis of an alcoholic specimen, thereby alleviating the laborious task of slide mounting the specimen. Large numbers of alcoholic specimens can be stored in a small amount of space as compared to the amount of space required for a similar number of pinned specimens. Jones (1955) states that 4,000 specimens of a medium sized species will only half fill a vial measuring 21 x 70 mm.

In spite of the advent of the so-called "biological species concept," the criteria for specific and subspecific categories are ordinarily still morphological. Since the morphological discontinuities between individuals or groups of individuals must be analyzed and interpreted by the taxonomist, taxonomic procedures have been made more and more complex and sophisticated in order to reduce the amount of subjective interpretation.

It has become increasingly apparent in recent taxonomic works involving the genus *Culicoides* that the traditional approach of using wing and mesonotal disc patterns to differentiate species is no longer sufficient. Refined taxonomic methods have shown that many of what were considered for many years to be species are actually species complexes. Pointed specimens, therefore, although they show mesonotal disc patterns, etc., are of considerably less taxonomic value than dissected slide-mounted specimens. Many important taxonomic characters, e.g., antennal sensoria, mandibular teeth, spermathecal structure, are at best not easily discernible on pointed specimens but are readily observable on dissected specimens.

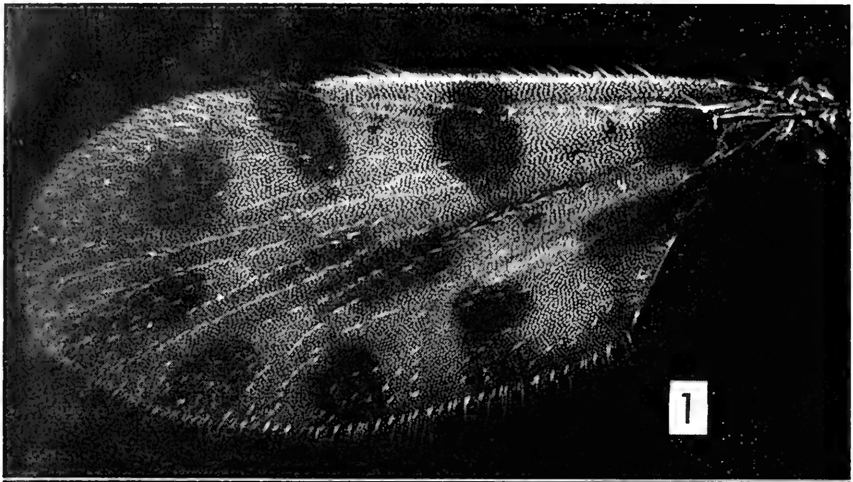
There are several good methods currently in use for slide mounting ceratopogonids. The technique employed in this study was to clear the specimens in 10% potassium hydroxide. The specimen to be mounted was first transferred from 70% alcohol to 95 or 100% alcohol, where one wing was dissected away and mounted under a separate cover glass, using Diaphane, a synethetic resinous medium. The wing can be removed in 70% alcohol and passed through 95 or 100% alcohol and then mounted; however, on several occasions when attempts were made to transfer the wing to the higher gradient of alcohol, it became torn or otherwise damaged.

After the wing was removed, the specimen was placed in 10% potassium hydroxide for clearing. I found chemical spot plates useful for clearing specimens. The specimen was retained in the KOH solution, which may be heated or used cold, until the proper degree of clearing had been achieved. The amount of time needed to clear a specimen properly depends on the amount of sclerotization, as well as size, and can only be learned through experience. Next, the specimen was washed in distilled water to which a drop of 10% glacial acetic acid had been added to stop the macerating process. After washing, the specimen was dehydrated in absolute alcohol and transferred to a drop of mounting medium on the slide, where the head and abdomen (or genitalia, if the individual is a male) were dissected away from the thorax under a wide field microscope. On the slide, the head was oriented dorsal surface up, the antennae and palps arranged and the mouthparts manipulated in such a fashion as to make the mandibular teeth visible. Special attention must be given to mounting the head and genitalia in order that they present a good symmetrical view. The coverglass was then applied, the slide labeled and then put away, preferably in an oven, to dry.

The use of Diaphane instead of balsam is advantageous, since it does not become tacky during arrangement of the dissected parts of the fly on the slide and permits mounting of the wing directly from alcohol.

A second technique for mounting ceratopogonids, preferred by Dr. Willis Wirth, is the phenol-balsam method. Specimens are placed overnight in a warm saturated solution of liquid phenol, prepared by mixing phenol crystals in absolute alcohol. They are then transferred to a solution containing equal parts Canada balsam and liquid phenol and, after standing a few minutes, are transferred to the slide for dissection. Small pieces of broken coverglass are added to prevent excessive flattening by the coverslip. The slides are then oven dried, and pure balsam is occasionally added to replace evaporating phenol. This method allows the preparation of large numbers of specimens at one time.

Many times, when attempting to observe the pattern of pale spots on the wings of *Culicoides,* one is handicapped by the lack of contrast between the pale spots and the remainder of the wing. I have found it very useful to observe the wing pattern by a false dark field illumination of a phase contrast microscope. This is accomplished by turning the phase condenser one or two stops too far while the low power objective is in position. With this false dark field microscopy the pale spots, which are due to the scarcity or absence of microtrichia, appear distinctly dark against a white background and are easily delimited (Figs. 1, 2). Even very small or indistinct spots are evident when viewed under these conditions. This technique, when supplemented by bright field illumination for studying the color pattern, presents an excellent method for examining *Culicoides* wings.



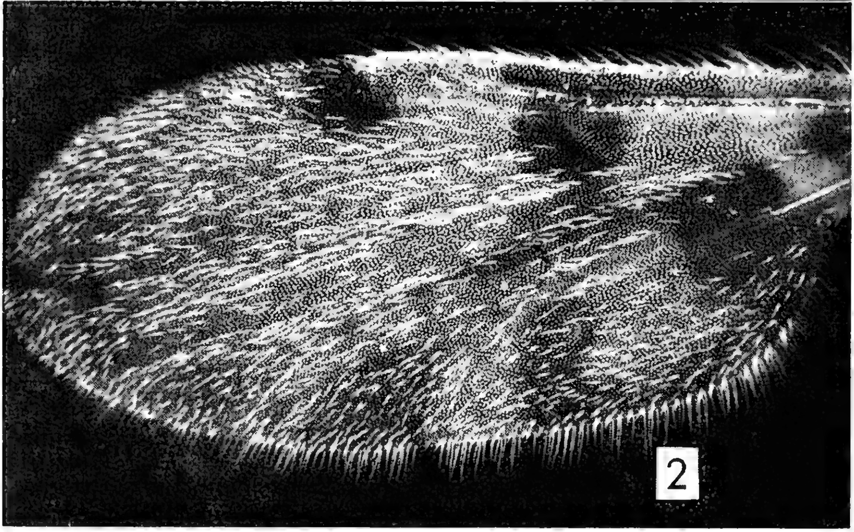


FIG. 1. Phase contrast dark field of wing of *Culicoides byersi*, new species. FIG. 2. Phase contrast dark field of wing of *Culicoides sublettei*, new species.

Types of the species described as new in this paper will be deposited in the United States National Museum, and as many paratypes as possible will be deposited in the Snow Entomological Museum of the University of Kansas and the American Museum of Natural History. A determined series of the New Mexico species will be deposited in the Snow Entomological Museum.

All measurements used were made with an ocular grid calibrated with a stage micrometer and most were taken from slide-mounted specimens which had been cleared in potassium hydroxide or from specimens cleared in phenol. Measurements, when possible, were made of a series of specimens so as to give some insight into the variation of the structures. The results are presented as the mean followed (in parentheses) by the range of variation and N, the number of specimens measured; for example, 1.68 (1.5-1.8; N=3). Measurements not given in this fashion refer to single specimens.

Drawings were made with the aid of a Bausch and Lomb V-H microprojector. No attempt was made to correct the symmetry of most of the drawings, since this could have led to distortion of some of the structures.

The illustration of the dark and pale wing spots in this paper was achieved by using Craf-Tone, a commercial stippling paper. This technique is limited in that one cannot show decreasing or increasing intensity of the wing color. This, however, is not of great taxonomic value and the ease by which this material can be applied compared to stippling by hand greatly overshadows this limitation.

MORPHOLOGY

The head is subspherical, anteriorly flattened and possesses a broad postocciput. The vertex is undifferentiated and usually contains scattered setae. The eyes are large reniform structures and are bare or rarely have short pubescence among the ommatidial facets. The eyes may be contiguous or separated; the degree of marginal contact or separation is of importance in distinguishing some species. The ocelli are more or less poorly differentiated. The frons can be arbitrarily delimited posteriorly in most species by a transverse transocular suture, which arose secondarily. It probably gives support in the area of the eyes and is quite evident, particularly in species with rather widely separated compound eyes.

One can readily postulate that if this secondary suture functions for support of this area, the appearance of a second suture with a similar function is possible. Indeed, this appears to be borne out in certain species of *Culicoides,* e.g., *C. sublettei* n. sp., and *C. stellifer,* in which there is a small interocular suture anterior to the transocular suture.

The frontoclypeus surrounds the antennal bases in the region of the frons and is expanded anteriorly to form the convex clypeal region. Its strongly incurved border is joined with the labrum-epipharynx by two small, triangular sclerites designated by Peterson (1916) as tormae. An important taxonomic character involves a ratio of the head and proboscis. The length of the proboscis is measured from the distal end of the labrum-epipharynx to the anterior margin of the tormae. This length is divided into the length measured from the anterior margin of the tormae to the median hair socket.

Jamnback (1965), in his paper on the *Culicoides* of New York, has defined this character as given here; however, he has inverted the fraction when applying it to a description and said that a "proboscis-to-head ratio" of less than 0.65 should be indicative of a short proboscis; however, it should indicate a long proboscis. Therefore, no comparison could be made with regard to this character between eastern and southwestern representatives of several species.

The biting apparatus includes the labrum-epipharynx, mandibles, maxillae, labium and the hypopharynx. The mandibular, hypopharyngeal and maxillary stylets are enclosed in a labial gutter, covered dorsally by the labrum; the sucking apparatus consists of cibarial and pharyngeal pumps (=pharynx and oesophageal pumps, respectively, of Jobling, 1928). The mandibles of the females are thin blades, finely toothed on the distal margins, the number of mandibular teeth being of value in separation of closely related species. Various authors have shown a device which interlocks the mandibles to give a scissor-like appearance. The endite lobe of the maxilla, usually extended as a maxillary stylet, is believed to be the galea or fused galea and lacinia. On the basis of musculature, the action of the maxillae appears to be protraction and retraction. The labium and hypopharynx are distally toothed.

The mandibles of the females in the majority of blood-feeding species in the genus *Culicoides* are prominently denticulate. The females of other species have weakly developed mouthparts and are apparently incapable of taking a blood meal. Jamnback (1965) has illustrated both hematophagous and non-hematophagous types of mouthparts.

The maxillary palps are five-segmented, the first segment short and incompletely sclerotized, the third segment large and more or less swollen. The third palpal segment bears on the mesal surface a specialized sensory organ which contains many small sensillae. Barth (1961) described the histological aspects of this organ in *Forcipomyia,* a genus related to *Culicoides.*

The maxillary palps of females possess characters, such as the ratio of lengths of segments and the shapes of the third segment and sensory pit, which have been used by many workers for the delimitation of species. The palpal ratio (PR) is obtained by dividing the length of the third palpal segment by its greatest breadth. This measurement is subject to variation, particularly in slide-mounted specimens, due to the orientation of the palpus on the slide; however, it is still of importance in the separation of some species. The relative lengths of the palpal segments is another useful character. In this paper the basal segment is not included in palpal measurements, since its degree of sclerotization appears to vary among individuals of the same species.

The mouthparts of the males, although structurally similar to those of the females, are less well developed. They have no distal mandibular teeth; the mouthparts are not fitted for piercing; and the maxillary palps are not as well developed as in females.

The antennae provide some of the most useful characters for distinguishing species. They are divided into 15 units: a small ring-like scape, which is more or less hidden by the enlarged pedicel, and a flagellum composed of 13 sub-segments. In various instances in the remainder of this paper the antennal sub-segments, or flagellomeres, will be referred to as "segments." In the females the proximal eight flagellomeres are short, being slightly longer than wide, while the distal five are elongate, usually much longer than wide. Segment 3 is elongate and somewhat larger than 4-10. Segments 3-10 in the female possess long verticils. In males the pedicel is more enlarged than in females, and the transition in flagellar structure occurs between segments 12 and 13. Segments 3-12 each have dense verticillate hairs, giving the male antenna a plumose appearance.

The antennal segments contain various types of sensory organs, one of which is very important taxonomically. Jobling (1928) first demonstrated the presence of small pits on various segments and referred to them as olfactory pits. These pits, which are surrounded by a number of minute setulae, are found on the third segment of both sexes and various other segments in females and some males. First used taxonomically by Ortiz (1951), their pattern of distribution is more or less consistent for a species and, therefore, very useful in the separation of species and species groups. Antennal sensillae (*sensu* Jobling) are usually evident under low magnification in slide-mounted preparations. A second type of sensilla on the antennal segments has been described by Campbell and Pelham-Clinton (1960). According to these authors, small flask-shaped structures occur on various antennal segments and correspond to the sensilla coeloconica described by Snodgrass (1935). No taxonomic significance has yet been assigned to the sensilla coeloconica. The use of the term sensilla in this paper, unless otherwise stated, refers to the "olfactory pits" described by Jobling.

Jamnback (1965) has shown some correlation between the number of antennal olfactory pits and the host preferences of the females. He has pointed out that females of ornithophilic species appear to have more olfactory pits than mammalophilic species preferring large mammals.

The antennal ratio is obtained by dividing the combined lengths of the distal five segments by the combined lengths of the preceding eight.

In addition to the antennal ratio, another antennal character is more or less constant for a species. This relationship involves the length of segment 11 divided by the combined lengths of segments 9 and 10.

The thorax is dorsally convex and protruding anteriorly, so as to cover the posterior region of the head slightly. The mesonotum possesses a pair of large and distinct sensory or humeral pits, which are located near the anterior margins of the humeri and are possibly remnants of the pupal respiratory horns. A pair of faint lines, the pseudosutural foveae, extend posteriorly from the pits to near the sides of the scutellum. The large, somewhat flattened, caudal portion of the mesonotum, the prescutellar depression, possesses a pair of sensory areas known as the prescutellar spots. The postscutellum is bare and arched. In many species the mesonotal disc is ornamented by a distinct pattern, which along with various other thoracic markings, is of use in species differentiation.

The legs are slender; however, the femora occasionally may be slightly expanded, but are not spinous and bear no scales, as in many of the other ceratopogonid genera. The hind tibiae bear a comb of spines, which is sometimes useful in differentiating species. The basal tarsomere is at least twice as long as the second, and the fourth tarsomere is shorter than the fifth. The shape of the fourth tarsomere is important in distinguishing the subgenus *Macfiella* Fox and some other unrelated species. The pretarsal claws are small, simple, and equal in both sexes and a very minute empodium arises from the apical end of the unguitractor.

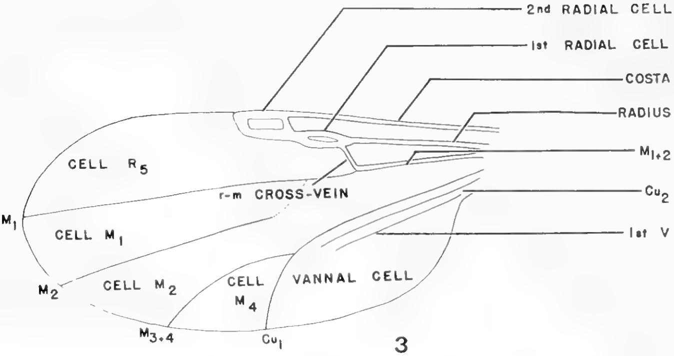
The wings possess two types of hairs: macrotrichia, which are long hairs whose abundance may vary between species, and dense microtrichia, whose presence or scarcity at a particular location makes a pattern of light or dark spots, which are of great importance in the recognition of species. These pale spots can be very stable in position and distinctiveness in some species, but certain spots may be highly variable in others.

The costa extends approximately one-half the length of the wing, the proportion being a useful taxonomic character in some species. There are two radial cells which are usually of subequal length, the distal cell being broader than the slit-like proximal cell. The nomenclature of the wing veins used in this study follows the Tillyard modification of the Comstock-Needham system, in which the anterior branches are M_1 and M_2, and the posterior branches are M_{3+4} and Cu_1 (Fig. 3).

The terms vannal vein and vannal cell used in this work are considered to be morphologically more correct than the terms anal vein and anal cell used by previous authors. The vannal portion of the wing refers to the fan-shaped area delimited basally by the third axillary sclerite and anteriorly by the vannal fold. Although the term anal vein is firmly entrenched in the taxonomic literature of this group, it is incorrect, according to current morphological thinking and is in need of change.

The wings of the males are usually more elongate than those of females, and the pattern of light spots usually lacks the contrast seen in the female wing. The measurement of wing length was made from the basal arculus to the tip. This measurement appears to be more accurate than the practice of adding one-seventh to the wing length to account for that part of the wing basad to the basal arculus, utilized by some workers.

The external features of the female abdomen are usually of little taxonomic importance and are easily discolored as a result of engorgement. The internal abdominal structures are, however, of paramount importance. The sclerotized



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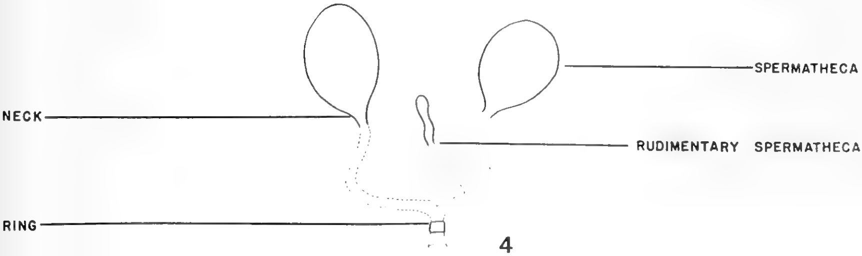

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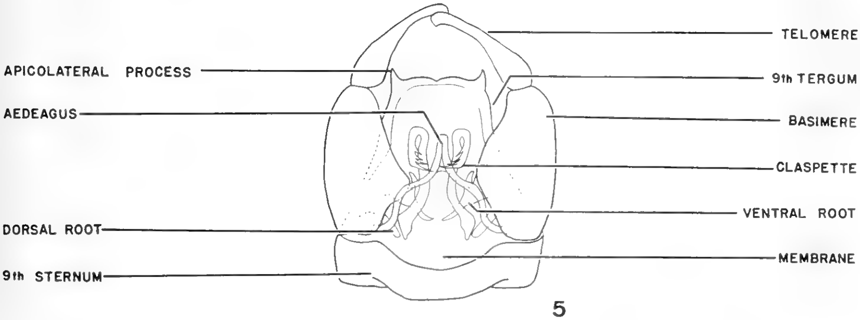

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Fig. 3. Wing of *Culicoides*. Fig. 4. Spermathecal system of *Culicoides*. Fig. 5. Male genitalia of *Culicoides baueri* Hoffman.

parts of the spermathecal system (Fig. 4) are very significant, and females of many species cannot be accurately identified without reference to it. The spermathecae may or may not be sclerotized and may vary in number from one to three, the number being constant for a particular species. Those species having two functional spermathecae usually have a rudimentary sclerotized spermatheca, which is rarely expanded to resemble a small third functional spermatheca. The spermathecal ducts may be sclerotized for some distance distally but are unsclerotized proximally near their connection to the bursa copulatrix. The junction, which forms the union of the spermathecal ducts and the bursa, may be marked by a small sclerotized ring. Length of the spermathecae was measured from the distal end to the proximal end of the sclerotized portion of the duct, and width was measured at the widest point.

The abdomen of the male is considerably more slender than that of the female. The genitalia of the male (Fig. 5) are of primary importance in the recognition of species and higher taxa. In this study I have followed the revised interpretation of the male genitalia proposed by Snodgrass (1957, 1959). This concept is in agreement with the earlier morphological ideas of Crampton (1942) and more recently the studies of Matsuda (1958). It is supported in the Diptera by the embryological studies of Christophers (1922), Christophers and Barraud (1926) and Abul-Nasr (1950), and in my opinion is more plausible than the earlier idea of appendicular origin of genitalia.

Taxonomists of the Ceratopogonidae have long chosen to follow a terminology for the male genitalia that is, in many instances, without meaningful morphological basis. This condition, however, is not limited to the Ceratopogonidae. Crampton (1942) pointed out some of the confusion that exists regarding the nomenclature of various structures and made a plea for uniformity. This uniformity has been met in some groups by the use of taxonomically adequate, but morphologically inaccurate, terms. Although there is something to be said for uniformity of nomenclature, one should strive for morphological accuracy to facilitate uniformity in concepts of homology.

The ninth abdominal segment of the male is in the form of an irregular scleroma composed of the fused tergum and sternum. The ninth tergum is a posteriorly tapering, platelike expansion, the posterior margin of which may or may not bear apicolateral processes. The ninth sternum is a narrow structure, usually emarginate on the posterior surface. The outermost genital claspers, the parameres, articulate on the ninth sternum and are divided into a proximal basimere and a distal telomere (basistyle and dististyle, respectively, of authors). The suffix "-style," used by many authors in the terminology for the outermost male genital claspers, invokes the old idea of the appendicular origin of the male genitalia and is not consistent with the terminology proposed in this paper. The term "paramere" has been affixed to many different structures of the genitalia, but in reality is the lateral genital clasper. Some workers have gone so far as to suggest abandoning this term because of the confusion as to its true identity. The basimere (Fig. 5), in the generalized condition, has two internal processes on the anterior surface, the inner ventral root and the outer dorsal root. The telomere generally has an expanded base and narrows distally and may have a curved-tipped apical spine. The claspettes (parameres of authors) are usually elongate with an expanded base and a simple, slender to greatly modified apex. In the subgenus *Selfia* Khalaf, the claspettes are fused into a platelike structure. The aedeagus is usually a V-or Y-shaped structure, less sclerotized distally, with a pair of basal arms. Its basal arch is usually curved and is connected to the ninth sternum by a membrane, which may or may not be spiculate.

SYSTEMATICS

The Ceratopogonidae show morphological affinity to the Chironomidae but differ in that they possess complete mouthparts, having developed mandibles in both sexes, and a branched M_{1+2} wing vein, and a postscutellum lacking a median furrow or keel. The legs of ceratopogonids appear stouter and the metathoracic pair is usually longer, as is the prothoracic pair of chironomids. Edwards (1939) is of the opinion that the ceratopogonids have much in common with the Simuliidae.

The genus *Culicoides* can be differentiated from other ceratopogonids by the presence of two more or less equal radial wing cells, small and equal tarsal claws in both sexes, the absence of a hairy empodium, and large pronounced thoracic humeral pits.

Root and Hoffman (1937) proposed the first supraspecific categories of *Culicoides* when they divided the North American species into two series on the basis of male genitalia and certain external characters. Edwards, in his monograph of the British species (1939), was able to substantiate such a division and placed the European species into two apparently natural groups on the basis of the male genitalia.

Fox (1948) proposed the subgenus *Hoffmania* for 12 neotropical species, which he distinguished from *Culicoides s. str.* The known species of *Hoffmania* were later reviewed by Ortiz (1950), who expanded the subgenus to include several additional species.

Khalaf (1954) made the first major attempt to establish interrelationships and deduce phylogenies among species of *Culicoides*. Using primarily external male genitalia and female spermathecae, he was able to divide the known world fauna into four subgenera: *Culicoides s. str., Monoculicoides* Khalaf, *Oecacta* Poey and *Selfia* Khalaf, lumping the subgenus *Hoffmania* of Fox into the subgenus *Oecacta* Poey. Khalaf further subdivided these subgenera into complexes and species groups, and although his concepts were fundamentally sound, he was handicapped in that he had to draw much of his information from the literature, which was, no doubt, vague in many instances. Many of the species descriptions in the literature made little reference to the genitalia; therefore, the true relationship of these with other species could not be accurately determined.

Vargas (1953) erected the subgenus *Beltranmyia* for the *crepuscularis* group, which Khalaf had included in *Monoculicoides*. Fox (1955), in his catalog of bloodsucking midges, arranged the species of *Culicoides* known to occur in the Americas into subgenera, introduced the subgenus *Macfiella* for the *phlebotomus* group and *Avaritia* for the *obsoletus* group, and augmented the subgenus *Beltranmyia* as Vargas had outlined it. In spite of these changes, the subgeneric classification of Fox is not entirely in agreement with the earlier attempt by Khalaf with respect to the content of the various subgenera.

More recently Wirth and Hubert (1959) have proposed the subgenus *Trithecoides* for the Ethiopian and Oriental species whose females have three well-developed spermathecae and a long second radial cell.

Vargas (1960), attempting to correlate genitalia and wing characters, proposed the following new subgenera for the species occurring in the Western Hemisphere: *Anilomyia, Diphaomyia, Drymodesmia, Glaphiromyia* and *Mataemyia.* In addition he resurrected the name *Haematomyidium* Goeldi 1905 for many species usually placed in the subgenus *Oecacta.*

Incorporating two of the subgeneric names of Vargas (1960), i.e., *Drymodesmia* for the *copiosus* group and *Diphaomyia* for the *iriartei-baueri* group, with previously known names, Wirth (1965) arranged the North American species into nine subgenera. In my opinion the classification by Wirth (1965), which differs from that of Vargas (1960) in the content of several of the subgenera, reflects more correctly in many instances the natural affinities of the genus. It is the classification followed in this paper.

Some subgenera, e.g., *Oecacta,* in the past have been considered as "catch-alls" for a rather heterogeneous accumulation of species. Attempts have recently been made to divide various subgenera into much smaller units. Although in some instances such divisions may be useful in pointing out interspecific relationships, there is little to be gained at present by assigning subgeneric names to a large number of species groups that would contain only a few species. As more information becomes available, much shifting of taxa may become necessary. It is only after more distributional data are available and extensive taxonomic studies, such as that of Wirth and Blanton (1959), have been made that more accurate conclusions regarding phylogenetic relationships can be drawn.

Further studies, such as those of Jones (1961), are needed to correlate the classification of the immature stages with that of the adults. These studies should reveal interspecific relationships not evident in classifications based on adults. Several of the newer systematic techniques, e.g., numerical taxonomy, should show considerable promise at the subgeneric level.

At the outset of this investigation nine species of *Culicoides* were reported in the literature as occurring in New Mexico (Wirth, 1952, 1965; Foote and Pratt, 1954). Extensive collecting has increased this number to 35. Nineteen species can be assigned to previously existing names, the remainder are considered as new to science. Adequate material is available to describe four of these as new species. It is hoped that subsequent collection will allow description of the remaining species. One species, *C. pampoikilus* Macfie, previously reported from Mexico, Panama and Venezuela, was taken during this study at Ruidoso, Lincoln County, and is a new United States record.

The *Culicoides* fauna of New Mexico can be divided into eight subgenera. In the descriptive portion of this paper many species, particularly those placed in the subgenus *Oecacta,* are listed, when applicable, with the name of their respective species group. The following table gives the systematic arrangement of New Mexico species together with a summary of the mean values of a number of quantitative characters. The range of variation is given in the respective species descriptions.

TABLE 1. Systematic arrangement and summary of quantitative characters of New Mexico *Culicoides.*

Species	Wing Length	Costal Ratio	Antennal Ratio	Ratio of Antennal Segments 9+10 to 11	Sensorial Pattern	Palpal Ratio	Head Length to Proboscis Ratio	No. Mandibular Teeth	No. Tibial Spines
Subgenus *Avaritia*									
obsoletus	1.19	0.60	1.14	0.72	3, 11-15	2.74	1.0	12-16	5
Subgenus *Beltranmyia*									
crepuscularis	1.41	0.56	1.35	0.90	3-14(15)	2.27	1.05	10-16	4
Subgenus *Culicoides*									
cockerellii	1.84	0.60	1.07	0.71	3, 5, 7, 9-15	3.26	1.05	14-16	6
Subgenus *Diphaomyia*									
baueri	1.35	0.52	1.07	0.66	3, 5-10	2.17	1.24	10-12	4
haematopotus	1.17	0.55	1.43	0.91	3, 5, 7, 9-15	2.5	1.11	12-15	4
Subgenus *Drymodesmyia*									
sitens	1.34	0.51	1.07	0.69	3-9, (10) 11-15	2.33	1.0	14	4
byersi	0.89	0.54	1.13	0.73	3, 5, 7, 9, 11-15	1.7	1.67	9-10	4
Subgenus *Monoculicoides*									
variipennis sonorensis	1.55	0.55	0.86	0.59	3, (4) (5) (6) (7), 8-10	2.38	1.10	11-15	6-7
Subgenus *Oecacta*									
doeringae	1.24	0.58	1.63	1.11	3, 5, 7, 9, 11, 13-15	2.61	1.12	12-15	4
luglani	1.22	0.53	0.95	0.59	3-10	2.12	1.05	13-16	4
novamexicanus	1.23	0.56	1.02	0.58	3-5, 7, 9, 11, 13-15	2.12	1.04	14-16	4
oklahomensis	1.21	0.56	1.29	0.82	3, 5, 7, 9, 11-15	3.0	1.04	14	5
palmerae	1.48	0.56	1.28	0.77	3-15	2.26	1.02	14	4
pampoikilus	1.52	0.54	1.55	0.89	3, 5, 7, 9, 11-15	2.0	1.32	15	4

TABLE 1. Systematic arrangement and summary of quantitative characters of New Mexico *Culicoides* (concluded).

Species	Wing Length	Costal Ratio	Antennal Ratio	Ratio of Antennal Segments 9+10 to 11	Sensorial Pattern	Palpal Ratio	Head Length to Proboscis Ratio	No. Mandibular Teeth	No. Tibial Spines
pecosensis	1.22	0.54	1.25	0.81	3-7, 9, 11-14	2.48	0.93	17-18	5
reevesi	0.85	0.56	0.65	0.33	3, 8-10	2.1	1.16	14-16	4
stellifer	1.24	0.54	0.96	0.62	3, 7-10	2.47	1.22	12-14	5
stonei	1.17	0.56	1.10	0.69	3-14(15)	2.3	1.04	12-13	4
sublettei	1.19	0.55	1.07	0.67	3, 11-15	2.37	1.05	14-16	4
utahensis	1.43	0.55	1.12	0.75	3-15	1.85	1.30	14	4
Subgenus *Selfia*									
brookmani	1.14	0.53	0.92	0.62	3-10	1.97	1.39	11	4
hieroglyphicus	1.20	0.54	1.03	0.66	3, 5-10	2.11	1.24	11-13	4-5
jamesi	1.27	0.56	1.0	0.63	3-10	2.26	1.27	11-13	4-5

KEY TO FEMALES OF NEW MEXICO *CULICOIDES*

1. Spermathecae unsclerotized; wings without pattern of light and dark spots. 2
Spermathecae sclerotized; wings with or without pattern of spots. 3

2. Sensoria on antennal segments 3-10. .... *brookmani*[1]*
Sensoria on antennal segments 3, 5-10. .... *jamesi*[3]
.... *hieroglyphicus*[2]

3(1). Second radial cell with distal portion in a pale area (Fig. 18, 23) eyes contiguous. 4
Second radial cell in a dark area; eyes may or may not be contiguous. 5

4(3). Wings poorly marked; sensoria on segments 3, 11-15; hind tibial comb with 5 spines; a small to medium sized species, WL 1.0-1.3 mm. .... *obsoletus*[5]
Wings well marked, with 3 transverse bands (Fig. 18) which may be reduced in some forms; sensoria irregularly distributed, usually 3, 5, 7, 9, 11-15; hind tibial comb with 6 spines; a large species, WL 1.6-2.0 mm. .... *cockerellii*[4]

5(3). One spermatheca. 6
Two spermathecae. 8

6(5). Wing pattern with irregular gray streaks (Fig. 33); hind tibial comb with 6-7 spines; spermatheca C-shaped. .... *variipennis*[7]
Wing pattern with definite pattern of spots; hind tibial comb with 4 spines; spermatheca not as above. 7

7(6). Antennal segments 9+10 to 11 in ratio of 0.90; sensoria on segments 3-15; a large species, WL 1.1-1.5. .... *crepuscularis*[6]
Antennal segments 9+10 to 11 in ratio of 0.30; sensoria on segments 3, 8-10; a small species, WL 0.8 mm. .... *reevesi*[17]

8(5). Hind tibial comb with 5-6 spines. 9
Hind tibial comb with 4 spines. 11

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* Number in brackets refers to location in species descriptions.

9(8). Apices of veins M_1, M_2, M_{3+4} dark; cell R_5 with inverted U-shaped pale spot (Fig. 69); sensoria usually on segments 3, 7-10. .... *stellifer*[13]
Apices of veins M_1, M_2, M_{3+4} pale; cell R_5 not as above; sensoria on various proximal segments and on 11-15. 10
10(9). Vein Cu_1 bordered by a pale spot for at least part of its length (Fig. 105). .... *oklahomensis*[19]
Vein Cu_1 dark (Fig. 99). .... *pecosensis*[18]
11(8). Wing without distal pale spots (Figs. 77, 82). 12
Wings with distal pale spots. 13
12(11). Wings completely lacking pattern of spots; sensoria on segments 3-14(15). .... *stonei*[14]
Wings with very faint markings; sensoria on segments 3, 11-15. .... *sublettei*[15]
13(11). Spermathecae very unequal, lacking necks (Fig. 122); antennal segments 9+10 to 11 in ratio of at least 1.0; sensoria on segments 3, 5, 7, 9, 11, (12) 13-15. .... *doeringae*[23]
Spermathecae equal or subsequal, necks usually present; segments 9+10 longer than 11, in ratio of less than 1.0; sensoria various. 14
14(13). Cell R_5 with 3 pale spots (Fig. 88). .... *pampoikilus*[16]
Cell R_5 with 2 pale spots. 15
15(14). Pale bands absent on femora; eyes separated by approximately diameter of an ommatidial facet; macrotrichia abundant over entire surface of wing. 16
Some or all femora with pale bands; eyes usually separated less than diameter of ommatidial facet to contiguous; macrotrichia usually confined to distal and posterior regions of wing. 18
16(15). Sensoria on segments 3-5, 7, 9, 11, 13-15. .... *novamexicanus*[22]
Sensoria on segments 3-15. 17
17(16). Proboscis long, HR 0.8-1.1; wing well marked; third palpal segment moderately swollen, PR 2.0-2.4; spermathecae without necks. .... *palmerae*[20]
Proboscis of medium length, HR 1.30; wing poorly marked; third palpal segment greatly swollen, PR 1.85; spermathecae with necks. .... *utahensis*[21]
18(15). Sensoria on segments 3, 5-10, 3, 7-10, or 3-10, never on distal five segments. 19
Sensoria on segments 3, 5, 7, 9, (10) 11-15 or 3-15. 20
19(18). Spots in cells M_1, M_2 and M_4, small, round, well removed from wing margin (Fig. 55) veins M_{3+4} and Cu_1 bordered by pale area; spot in cell R_5 constricted mesally; sensoria on segments 3, (5), (6), 7-10. .... *baueri*[10]
Spots in cells M_1, M_2 and M_4 large, those in M_2 and M_4 attaining wing margin (Fig. 66) veins M_{3+4} and Cu_1 not as above; spot in R_5 large, not constricted; sensoria on segments 3-10. .... *luglani*[12]
20(18). Antennal segments 9+10 to 11 subequal, in ratio of 0.83-1.0; AR 1.25-1.57; pale spot in cell R_5 small at distal end of cell (Fig. 60). .... *haematopotus*[11]
Segments 9+10 to 11 unequal, in ratio of approximately 0.69-0.75; AR not more than 1.15; pale spot in cell R_5 mesally located. 21

21(20). Proboscis very short, HR 1.5-1.7; pale spot on basal portion of vein M$_1$ absent (Fig. 49); a small species, WL 0.89 mm. ..... *byersi*[9]
Proboscis of medium length, HR 1.0; mesally constricted pale spot in cell R$_5$, attaining anterior wing margin; pale spots over basal portions of veins M$_1$ and M$_2$ (Fig. 44); a medium sized species, WL 1.3 mm. ..... *sitiens*[8]

KEY TO MALES BASED UPON GENITALIA*

1. Claspettes fused for part or all of length (Figs. 12, 38). 2
Claspettes free and separate for entire length. 5

2(1). Claspettes fused basally, apices free; aedeagus with bifid tip (Fig. 38). ..... *variipennis*[7]**
Claspettes completely fused over entire length. 3

3(2). Ninth sternum without mesal notch or lobes; telomere unmodified; boomerang-shaped sclerites present. ..... *brookmani*[1]
Ninth sternum with prominent lobes or mesal notch; telomere modified apically; boomerang-shaped sclerites absent. 4

4(3). Ninth sternum with prominent caudo-median lobes; aedeagal arms widely separated. ..... *hieroglyphicus*[2]
Ninth sternum with medio-posterior notch; aedeagal arms not widely separated; telomere distinctly modified with large foot-shaped apex (Fig. 17). ..... *jamesi*[3]

5(1). Ninth tergum with apicolateral processes absent or very small (Figs. 22, 27); if small, medio-caudal margin very convex and extending posteriorly beyond tip of apicolateral processes; mesal notch of posterior border of ninth tergum absent. 6
Apicolateral processes present and usually well developed; mesal notch present. 7

6(5). Ventral root very long and slender, much longer than dorsal root; ninth sternum with deep mesal notch (Fig. 27); apicolateral processes absent. ..... *obsoletus*[5]
Dorsal and ventral roots subequal in length; ninth sternum with only slight emargination; ninth tergum with apicolateral process very small, medio-caudal margin very convex (Fig. 22). ..... *cockerellii*[4]

7(5). Claspette with distinct apical and subapical spines (Figs. 64, 70, 87, 122). 8
Claspette with simple apex (Figs. 32, 104, 115). 13

8(7). Ventral root with process on posterior margin (Figs. 65, 129). 9
Ventral root lacking process. 12

9(8). Aedeagal arms with blade-like processes on posterior margin (Fig. 65). 10
Aedeagal arms without blade-like processes. 11

10(9). Claspette with distinct thumb-like lobe on lateral margin, apex greatly expanded with row of prominent spines. ..... *haematopotus*[11]
Claspette lacking thumb-like lobe, apex not expanded. ..... *baueri*[10]

11(9). Claspette with small lateral lobe at approximately two-thirds of length; aedeagus in shape of inverted V, basal arch mesally notched, median posterior process short, conical. ..... *stellifer*[13]

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* Male of *reevesi* unknown.

** Number in brackets refers to location in species descriptions.

Claspette tapering to distal point bearing row of spines along margin; aedeagus with elongate, truncate median process, basal arch rounded. .... *doeringae*[23]

12(8). Claspette with fringe of spines, stem with prominent blade-like process on lateral margin (Fig. 69); median process of aedeagus with pointed lateral subapical processes. .... *luglani*[12]
Claspette with 2-3 subapical spines, stem simple (Fig. 86); aedeagus truncate, lacking subapical projections. .... *sublettei*[15]

13(7). Ventral root greatly reduced or absent (Fig. 33); membrane spiculate. .... *crepuscularis*[6]
Ventral root present and distinct; membrane may or may not be spiculate. 14

14(13). Telomere bulbous basally, abruptly bent (Fig. 109); apicolateral processes distinct, of uniform width for most of length, much longer than wide; medio-caudal border of ninth tergum convex with distinct mesal notch. 15
Telomere not abruptly bent; apicolateral processes usually triangular; medio-caudal border of ninth tergum not distinctly convex. .. 17

15(14). Aedeagus with lateral shoulder-like processes on median posterior process (Fig. 112); claspette with tapering, usually recurved apex. .... *palmerae*[20]
Aedeagus lacking processes; apex of claspette usually not recurved. 16

16(15). Claspette slender with contorted apex. .... *novamexicanus*[22]
Claspette stout with laterally directed apex. .... *utahensis*[21]

17(14). Median posterior process extended to slender point with subapical processes (Fig. 105). .... *oklahomensis*[19]
Median process not as above, lacking subapical processes. 18

18(17). Claspettes with median portion of stems distinctly swollen, apex abruptly narrowed (Fig. 101); median posterior process elongate, parallel-sided truncate, about equal in length to basal arms. .... *pecosensis*[18]
Claspettes tapering distally to simple pointed apex; median process not elongate or parallel-sided. 19

19(18). Apicolateral processes broad, very prominent, triangular (Figs. 79, 91); claspette with distinct, anteriorly directed basal process. 20
Apicolateral processes slender, pointed; claspettes not as above. 21

20(19). Median posterior process slender with slight subapical swelling (Fig. 93); basal arch notched mesally; claspette slender, tapering to mesally recurved apex; membrane bare. .... *pampoikilus*[16]
Median process broad, subtruncate without median swelling; claspette with rather stout, laterally turned sickle-shaped apex; apicolateral processes very large (Fig. 81); membrane spiculate. .... *stonei*[14]

21(19). Aedeagus very stout, conical, arms and basal arch short; claspettes with basal portion of stem swollen, knob-like, tapering to slender pointed, laterally directed tips; ninth sternum very narrow. .... *sitiens*[8]
Aedeagus with long slender arms, basal arch of medium length; claspettes tapering for entire length, apices entwined. .... *byersi*[9]

Subgenus *SELFIA* Khalaf, 1954:38

Type species *hieroglyphicus* Malloch (orig. des.).

This group of small to medium sized species contains females which have unsclerotized, therefore unapparent, spermathecae and plain wings, without a pattern of pale and dark spots. The antennal sensoria are located on various of the proximal 8 segments, depending on the species, but never on the distal 5. The hind tibial comb contains 4 or 5 spines. The claspettes of the male genitalia are fused into a platelike structure. The ventral root of the basimere is prominent; however, the dorsal root is often unapparent. Two lateral sclerites, often fused distally, usually comprise the adeagus. The unmarked wings of *stonei* James and *bottimeri* Wirth superficially resemble those of the *Selfia* species; however, these species can be readily distinguished by the well sclerotized spermathecae and the distinctive male genitalia.

Selfia is apparently restricted to the Nearctic region, as no neotropical forms have been described. This group reaches its highest development in the western portion of the United States, and only one species is reported east of the Mississippi.

Three species, *brookmani, hieroglyphicus* and *jamesi,* were found in New Mexico. Unless otherwise stated, all distribution records of *Selfia* species in this paper refer to males which have characteristic genitalia.

1. **Culicoides (S.) brookmani** Wirth

(Figs. 6-9)

Culicoides brookmani Wirth, 1952, Univ. Calif. Pub. Ent. 9:179 (male, female; California; fig. male genitalia, wing and palp).

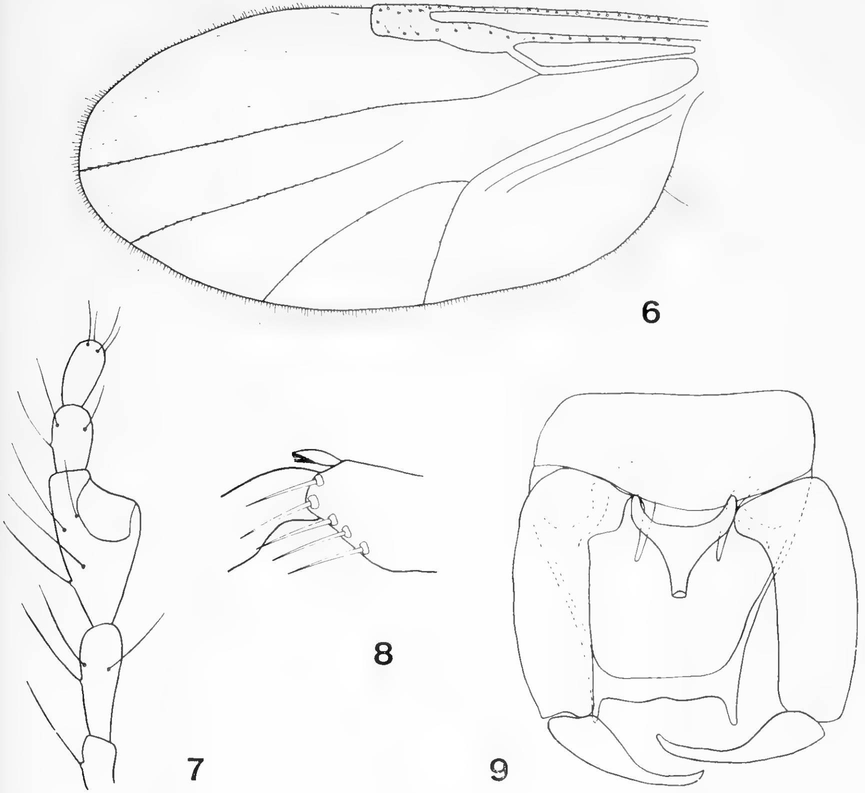
FEMALE—Length of wing 1.14 (1.04-1.27; n=4) mm.

Head: Eyes separated less than diameter of a facet. Antenna with flagellomeres in proportion of 13:10:10:11:12:12:12:13:14:14:15:15:21; antennal ratio 0.92 (0.82-0.97; n=4); distal sensory tufts present on segments 3-10; segments 9+10 to 11 in ratio of 0.62 (0.61-0.65; n=4). Distal four palpal segments in proportion of 15:25:8:12; third palpal segment short, very swollen, 1.97 (1.8-2.09; n=4) times as long as greatest breadth, with a large, very deep sensory pit; interior of pit lined with stalked sensillae (Fig. 7). Ratio of length of head to proboscis 1.39 (1.38-1.42; n=4). Mandible with 11 teeth.

Thorax: Legs unicolorous light brown; hind tibial comb with 4 or 5 spines (Fig. 8).

Wing: (Fig. 6). No pattern of pale and dark spots. Costa extending 0.53 (0.51-0.56; n=4) of total length of wing. Macrotrichia sparse, occurring in small numbers on veins M_1, M_2, M_4 and vannal cell.

Abdomen: Spermathecae unsclerotized.



FIGS. 6-9. *Culicoides brookmani* Wirth. Female: 6, wing; 7, palpus; 8, tibial comb. Male: 9, genitalia.

MALE—(Fig. 9). Genitalia with ninth sternum broad, posterior margin indefinite; membrane spiculate. Ninth tergum tapering posteriorly, mesal notch slight, apicolateral processes rather small and tapering distally. Basimere with ventral root prominent, having a slightly curved apex; dorsal root evidently included in basal portion of basimere. Telomere broad basally, tapering to a slender tip. Aedeagus Y-shaped with widely separated basal arms; median posterior process conical, distally truncate; two distinct boomerang-shaped structures present, the posterior end of each forming an oblique angle with the anterior end. Occasionally these structures form the lateral margins of the aedeagus. Claspettes ventrally turned, invisible in most specimens or, at best, visible as narrow band. Jones and Wirth (1958) dissected the males of this species and found the claspettes fused into a plate with narrow, slightly curved, basal arms that join narrowly for approximately the middle one-third of their combined length.

DISTRIBUTION: Present records indicate that this species is probably restricted to the southwestern United States. It has previously been reported from Calif., Ariz., N. Mex. and Texas. New Mexico County Records: Catron, Grant.

DISCUSSION: At present, alcoholic and slide-mounted females in the subgenus *Selfia* are virtually inseparable. The descriptions of the females of the *Selfia* species in this paper are based on specimens from a locality where collection yielded large numbers of males of a single *Selfia* species. An extensive study is needed to determine characters useful in the separation of the species of this group.

Slide-mounted specimens of *brookmani* tentatively can be separated from those of *hieroglyphicus* by the fact that *hieroglyphicus* usually has sensory tufts on antennal segments 3, 5-10. In pointed specimens, the pattern of the mesonotal disc of *hieroglyphicus* is sufficient to distinguish it from *brookmani,* which has either an unadorned mesonotum or three longitudinal vittae, as reported by Jones and Wirth (1958) for Texas specimens.

Although no good taxonomic character exists to distinguish slide-mounted and alcoholic specimens of *brookmani* from *jamesi,* separation can sometimes be made on the basis of the large size of *jamesi,* particularly its wing length. Pointed specimens can be distinguished on the basis of two submedial, longitudinal mesonotal stripes found in *jamesi.*

2. **Culicoides (S.) hieroglyphicus** Malloch

(Figs. 10-13)

Culicoides hieroglyphicus Malloch, 1915, Ill. State Lab. Nat. Hist. Bull. 10:297 (female; Arizona; fig. mesonotal disc).

FEMALE—Length of wing 1.20 (1.12-1.23; n=8) mm.

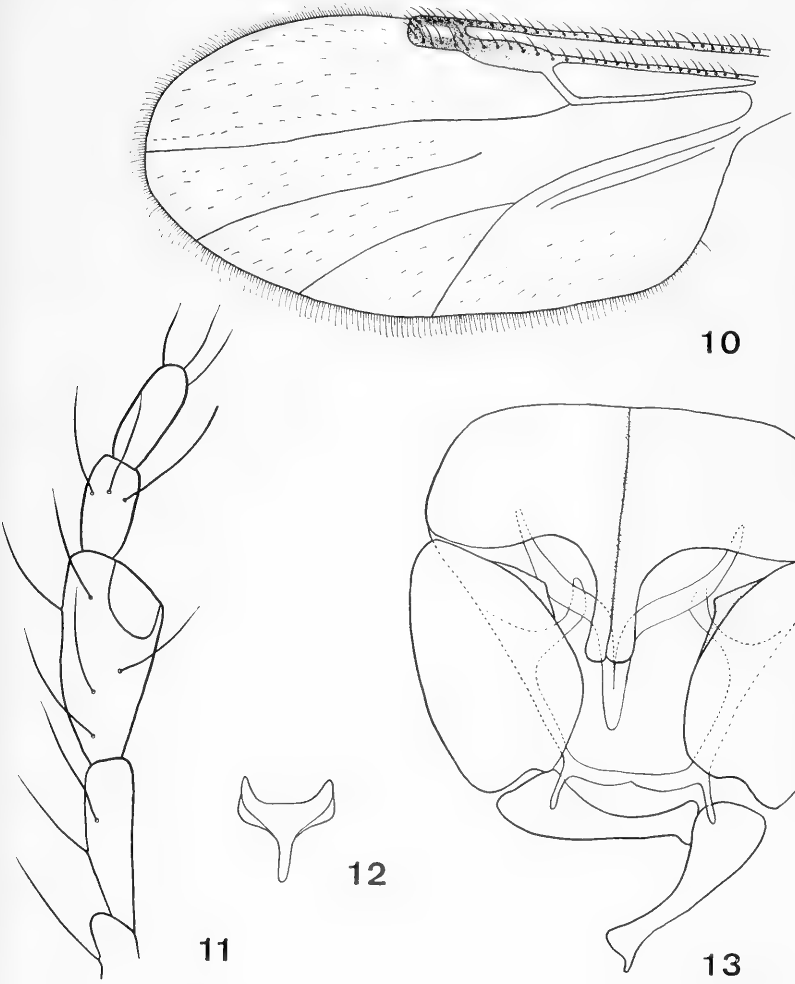
Head: Eye separation greater than diameter of a facet. Antenna with flagellomeres in proportion of 11:8:8:8:9:9:9:10:13:13:15:16:24; antennal ratio 1.03 (0.96-1.12; n=9); segments 9+10 to 11 in ratio of 0.67 (0.61-0.72; n=9); distal sensory tufts on segments 3, 5-10. Distal 4 palpal segments in proportion of 18:27:10:10; third palpal segment swollen, 2.11 (2.0-2.25; n=9) times as long as greatest breadth, with deep sensory pit (Fig. 11). Ratio of head length to proboscis 1.24 (1.10-1.46; n=8). Mandible with 11-13 (n=9) teeth.

Thorax: Legs yellowish brown; indistinct pale rings pre-apical on fore femora and subbasal on tibiae. Hind tibial comb with 4-5 spines.

Wing: (Fig. 10). Wing without pattern of pale and dark spots. Costa extending 0.54 (0.53-0.55; n=8) of entire wing length. Macrotrichia abundant.

Abdomen: Spermathecae unsclerotized.

MALE—Genitalia (Figs. 12, 13) with ninth sternum divided, with elongate mesal lobes extending posteriorly to almost same length as aedeagus. Ninth tergum tapering; caudal portion laterally convex, mesal notch present in some specimens, absent in others; apicolateral processes small, very slender. Basimere short, tapering slightly; ventral root well developed, slender with apically expanded end; dorsal root apparently consolidated into base of basimere; many large spines on mesal surface of basimere. Telomere swollen basally, narrowing distally with more or less blunt foot-shaped apex. Aedeagus composed of 2 slender sclerites, the basal or arm portions widely separated proximally, converging mesally, then turned caudad to form



FIGS. 10-13. *Culicoides hieroglyphicus* Malloch. Female: 10, wing; 11, palpus. Male: 12, claspettes; 13, genitalia, claspettes removed.

more or less parallel-sided median process. Claspettes fused to form modified triangular structure with long, slender caudomesal extension.

DISTRIBUTION: This species is a common western form occuring from South Dakota southward to Mexico and westward to California. New Mexico County Records: Bernalillo, Catron, Chaves, Colfax, DeBaca, Dona Ana, Eddy, Lincoln, Otero, Quay, Roosevelt, Sandoval, San Miguel, Santa Fe, and Sierra.

VARIATION: A large number of specimens collected near Glenwood, N. Mex., exhibited both male and female characteristics. These intersexes had normal male genitalia but possessed certain female head structures. The eyes were broadly contiguous, as one would expect in a male, but the third palpal segment was distinctly swollen with a deep sensory pit and many had denticulate mandibles. The most striking peculiarity were the antennae. These intersexes have the first eight antennal segments only slightly longer than wide and the transition between segment types occurs between segments 10 and 11. In a few specimens segment 11 was shortened. The pedicel, which is enlarged in normal males, apparently due to the presence of Johnstons organ, is reduced to the femalelike structure. A slightly reduced type of verticillate hairs occurs on these forms.

Downes (1958) has discussed a correlation between modification in head structures of males and mating behavior. *Culicoides utahensis* males, for instance, have femalelike antennae and palps, and this condition is apparently related to mating. Females of this species are often found in the ears of rabbits. The males, therefore, appear to be attracted to the rabbit, where they locate the females and mating occurs. A situation of this type is feasible for *hieroglyphicus* since females of this species are known to feed in the ears of rabbits in California. I do not know whether the high incidence of intersexes in this population represents a behavioral modification associated with mating or an extremely high infestation of mermithial nematodes, which also is known to induce the formation of intersexes.

FEEDING HABITS: Hoy (1966) has reported that in California this species attacks deer, feeding by day on the inner surfaces of the ears, and Jones (1965) found that it feeds on sheep in Colorado. These records, coupled with that of rabbits as hosts, indicate a rather broad host range for the species.

DISCUSSION: The difficulty of separating the *Selfia* species has been explained previously in the discussion of *brookmani*. The males of *heiroglyphicus* are readily separated from other species by the distinctive genitalia; however, with the possible exception of the mesonotal pattern, no clear-cut character is now known to distinguish the females from those of other *Selfia* species.

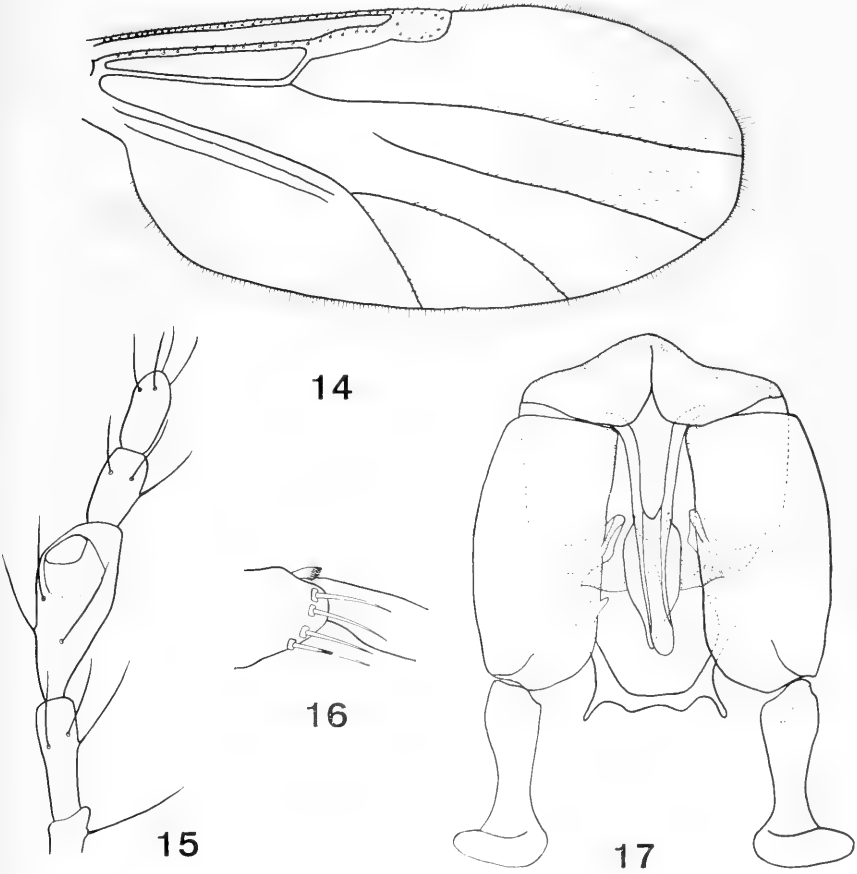
3. **Culicoides (S.) jamesi** Fox

(Figs. 14-17)

Culicoides jamesi Fox, 1946, Ent. Soc. Wash. Proc. 48:244 (male, female; Montana; fig. wing, mesonotal disc, palpus and male genitalia).

FEMALE—Length of wing 1.27 (1.20-1.39; n=15) mm.

Head: Eye separation equal or subequal to diameter of a facet. Antenna with flagellomeres in proportion of 14:11:10:10:11:12:12:13:15:17:17:18:25; antennal ratio 1.0 (0.94-1.13; n=16); distal sensory tufts present on segments 3-10; segments 9+10 to 11 in ratio of 0.63 (0.59-0.70; n=16). Distal 4 palpal segments in proportion of 16:27:8:13; third segment long and swollen, 2.26 (2.08-2.5; n=15) times as long as greatest breadth, with a deep sensory pit with many stalked sensillae lining proximal end (Fig. 15). Ratio



Figs. 14-17. *Culicoides jamesi* Fox. Female: 14, wing; 15, palpus; 16, tibial comb. Male: 17, genitalia.

of length of head to proboscis 1.27 (1.20-1.39; n=15). Mandible with 11-13 (n=16) teeth.

Thorax: Legs brown. Hind tibial comb with 4 or 5 spines, in some specimens 4 on 1 tibia, 5 on the other (Fig. 16).

Wing: (Fig. 14). Wing without pattern of light and dark spots. Macrotrichia present in distal and posterior portions of wing. Costa extending to 0.56 (0.54-0.59; n=9) of distance to wing apex.

Abdomen: Spermathecae unsclerotized.

MALE—Genitalia (Fig. 17) with ninth sternum expanded mesally, very deep medial posterior cleft extending almost to base. Ninth tergum tapered with narrow, divergent apicolateral processes, mesal cleft poorly defined. Basimere long; ventral root small; dorsal root well developed and elongate; rugose membrane connecting basimere in area of dorsal root with lateral margin of the fused claspette. Telomere with large, distinctive, footlike apical expansion; apex turned at right angle to remainder of telomere. Aedeagus very long and slender with high rounded basal arch; aedeagal arms long, extending anteriorly almost parallel, with bases turned antero-laterally. Claspettes fused to form a posteriorly pointed plate-like structure; anterior arms curved mesally and slightly laterad to give an almost semi-circular anteromedial emargination.

DISTRIBUTION: *Culicoides jamesi* is a western species occurring from New Mexico to Montana, westward to California. New Mexico County Records: Catron, Lincoln, Grant and Sandoval.

DISCUSSION: For distinguishing features see the discussion of *brookmani*.

Subgenus *CULICOIDES* Latreille 1809:251

Type species *Culex pulicaris* Linneaus as *Ceratopogon punctatus* Meigen (monobasic).

Large species with the apical portion of the second radial cell ending in a pale spot. Cell M_4 is dark at the base of the mediocubital fork, and the apices of veins M_1, M_2, M_{3+4} and Cu_1 are dark.

The North American species of this subgenus belong to the *cockerellii* group.

4. **Culicoides (C.) cockerellii** (Coquillett)

(Figs. 18-22)

Ceratopogon cockerellii Coquillett, 1901, U.S. Natl. Mus. Proc. 23:603.
Culicoides cockerellii Coquillett; Kieffer, 1906, Gen. Insectorum, fasc. 42:54.

FEMALE—Length of wing 1.84 (1.61-2.04; n= 5) mm.

Head: Eyes contiguous, meeting only at a point. Antenna with flagellomeres in proportion of 16:13:15:15:15:15:15:15:21:23:27:30:36; antennal ratio 1.07 (1.03-1.10; n=5); segments 9+10 to 11 in ratio of 0.71 (0.68-0.75;

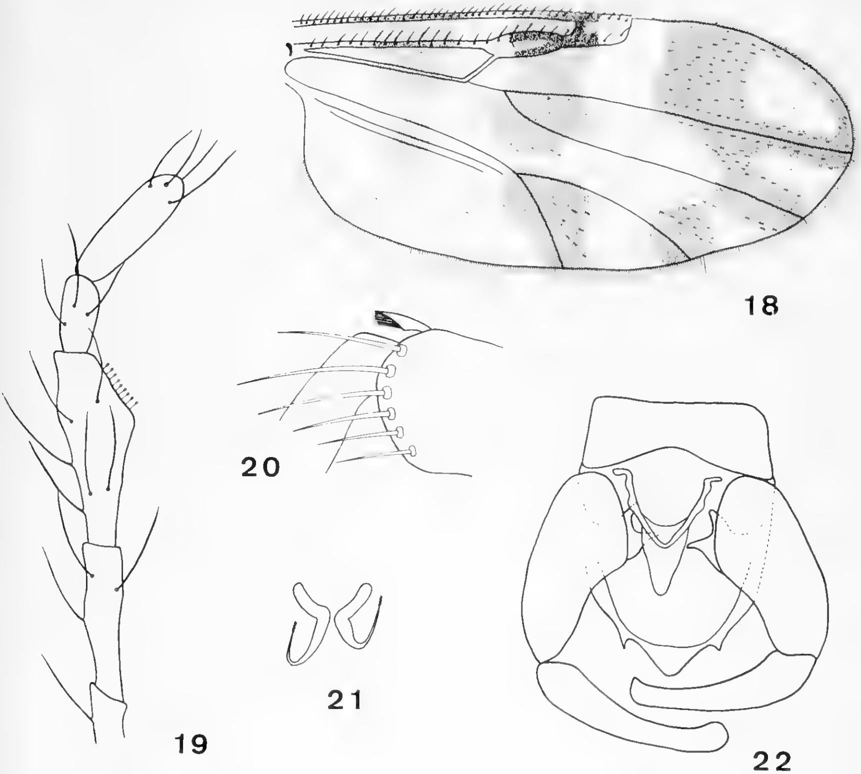


Fig. 18-22. *Culicoides cockerellii* (Coquillett). Female: 18, wing; 19, palpus; 20, tibial comb. Male: 21, claspettes; 22, genitalia, claspettes removed.

n=5); distal sensory tufts on segments 3, 5, 7, 9-15, occasionally absent from 10 or from 7, 9 and 10 (see discussion). Distal 4 palpal segments in proportion of 26:36:13:18; third palpal segment very slender and lacks a pit (Fig. 19), 3.26 (2.7-3.8; n=5) times as long as greatest breadth, possessing numerous stalked sensillae. Ratio of head length to proboscis 1.05 (0.84-1.20; n=4). Mandible with 14-16 (n=5) teeth.

Thorax: Legs dark brown. Hind tibial comb with 6 spines (Fig. 20).

Wing: (Fig. 18). Distal half of second radial cell in a light area; wing with 3 transverse bands: first band lying between r-m crossvein and base of wing, extending posteriorly from costa to beyond vein M_{1+2}, interrupted by pale area which extends to slightly anterior of Cu_1, another dark spot over Cu_1, Cu_2, and 1st V and extending slightly into vannal cell, majority of vannal cell in pale area; second dark band arising midway between r-m crossvein and distal end of second radial cell, extending to just behind M_1-M_2 fork, there interrupted by a light area, dark area in proximity of medio-cubital fork where it follows vein Cu_1 to margin; third dark band distal to poststigmatic spot, band very intense in anterior portion of wing. Macrotrichia long, rather dense in distal and posterior parts of wing. Costa extending 0.60 (0.54-0.62; n=5) of entire wing length.

Abdomen: Two oval spermathecae (crumpled in New Mexico specimens seen); ducts sclerotized at base; rudimentary spermatheca and ring present. MALE—Genitalia (Figs. 21, 22) with ninth sternum broad, with shallow caudomedian excavation. Ninth tergum tapering posteriorly, with distinct, rounded, caudal lobe; apicolateral processes very small. Basimere narrowing apically; roots small, subequal, tapering apically. Telomere large, gradually tapering to slightly expanded apex. Median posterior process of aedeagus broadly rounded apically, aedeagal arms slender, with slight swellings on lateral margins, basal portions turned laterally to give foot-shaped structure; lateral membraneous extensions extending from arms to lateral portion of median posterior process; basal arch rounded. Claspette with antero-laterally directed bases; stem swollen proximally, tapering to very slender anteriorly directed apex bearing fine fringe of subapical spines.

DISTRIBUTION: This species has previously been recorded from Alaska southward to California and Colorado. This is the first record of it from New Mexico. New Mexico County Records: Poorly marked form—Colfax, San Juan and Lincoln; well-marked form—Taos.

VARIATION: Wirth (1952), in discussing the *cockerellii* group in California, lists three varieties or forms in addition to *cockerellii sensu stricto.* Of the seven females of *cockerellii* taken during this investigation, four can readily be assigned to *cockerellii s. str.* as defined by Wirth, while the remainder had a reduced wing pattern and different sensorial configuration and closely agreed with the description of Wirth's variety "C." The culmination in reduction of wing pattern is exhibited by a specimen from San Juan River, San Juan Co., in which the wing pattern is reduced to the usual spot over the r-m crossvein, poststigmatic spot and two other very small round spots, one in the middle of cell M_4 and one lying just below the 1st vannal vein in the vannal cell. The poorly marked form has a sensorial pattern of 3, (5), 7, (9), (10), 11-15 as opposed to 3, 11-15 for the well-marked form. Since no males of *cockerellii* were taken during this study, information as to variation in the male genitalia is not available.

DISCUSSION: Vargas (1960) proposed the new subgenus *Anilomyia* for the *covagarciai* group, in which he includes *cockerellii* and *luteovenus* Root and Hoffman, as well as the neotropical species *rostratus* Wirth and Blanton. The *covagarciai* group as originally outlined by Wirth and Blanton (1959) did not include *luteovenus,* which was placed in the *pulicaris* group. There appears to be little gained by dividing this rather homogeneous group of species, previously known as the subgenus *Culicoides,* into two subgenera.

Subgenus *AVARITIA* Fox, 1955:218

Type species *Ceratopogon obsoletus* Meigen (orig. des.).

This subgenus is composed of a group of small species with poorly marked wings. The distal portion of the second radial cell is in a pale spot, and macrotrichia are usually sparse. Antennal sensoria are located on segments 3 and 11-15, and the eyes of the females are contiguous. There are two subequal spermathecae with very short necks, and the hind tibial comb possesses 5 spines. The ninth tergum of the male genitalia usually lacks the mesal notch, the apicolateral processes are absent (except in *chiopterus,* in which they are poorly developed, blunt structures), the claspettes are separate and taper distally to a fine point which may or may not possess apical hairs, and the basimere has long, simple, subequal roots.

The members of this subgenus are widespread, two species occurring in the Palearctic and Nearctic regions, while a third species is Nearctic and Neotropical. One species, *obsoletus* (Meigen) occurs in New Mexico.

5. **Culicoides (A.) obsoletus** (Meigen)

(Figs. 23-27)

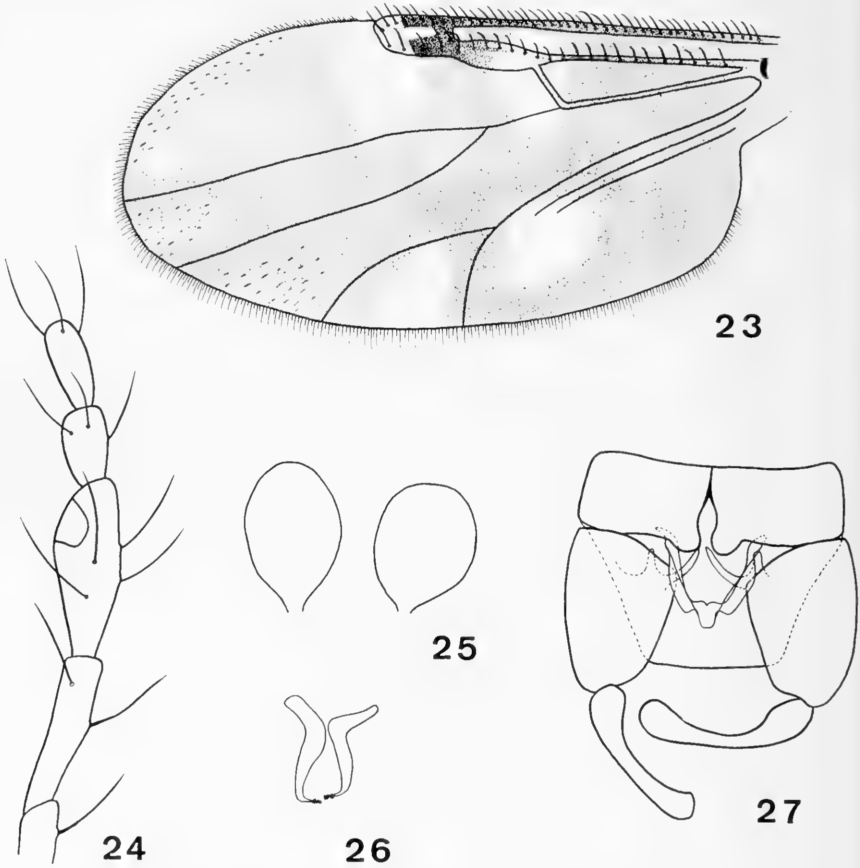
Ceratopogon obsoletus Meigen, 1818, Syst. Beschr. Gur. Zweifl. Ins., 1:76.
Culicoides obsoletus (Meigen); Goetghebeur, 1921, Mem. Mus. Roy. Hist. Nat. Belg., 8:180.
For additional synonomy see Fox (1955).

FEMALE—Length of wing 1.19 (1.01-1.36; n=9) mm.

Head: Eyes broadly contiguous. Antenna with flagellomeres in proportion of 11:10:10:10:11:11:12:13:17:17:17:18:30; antennal ratio 1.14 (1.0-1.23; n=9); segments 9+10 to 11 in ratio of 0.72 (0.65-0.79; n=9); distal sensory tufts on segments 3, 11-15. Distal four palpal segments in proportion of 17:18:8:10; third segment very slender, only slightly swollen (Fig. 24), 2.74 (1.8-3.7; n=7) times as long as greatest breadth (the specimen measuring 1.8 had an extremely short and slender third segment, hence the very small value); shallow sensory pore. Ratio of head length to proboscis 1.0 (0.87-1.24; n=6). Mandible with 12-16 (n=6) teeth.

Thorax: Legs brown; lacking distinct banding pattern. Hind tibial comb with 5 spines, one nearest spur usually longest.

Wing: (Fig. 23). Pattern indistinct and variable; apical half of second radial cell in a pale area; pale spot over r-m crossvein small, extending posteriorly beyond vein M_{1+2}, not attaining anterior wing margin; post-stigmatic spot rather elongate, extending to just anterior of vein M_1; rather vague pale spots in distal portion of cells R_5, M_1 and M_2, their position and intensity variable; pale spot in cell M_4 extending to posterior wing margin; small spot in anterior portion of vannal cell; poorly defined pale area in medial portion of wing. Costa extending 0.60 (0.57-0.63; n=9) of entire wing length. Macrotrichia sparse.



Figs. 23-27. *Culicoides obsoletus* (Meigen). Female: 23, wing; 24, palpus; 25, spermathecae. Male: 26, claspettes; 27, genitalia, claspettes removed.

Abdomen: Two slightly unequal spermathecae (Fig. 25) 56 x 33 and 46 x 40 μ, ducts sclerotized for a short distance; rudimentary spermatheca and ring present.

MALE—Genitalia (Figs. 26, 27) with ninth sternum broad; caudomedian excavation narrow, deep, anteriorly pointed; posterior lips of excavation distinctly lobe-like. Ninth tergum lacking apicolateral processes and mesal notch. Basimere with very long slender, pointed ventral roots; dorsal roots much shorter. Telomere only slightly swollen basally, mesal portion narrow, apex swollen, club-like. Aedeagus with short, sub-conical median posterior process; aedeagal arms with small, laterally directed bases, slightly sinuate posteriorly, abruptly bent mesally to form median process; basal arch very long, extending approximately 0.75 of entire length of aedeagus. Claspettes with very stout basilateral arms; stems swollen proximally, tapering to very slender apex bearing microscopic fringe of spines.

DISTRIBUTION: A very widespread species reported by Jamnback and Wirth (1960) as occurring in Eurasia, North Africa and North America. In North America *obsoletus* has been previously reported throughout the eastern United States and westward to include Colorado, Oklahoma and California. Canadian records include Alberta and British Columbia. New Mexico County Records: Lincoln, Otero.

VARIATION: The specimens from New Mexico designated in this paper as *obsoletus* do not completely agree with the species descriptions from the eastern United States. The most obvious discrepancy occurs in the male genitalia. There are apical hairs on the claspettes, as in typical *obsoletus,* and the mesal notch on the ninth sternum agrees closely with that species. The aedeagus, however, has a shape closely approximating that of *sanguisuga* (Coquillett). Because of the paucity of male specimens of this form from New Mexico, I have refrained from describing it as new. The *obsoletus* complex in the western United States is very poorly understood and is in need of extensive study, such as given the eastern spcies by Jamnback and Wirth (1960).

FEEDING HABITS: In many areas *obsoletus* constitutes a serious pest. Wirth (1952) has cited its annoyance in the mountains of the western states. Although various authors have described this species as pestiferous in the eastern states, Jamnback and Wirth (1960) state that many of these biting records actually refer to *sanguisuga.*

During this investigation, this species was collected biting man in the mountains of southern New Mexico. It appears to be crepuscular in its activity, as all specimens were taken at dusk.

Subgenus *BELTRANMYIA* Vargas, 1953:34

Types species, *crepuscularis* Malloch (orig. des.).

This subgenus contains species in which the females possess one spermatheca and the antennal sensorial configuration varies from 3-15 to a very reduced condition in some species in which sensoria are present only on the third and various of the distal 5 segments. The wing has the second radial cell in a dark area, and the pattern of pale and dark spots may be either faint or well defined. The ventral root of the basimere in the male is either very reduced or absent. The claspettes are separate, tapering to very fine, pointed, unadorned apices.

Numerous representatives of this subgenus are found in the eastern United States; however, the distributions of three continue into the western states: *bermudensis* Williams as far west as Texas, *wisconsinensis* Jones to California and Washington, and *crepuscularis* Malloch to California.

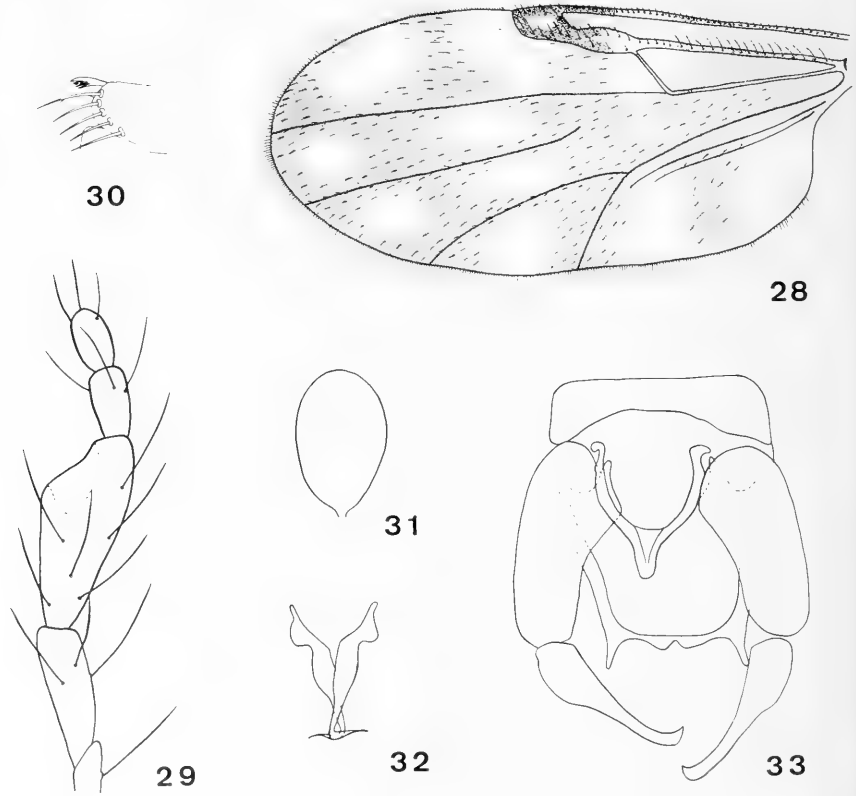
6. **Culicoides (B.) crepuscularis** Malloch

(Figs. 28-33)

Culicoides crepuscularis Malloch, 1915, Ill. State Lab. Nat. Hist. Bull. 10:303 (male, female; Illinois; fig. wing, mesonotal disc).

FEMALE—Length of wing 1.41 (1.14-1.56; n=22) mm.

Head: Eye separation about equal to diameter of a facet. Antenna with flagellomeres in proportion of 15:10:10:10:10:10:11:13:20:22:24:24:33; antennal ratio 1.35 (1.26-1.50; n=22); distal sensory tufts present on segments 3-14 (15), occasionally absent from segments 10 and 11; segments 9+10 to 11 in ratio of 0.90 (0.79-1.05; n=12). Distal 4 palpal segments in proportion of 20:33:11:13; third palpal segment swollen, 2.27 (2.0-2.56; n=25) times as long as greatest breadth, sensory pit deep with numerous stalked sensillae located on inner surface of pit (Fig. 29). Ratio of head length to proboscis 1.05 (0.95-1.14; n=23). Mandible with 14 (10-16; n=26) teeth.



FIGS. 28-33. *Culicoides crepuscularis* Malloch. Female: 28, wing; 29, palpus; 30, tibial comb; 31, spermatheca. Male: 32, claspettes; 33, genitalia, claspettes removed.

Thorax: Legs brown; fore femora with pre-apical pale ring, all tibiae with subbasal pale rings. Hind tibial comb with 4 spines (Fig. 30).

Wing: (Fig. 28). Second radial cell in a dark area; pale spot over r-m crossvein extending slightly posteriorly to vein M_{1+2} but not extending to anterior margin; remaining pale spots located as follows: immediately distal to second radial cell, in distal portion of cell R_5 but not attaining wing margin, in cells M_1, M_2, M_4; a double spot in distal portion of vannal cell, usually attaining the wing margin; two elongate spots in proximal portion of cells M_1 and M_2; medio-cubital fork in a dark area. Macrotrichia abundant over surface of the wing. Costa extending to 0.56 (0.51-0.64; n=22) of entire length of wing.

Abdomen: One large spermatheca (Fig. 31) with neck sclerotized for a very short distance. Rudimentary spermatheca, without sclerotized ring, occasionally evident in slide-mounted preparations.

MALE—Genitalia (Figs. 32, 33) with narrow ninth sternum, caudiomedial excavation, broad, deep; membrane spiculate. Ninth tergum tapering posteriorly, with prominent apicolateral processes. Basimere long and slender, dorsal root well developed, ventral root absent. Telomere expanded basally, tapering, with a slightly swollen, mesally tipped apex. Aedeagus with conical, distally truncate, median posterior process; aedeagal arms long and slender with small laterally directed bases, basal arch rounded. Claspettes with pronounced foot-shaped basal expansions; mesal margins of stem straight, lateral margins swollen at approximate mid-point, stems sharply bent at apex to form simple, ventrolaterally directed tips.

DISTRIBUTION: This species has been taken in most states from New England to California, Mexico into Canada. New Mexico County Records: Catron, Colfax, Dona Ana, Lea, Lincoln, Otero, Quay, Rio Arriba, Sandoval, San Juan, San Miguel and Socorro.

VARIATION: Considerable variation exists in the wing pattern of this species at several localities. In Rio Arriba County, poorly marked forms were taken that exhibited reduction in number and size of the distal wing spots. Some of these specimens lacked the pale spots in cell M_1, and the spots in cells R_5, M_2 and M_4 were greatly reduced. In other specimens pale spots were absent in these four cells. Dr. Willis Wirth (in litt.) informs me that this variation in wing markings as well as some additional characters appears to show regional trends. Together with other morphological and biological descrepancies reported by various authors, it suggests that there may be more than one species disguised under the name *crepuscularis.*

Two intersexes were taken at light, along with numerous normal specimens, at the Bosque del Apache Refuge along the Rio Grande.

DISCUSSION: Although the wing markings of *crepuscularis* superficially resemble the wing pattern of females of certain other New Mexico species, the presence of one large spermatheca will readily distinguish this species. Only two other New Mexico species, *reevesi* and *variipennis,* have a single spermatheca. Separation of the females of these three species is accomplished easily by the irregular wing markings, sensorial pattern and usual "C" shaped spermatheca of *variipennis* and the unusual shape of the antennal segments, sensorial pattern, etc., of *reevesi.*

This species is not closely allied to any of the other New Mexico species, but is very similar to several, particularly *hollensis* (Melander and Brues) and *wisconsinensis* Jones, which occur primarily in the eastern portion of the U.S.

FEEDING HABITS: With the exception of a reference by Edmunds and Keener (1954), in which they state that *C. crepuscularis* is a very severe pest in Nebraska, the proponderence of evidence accumulated for this species indicates an ornithophilic behavior. This is supported by reports of Williams (1955) and Snow (1955) that *crepuscularis* is active in considerable numbers in the forest canopy; and Messersmith (1965) has taken large numbers of engorged females of the species from chicken houses.

The importance of *crepuscularis* in the interrelationship between various pathogens and their avian hosts has recently been stressed. Robinson (1961) cited the development of an avian filarial worm in this species after having fed on an infested starling, while Bennett (1961) used *crepuscularis,* along with other species, in trypanosome transmission experiments involving several species of birds. Fallis and Bennett (1961) reported developing oöcysts and sporozoites of *Haemoproteus* in the gut wall of *crepuscularis* after the flies had fed on infected crows and purple finches.

Subgenus *MONOCULICOIDES* Khalaf, 1954:39

Type species *Ceratopogon nubeculosus* Meigen (orig. des.).

Large species with second radial cell in dark area and with moderately abundant macrotrichia. The eyes are widely separated, and one C-shaped spermatheca is present. The ninth tergum of the male has well developed apicolateral processes, the claspettes are fused basally, with the apices terminating in slender separate points, and the basimere possesses a moderately long ventral root, but a very short dorsal root.

Two species, *gigas* Root and Hoffman and *variipennis* (Coquillett), are included in the Nearctic fauna, although only *variipennis* is found within the boundaries of the United States.

7. **Culicoides (M.) variipennis sonorensis** Wirth and Jones

(Figs. 34-39)

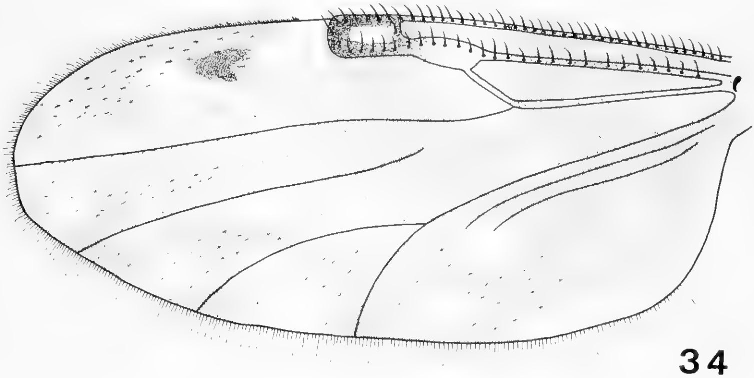
Ceratopogon variipennis Coquillett, 1901, U.S. Nat. Mus. Proc. 23:602.
Culicoides variipennis; Kieffer, 1906, Gen. Insectorum, fasc. 42:55.

Culicoides variipennis sonorensis Wirth and Jones, 1957, U. S. D. A. Tech. Bull. no. 1170, p. 18-20 (male, female; Arizona; fig. wing, spermatheca, mesonotal disc, palpus, male genitalia).

Culicoides variipennis australis Wirth and Jones, 1957, U. S. D. A. Tech. Bull. no. 1170, p. 15-17 (male, female; Louisiana; fig. wing, spermatheca, mesonotal disc, palpus, antenna). NEW SYNONOMY.

FEMALE—Length of wing 1.55 (1.30-1.79; n=14) mm.

Head: Eyes widely separated by much more than diameter of a facet. Antenna with flagellomeres in proportion of 13:13:13:13:13:13:13:14:16:17:18:18:26; antennal ratio 0.86 (0.79-0.90; n=13); segments 9+10 to 11 in ratio of 0.59 (0.54-0.70; n=7); distal sensory tufts always on segments 3, 8-10,



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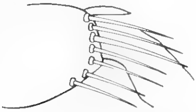

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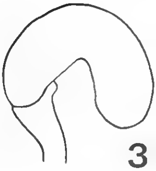

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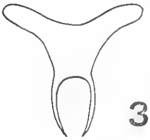

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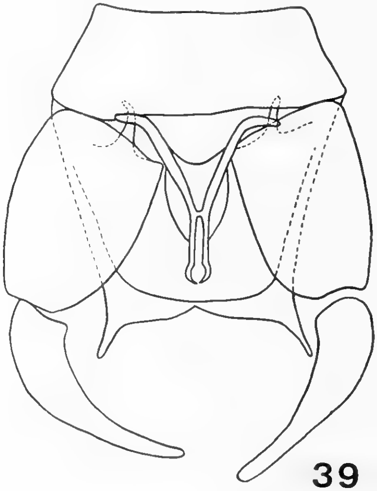

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FIGS. 34-39. *Culicoides variipennis sonorensis* Wirth and Jones. Female: 34, wing; 35, palpus; 36, tibial comb; 37, spermatheca. Male: 38, claspettes; 39, genitalia, claspettes removed, often on 5, 6 or 7, occasionally present on segment 4. Distal 4 palpal segments in proportion of 25:35:10:15; third palpal segment very swollen (Fig. 35), 2.38 (2.11-2.69; n=14) times as long as greatest breadth, with moderately deep sensory pore. Ratio of length of head to proboscis 1.10 (1.02-1.17; n=10). Mandible with 11-15 (n=14) teeth.

Thorax: Legs brown; fore femora with median pale band; all femora with pre-apical pale ring, tibiae with subbasal pale rings. Hind tibial comb with 6-7 spines (Fig. 36).

Wing: (Fig. 34). Second radial cell in a very dark spot; pattern of pale and dark spots irregular. Costa extending 0.55 (0.53-0.58; n=14) of entire wing length. Macrotrichia short, rather sparse.

Abdomen: One large, mesally bent, C-shaped spermatheca (Fig. 37).

MALE—Genitalia (Figs. 38, 39) with ninth sternum having little if any posterior excavation. Ninth tergum with prominent, triangular apicolateral processes. Basimere short, slightly tapered; ventral root small; dorsal root long, slightly curved laterally. Telomere curved, strongly swollen basally, abruptly narrowing approximately at mid-length, distal half gradually tapering to simple apex. Aedeagus elongate; median posterior process consisting of two narrow separate points with slight sub-apical expansion, lateral portion of median process membraneous; aedeagal arms short, gently curved laterally; basal arch short, rounded, extending only about 0.25 of entire length of aedeagus; membrane posterior to basal arch may or may not be spiculate. Claspettes fused basally, with slender, pointed, separate apices.

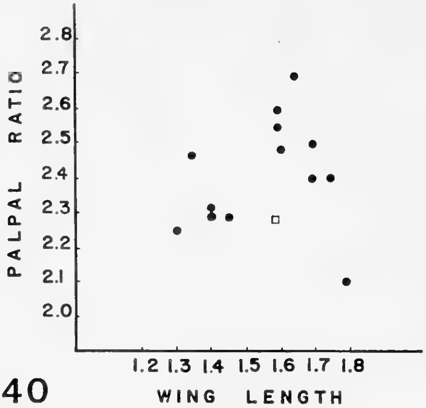
DISTRIBUTION: This subspecies of a widely distributed form found in the United States, Canada, Mexico and Baja California is limited to the more arid portions of the southwestern United States and Mexico. Wirth and Jones (1957) reported *sonorensis* from Arizona, California, Nevada, New Mexico, Oklahoma, Utah, Washington and Mexico, and under the name *australis* it has been recorded in Kansas, Louisiana, Missouri, Oklahoma, South Carolina, Texas and Virginia. It is probably the most common species occurring in New Mexico. New Mexico County Records: Chaves, Curry, DeBaca, Dona Ana, Eddy, Lea, Lincoln, Quay and Roosevelt.

DISCUSSION: Wirth and Jones (1957) proposed five subspecies for polytypic *Culicoides variipennis*. Consideration of the distributional data, ecological associations, as well as the critical examination of a number of specimens from various localities in New Mexico make evident the need for a discussion of the validity of certain aspects of this division.

Many times when attempting to analyze a taxonomic problem, it is desirable to define the taxonomic category under investigation. The *variipennis* situation is complicated by the omission of, or reference to, such an explanation of what these writers consider to be a subspecies. If we take one of the more widely used definitions of subspecies, i.e., "an aggregate of local populations of a species inhabiting a geographic subdivision of the range of the species and differing taxonomically from other populations of the species (Mayr 1963)," and apply it to the *variipennis* problem, several discrepancies become evident.

There can be little doubt that *variipennis sensu lato* is divisible into two forms. On the basis of morphological and particularly biological evidence, it would appear that *variipennis variipennis* and *variipennis sonorensis* are worthy of at least subspecific status. The former subspecies is restricted to the forested northern and eastern portions of North America and is not associated with saline environments. It is considered by Ross (1962) to be the oldest and most stable form. The *sonorensis* stock of the southwestern, arid portion of North America has been further divided into four subspecies on the basis of biological as well as morphological criteria. The *australis* form is typically found in saline environments and is characterized by Wirth and Jones as having long wings, more slender palps, higher number of antennal sensoria and a bare aedeagus (see Table 2 for numerical values). The *sonorensis* form typically inhabits polluted waters and is distinguished by shorter wings, stouter palps, lower number of supernumerary antennal sensoria and a spinose aedeagus (Table 2). As will be shown below, this habitat isolation apparently breaks down in southeastern New Mexico, and populations occur that exhibit all morphological intergradation between *sonorensis* and *australis*. No definite statement can be made regarding *occidentalis*, the west coast subspecies, or *albertensis*, which occurs in the Midwest, northward into Canada. These two forms lie outside the scope of this investigation; however, it should be noted that Wirth and Jones state that over much of its range the latter form cannot be distinguished from other forms of the *sonorensis* stock. Ross (1962) considers *occidentalis* to be the oldest and most stable form of the *sonorensis* stock; however, this is open to serious question.

A sample from the Pecos River, east of Roswell, provided an excellent opportunity to examine the extent of infraspecific variation in a given *variipennis* population. The range of variation among 28 specimens examined from this locality included individuals that could definitely be assigned to the typical *sonorensis* form to those that exhibited all the characteristics of *australis*. Of 14 males, 4 had very spinose aedeagi of the *sonorensis* form, 8 possessed bare aedeagi of the *australis* form and 2 specimens could be considered as intermediate in that they had only 5 or 6 spines. Among the females (Figs. 40, 41), 5 specimens having short wings, swollen palpi and 1 or 2 additional sensoria could be assigned to the *sonorensis* form. Eight of the remaining females could be designated as *australis*, although some resembled *sonorensis* in 1 or 2 characters. One female appeared to be intermediate (shown in scatter diagram by an open



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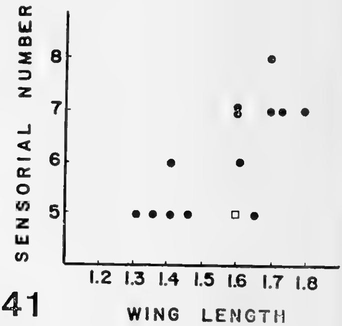

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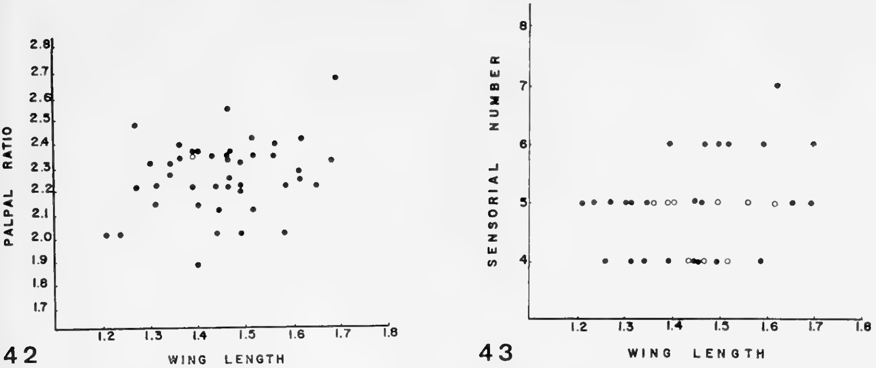
FIGS. 40-41. Scatter diagrams showing extent of intraspecific variation in a given population (Pecos River, east of Roswell, New Mexico) of *Culicoides variipennis*. Open square indicates apparent intermediate form between *C. variipennis australis* and *C. variipennis sonorensis* forms.

rectangle, having a long wing (1.58 mm.), one supernumerary sensoria and a very swollen palp (P.R.=2.23).

Genetically, a given local population can, if it occurs in a zone of intergradation, contain elements of more than one subspecies. If the zones of contact or overlap between subspecies have not been determined, however, or if the local population in question is remote from such a zone, the population should taxonomically be assigned to only one or another subspecies. That is, subspecies are generally thought of as being for the most part mutually exclusive.

The evidence described would imply that either *australis* is only an infrasubspecific form of *sonorensis,* or that the four characters Wirth and Jones used to differentiate supposed subspecific populations will not effectively do so. (A fifth character, the number of mandibular teeth of the females, is not included here because of the high degree of overlap that exists between the two forms).

One remaining criterion for subspecific distinction of these two forms is habitat isolation. A large number of specimens were examined from a salt lake near Loving, New Mexico. The extreme salinity of this habitat was evidenced by a salt crust at various places along the margin. Potash was mined nearby. Over 50 specimens were examined from this locality, and only one form was present (Figs. 42, 43), but these were not *australis,* as one would expect, but *sonorensis*! All the males examined had spinose aedeagi, and the number of antennal sensoria and palpal ratio of the females were almost precisely those given by Wirth and Jones as mean values for *sonorensis*. The mean wing length of this series was somewhat greater than would be expected for a *sonorensis* population; however, the agreement



FIGS. 42-43. Scatter diagrams showing extent of intraspecific variation in a given population (Salt Lake, near Loving, New Mexico) of *Culicoides variipennis.* Open circles indicate more than one individual exhibiting these character states.

in the other characters would definitely suggest that this is a population of *sonorensis.* Here again the range of such characters as wing length and palpal ratio encompassed almost the entire range of variation Wirth and Jones established as 95% limits of both subspecies.

If *australis* and *sonorensis* were actually subspecies, the long wing characteristic of the Loving population could be due to gene flow between them. Subspecific intergradation cannot account for the remaining ecological and morphological discrepancies, however, and the spinose aedeagi, low number of supernumerary sensoria and palpal ratio indicate that this population is definitely *sonorensis.*

The wide variation of characters found in the Pecos River sample might be ascribed to a zone of contact or overlap between two phenotypically distinct, allopatric populations. If these phenotypically different populations are considered as subspecies, i.e., *australis* and *sonorensis,* intergradation between them should not occur also at such distant localities as northern Oklahoma and southern Texas (cited by Wirth and Jones) and southern New Mexico, especially when both subspecies are shown to occur at various intermediate localities. The area enclosed by these sites of intergradation is almost half of the proposed range of *australis.*

Rowley (1965), in his study of the bloodsucking midges in the Columbia Basin of Washington, has also reported two subspecies of *variipennis,* i.e., *occidentalis* and *sonorensis,* occurring in the same area. In the Columbia Basin Crab Creek flows near numerous alkaline potholes producing, with regard to salinity, two distinct larval habitats in very close proximity. Each of these habitats is theoretically better suited for a different subspecies. If these two forms were subspecies of one species, they would be expected to become merged where they occur sympatrically. Rowley reports that individuals from this area, like those from the above mentioned localities in southeastern New Mexico, exhibit a great amount of variation in the characters used for subspecific designation by Wirth and Jones.

One possible explanation for the *variipennis* problem is that these forms of the *sonorensis* stock are ecotypes produced by the response of the immature stages to their particular environment. The relatively large amount of morphological variation that exists among *variipennis* populations, such as at the Washington and New Mexico localities, could therefore be attributed to selection by the habitat. The designation of ecotypes rather than subspecies would also clarify the many populations of *variipennis* in the western United States that are unassignable to "subspecies."

The preponderance of evidence accumulated in this investigation relating to *C. variipennis* would imply that, on the basis of the characters presented by Wirth and Jones, only one subspecies, *sonorensis,* occurs in New Mexico and that *australis* is only an infrasubspecific form of *sonorensis.* Accordingly, I consider *australis* a synonym of *sonorensis.*

FEEDING HABITS: Culicoides variipennis sonorensis is the most economically important species in the New Mexico fauna, due to its involvement with the transmission of bluetongue virus in sheep. Price and Hardy (1954) incriminated *C. variipennis* in the transmission of bluetongue virus when two sheep inoculated with macerated *variipennis* adults developed clinical bluetongue. Foster, Jones and McCrory (1963) obtained positive biological transmission of bluetongue in sheep when they allowed *variipennis* to feed on infected sheep and later on uninfected animals.

As shown above, this species fulfills one of the requirements of a vector in that it is capable of biological transmission of the bluetogue virus. Later investigations by Jones (1961, 1965) have shown that *sonorensis* will naturally approach sheep in the field in sufficient numbers, and during a major outbreak of bluetongue of sheep in Colorado, *sonorensis* was taken in large numbers by sheep baited traps.

TABLE 2. Summary of data regarding morphological variation of two populations of *Culicoides variipennis.*

Subspecies of Wirth and Jones 1957 or New Mexico locality	Wing Length		Palpal Ratio		Additional Antennal Sensoria		
	Mean	Range*	Mean	Range	Mean	Range	Aedeagus
australis	1.54	1.39-1.69	2.53	2.19-2.87	2.75	0.93-4.00	bare
sonorensis	1.26	1.16-1.36	2.23	1.99-2.47	0.83	0-2.01	spinose
Pecos River east of Roswell	1.55	1.30-1.79	2.38	2.11-2.69	2.0	1-4	bare to spinose
Salt Lake near Loving	1.46	1.21-1.70	2.42	1.86-2.66	0.8	0-3	spinose

* Represents 95% limits or Wirth and Jones (1957) for *australis* and *sonorensis.*

Although *sonorensis* feeds on man, Jones (1959) has shown that it prefers cattle, sheep and man in a descending sequence. Under laboratory conditions it will engorge on chickens.

Subgenus *DRYMODESMYIA* Vargas, 1960:40

Type species *copiosus* Root and Hoffman (orig. des.).

This subgenus contains species with hairy wings and more or less distinctly rounded pale spots. There is often a prominent pale spot lying on the basal portion of vein M_1 and usually a pale spot over the median portion of vein M_2. A distinct pale spot is usually present in cell M_4. The r-m crossvein is in a pale spot. The third palpal segment of the females is usually swollen with a deep sensory pit. Two sclerotized spermathecae, a rudimentary spermatheca and ring are present. The hind tibial comb has four spines. The male genitalia has the claspettes swollen basally with the basal portion anterio-laterally directed and usually knobbed. The stems are slender, lack lateral lobes and possess slender, simple and often turned, twisted or contorted apices. The basimere has simple roots and the aedeagus is usually broad with a low basal arch and stout basal arms.

8. **Culicoides (Dr.) sitiens** Wirth and Hubert

(Figs. 44-48)

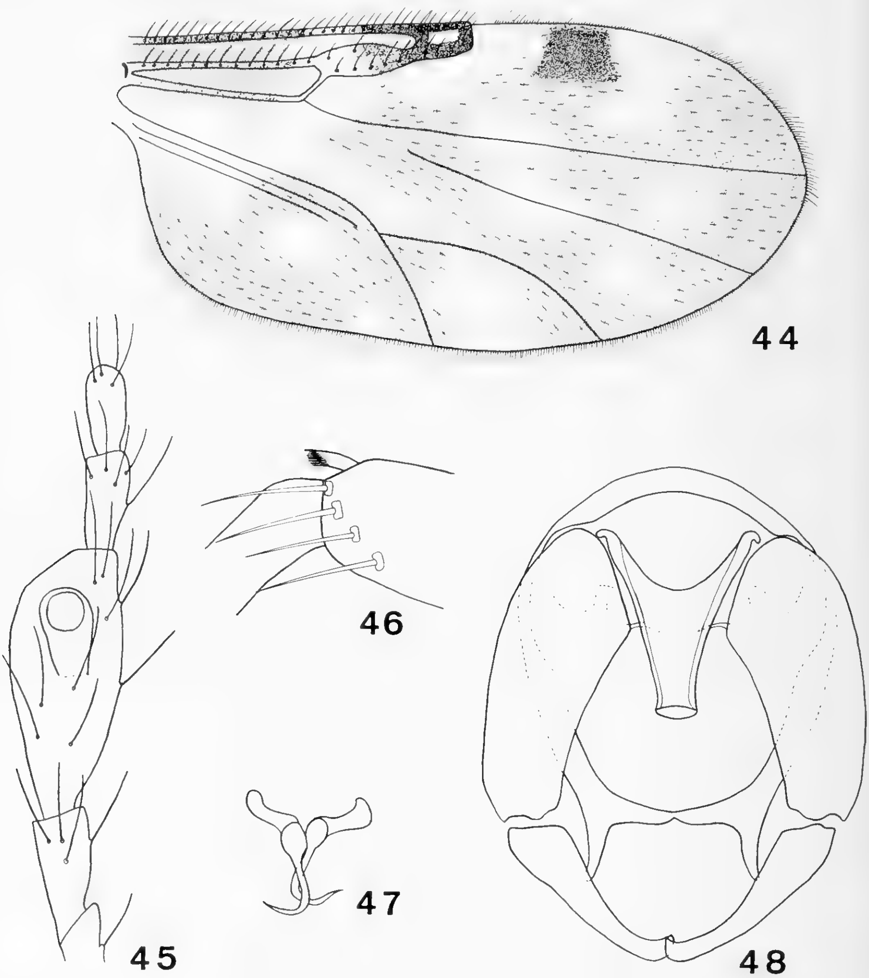
Culicoides sitiens Wirth and Hubert, 1960, Ent. Soc. Amer. Ann. 53:652 (male, female; California; fig. wing, palpus, spermathecae, male genitalia).

FEMALE—Length of wing 1.34 mm.

Head: Eyes separated by about half the diameter of a facet; inferior transocular suture present. Antenna with flagellomeres in proportion of 13:10:11:12:13:13:13:13:18:18:20:21:28; antennal ratio 1.07; distal sensory tufts present on segments 3-9, (10), 11-15; segments 9+10 to 11 in ratio of 0.69. Third palpal segment greatly swollen, 2.33 times as long as greatest breadth, with a deep slender sensory organ, opening by a small rounded opening (Fig. 45). Ratio of head length to proboscis 1.0. Mandible with 14 teeth.

Thorax: Legs with broad pre-apical pale rings on fore and midfemora, all tibiae with subbasal pale rings. Hind tibial comb with 4 spines (Fig. 46).

Wing: (Fig. 44). Second radial cell in a dark area; pale spot on r-m crossvein extending from costa posteriorly beyond vein M_{1+2}, uniting with elongate spot in extreme basal portion of cell M_2; poststigmatic spot curved proximally around second radial cell; mesally constricted pale spot located in median portion of cell R_5, extending from anterior wing margin to slightly before vein M_1; pale spots in distal portions of cells M_1 and M_2 not attaining wing margin; spot in cell M_4 broadly joining posterior margin of wing; 2 rounded spots in distal portion of vannal cell, posteriormost spot



Figs. 44-48. *Culicoides sitiens* Wirth and Hubert. Female: 44, wing; 45, palpus; 46, tibial comb. Male: 47, claspettes; 48, genitalia, claspettes removed.

smallest; pale spots present on basal portions of veins M_1 and M_2, spot over vein M_1 barely below posterior border of poststigmatic spot; a small spot resting on anterior surface of medio-cubital fork. Macrotrichia abundant over entire surface of wing. Costa extending to 0.51 of entire length of wing.

Abdomen: Two unequal, subpyriform spermathecae present, both crumpled in only female specimen seen, ducts absent; rudimentary spermatheca and ring present.

MALE—Genitalia (Fig. 47, 48) with ninth sternum very narrow, with shallow caudomedian excavation. Ninth tergum with prominent, distally divergent, apicolateral processes. Basimere with very slender ventral root; dorsal root broad, truncate. Telomere tapering distally with a slightly curved, mesally tipped apex. Aedeagus stout, broad, conical, truncate median posterior process; aedeagal arms short with small upturned bases; basal arch gently curved, extending about 0.30 of total length of aedeagus. Claspettes with strong basolateral arm; stem swollen, diminishing basally to a very slender, laterally directed apex.

DISTRIBUTION: This is a southwestern species previously reported from Arizona, California and Baja California. New Mexico County Record: Sandoval.

DISCUSSION: This species has been described by Wirth and Hubert (1960) from the rotting parts of cacti, having been reared from *Opuntia* and *Lophocereus*.

9. **Culicoides (Dr.) byersi** new species

(Figs. 1, 49-54)

FEMALE—Length of wing 0.89 (0.88-0.91; n=2) mm.

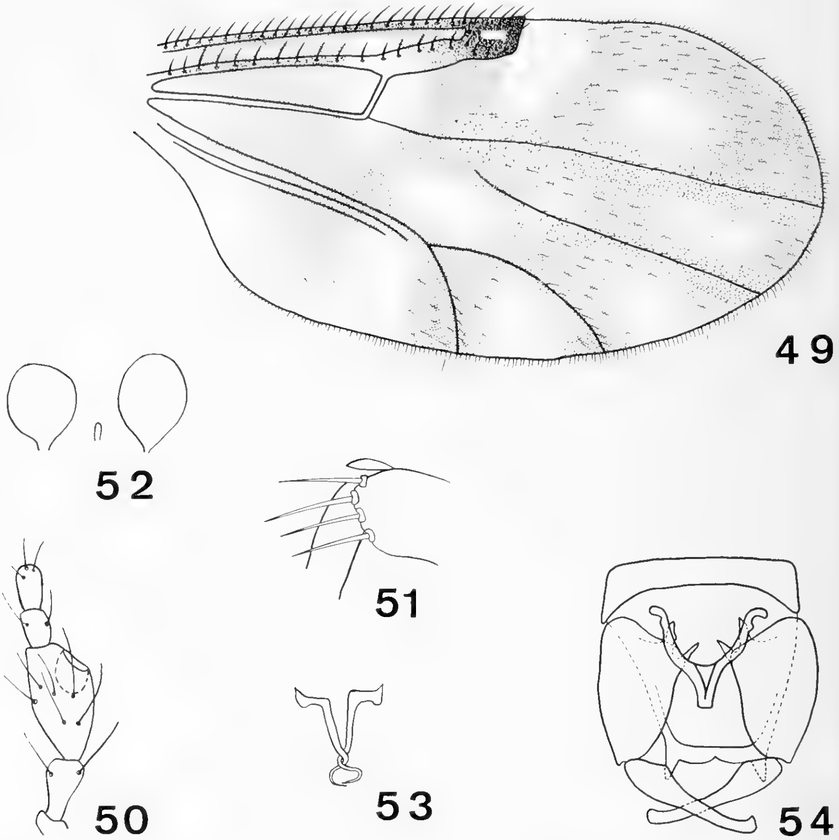
Head: Eyes barely separated to contiguous. Antenna with flagellomeres in proportion of 10:8:9:9:9:9:9:10:15:15:17:17:21; antennal ratio 1.13 (1.09-1.15; n=3); segments 9+10 to 11 in ratio of 0.73 (0.72-0.75; n=3); distal sensory tufts present on segments 3, 5, 7, 9, 11-15. Third palpal segment short, very swollen (Fig. 50), 1.7 (1.6-1.8; n=3) times as long as greatest breadth, with deep sensory pore. Ratio of head length to proboscis 1.67 (1.57-1.77; n=2). Mandible with 9-11 very small teeth.

Thorax: Legs dark brown; fore femora with pre-apical pale band, tibiae with subbasal pale band. Hind tibial comb with 4 spines (Fig. 51).

Wing: (Fig. 49). Second radial cell in a dark area; small round spot over r-m crossvein, barely extending beyond vein M_{1+2}; rather long, narrow poststigmatic spot; remaining spots as follows: small, round spot in median portion of cell R_5; pale spot in distal portion of cell M_1 not attaining wing margin; pale spots in distal portions of cells M_2 and M_4 may or may not extend to margin; a mesally constricted pale spot in distal portion of vannal cell attaining wing margin; a rather indefinite pale area anterior to mediocubital fork. Costa extending 0.54 of entire wing length. Macrotrichia usually confined to distal and posterior wing areas and veins.

Abdomen: Two subequal spermathecae (Fig. 52) 49 x 39 and 43 x 39 μ, ducts sclerotized for a very short distance; rudimentary spermatheca present.

MALE—Genitalia (Figs. 53, 54) with ninth sternum with shallow caudomedian excavation. Ninth tergum with prominent, divergent apicolateral processes. Basimere with slender, simple, ventral root; dorsal root more or less truncate. Telomere tapering, with swollen, tipped apex. Aedeagus with truncate median posterior process, in allotype male slightly flared apically;



FIGS. 49-54. *Culicoides byersi,* new species. Female: 49, wing; 50, palpus; 51, tibial comb; 52, spermathecae. Male: 53, claspettes; 54, genitalia, claspettes removed.

aedeagal arms arcuate, with knobbed, laterally directed bases, basal portion of stem with small lobe on lateral margin immediately distal to anterior bend of arms; basal arch curved. Claspette with stout basolateral arm; stem abruptly bent posteriorly, long, tapering to a very slender, contorted apex.

DISTRIBUTION: New Mexico (Catron Co.) and Arizona.

Specimens examined: Holotype female, Whitewater Forest Service Camp, 5 mi. E. of Glenwood, New Mexico, 24 June 1953, W. W. Wirth, at light. Allotype male, Glenwood Fish Hatchery, Glenwood, New Mexico, 2 Aug. 1965, W. R. Atchley, at light. Paratypes, 1 male, 1 female, same data as holotype; 1 female, Whitewater Forest Service Camp, 1 Aug. 1965, W. R. Atchley, at light. Additional specimens examined: 1 female, Mormon Lake, Coconina Co., Arizona, 8-15 July 1956, F. W. and F. G. Werner.

DISCUSSION: This species is very close to *hinmani* Khalaf and *borinqueni* Fox, tree-hole breeders of the *copiosus* group. *Culicoides byersi* can be distinguished from *hinmani* by the sensorial pattern and the presence of a single elongate pale spot immediately posterior to the second radial cell.

Both *hinmani* and *borinqueni* have two small spots immediately posterior to the second radial cell. The vannal cell of *byersi* has a large U-shaped spot broadly borderng the wing margin, whereas in *hinmani* the vannal cell is provided with two or three pale spots, the distalmost spot at best narrowly attaining the wing margin. *C. byersi* can be distinguished from *borinqueni* in that the combined length of antennal segments 9 and 10 is greater than 11; and the antennal ratio of *byersi* is 1.13 as opposed to approximately 1.7 of *borinqueni.*

I am very happy to name this species for my Major Professor at the University of Kansas, Dr. George W. Byers.

Subgenus *DIPHAOMYIA* Vargas, 1960:40

Type species *baueri* Hoffman (orig. des.).

Vargas (1960) erected this subgenus for the *iriartei* group as defined by Wirth and Blanton (1959). The species of this subgenus have the second radial cell in a dark area and a pale spot over vein M_2. The hind tibial comb has 4 spines. Two spermathecae are present, each with a long sclerotized neck. The ventral root of the basimere is long, slender and curved, with a prominent posterior process. The claspette is knobbed basally, with an apical fringe of spines. There are distinct bladelike processes located on the postero-lateral margins of the basal arms of the aedeagus.

Two species of the subgenus, *baueri* and *hematopotus,* are found in the New Mexico fauna.

10. **Culicoides baueri** Hoffman

(Figs. 55-59)

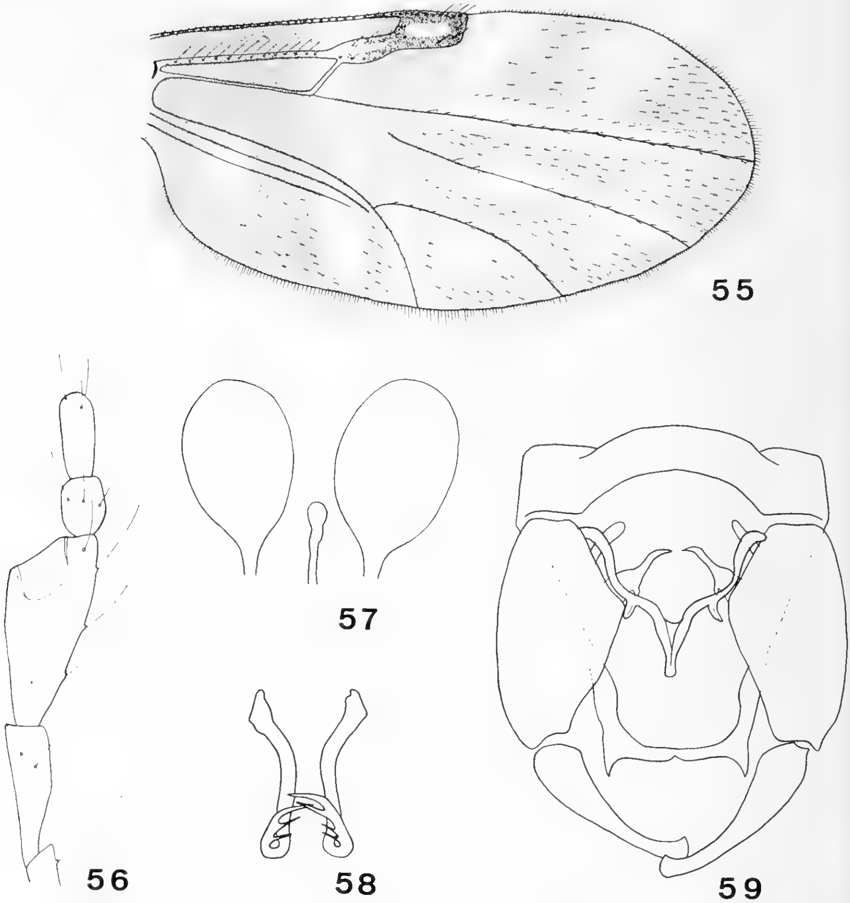
Culicoides baueri Hoffman, 1925, Amer. Jour. Hyg. 5:297 (male, female; Maryland; fig. wing, mesonotal disc).

FEMALE—Length of wing 1.35 (1.19-1.40; n=10) mm.

Head: Eyes separated less than diameter of a facet. Antenna with flagellomeres in proportion of 11:10:9:10:11:10:10:12:15:15:18:19:30; antennal ratio 1.07 (0.98-1.28; n=9), segments 9+10 to 11 in ratio of 0.66 (0.65-0.70; n=6); distal sensory tufts on segments 3, 5-10, occasionally present on segment 4 or absent from segment 5 and/or 6. Distal 4 palpal segments in proportion of 17:24:7:10; third palpal segment swollen, 2.17 (1.9-2.5; n=12) times as long as greatest breadth (Fig. 56). Ratio of head length to proboscis 1.24 (1.0-1.44; n=9). Mandible with 10-12 (n=9) teeth.

Thorax: Legs dark brown; fore and middle femora with pre-apical pale rings, all tibiae with subbasal pale rings. Hind tibial comb with 4 spines.

Wing: (Fig. 55). Second radial cell in a dark area; poststigmatic spot usually small, sometimes divided into 2 spots; pale spot in cell R_5 with mesal constriction, rarely divided into 2 spots; pale spots in cells M_1, M_2, M_4 and



FIGS. 55-59. *Culicoides baueri* Hoffman. Female: 55, wing; 56, palpus; 57, spermathecae. Male: 58, claspettes; 59, genitalia, claspettes removed.

vannal cell, all well removed from wing margin; pale spot present over vein M_2; medio-cubital fork bordered posteriorly by a rather long pale spot; a small spot just posterior to r-m crossvein, separated from spot on r-m and spot forming posterior border of medio-cubital fork. Macrotrichia abundant. Costa extending 0.52 (0.48-0.55; n=10) of distance to wing apex.

Abdomen: Two subequal spermathecae (Fig. 57) 49 x 66 and 42 x 66 μ, necks well developed; rudimentary spermatheca and ring present.

MALE—Genitalia (Figs. 58, 59) with ninth sternum broad, caudomedian excavation deep; membrane spiculate. Ninth tergum tapering posteriorly, with 2 pointed apicolateral processes and slight mesal notch. Basimere with long prominent roots; ventral root slender, tapering, almost touching opposite root mesally, with boat-shaped hook; dorsal root elongate but stouter.

Telomere tapering distally, with knobbed apex. Aedeagus with median posterior process sub-truncate; aedeagal arms widely separated anteriorly, bases sharply curved laterad, converging posteriorly to form median process; arms more or less sinuate with blade-like processes on posterior margin of shoulders. Claspette stout; broad basally, distal one-third strongly recurved, apex with a fringe of long slender spines.

DISTRIBUTION: *Culicoides baueri* is a widespread species that has been reported from Calif., Colo., Fla., Ga., Md., N.Y., Okla., Tenn., Texas, and Wis. New Mexico County Records: DeBaca, Catron, Lincoln, Otero, Quay and Sandoval.

VARIATION: There exists some variation in the pattern of pale wing spots in New Mexico specimens. When compared with the well defined patterns of the low-land specimens, representatives from some of the mountainous areas, such as at Alto (Lincoln County) exhibit some reduction in spot definition.

The distal pale spot in cell R_5 may vary from large and mesally constricted to two small spots.

11. **Culicoides haematopotus** Malloch

(Figs. 60-65)

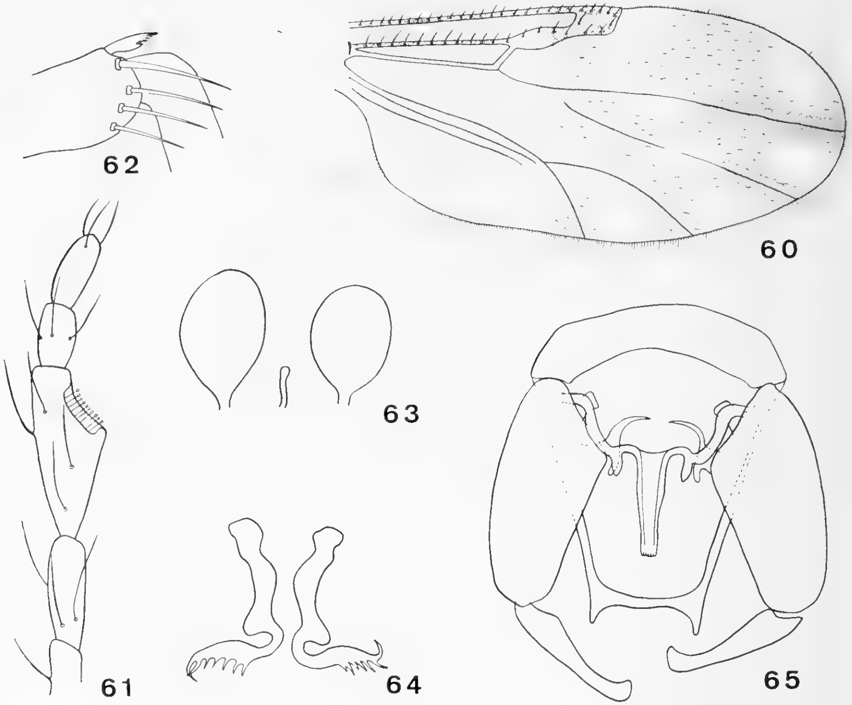
Culicoides haematopotus Malloch, 1915, Ill. State Lab. Nat. Hist. Bull. 10:302 (male, female; Illinois; fig. wing, male antenna, male genitalia).

FEMALE—Length of wing 1.17 (1.0-1.3; n=15) mm.

Head: Eyes separated less than diameter of a facet. Antenna with flagellomeres in proportion of 12:8:8:8:8:8:8:9:19:19:21:22:30; antennal ratio 1.43 (1.25-1.57; n=13); distal sensory tufts on segments 3, 5, 7, 9-15, occasionally present on segment 8 and rarely on 6 and 8 together (see discussion on variation for second form of *haematopotus*); segments 9+10 to 11 in ratio of 0.91 (0.83-1.0; n=12). Distal 4 palpal segments in proportion of 15:25:8:11; third segment moderately swollen, 2.5 (2.3-2.7; n=14) times as long as greatest breadth, with a broad but moderately shallow sensory organ (Fig. 61). Ratio of head length to proboscis 1.11 (0.97-1.25; n=11). Mandible with 12-15 (n=16) teeth.

Thorax: Legs brown; fore and middle femora with pre-apical pale rings, all tibiae with sub-basal pale rings; knees dark. Hind tibial comb with 4 spines, the spine nearest the spur usually longest (Fig. 62).

Wing: (Fig. 60). Second radial cell in a dark area; spot over r-m crossvein extending from anterior wing margin to just beyond vein M_{1+2}, may be connected to a second small pale spot and apparently extending to immediately anterior of medio-cubital fork; poststigmatic spot present, usually connected to spot over vein M_1; distal spots in cells R_5, M_1, M_2, M_4 and vannal cell, all attaining wing margin; 2 spots in vannal cell sometimes con-



FIGS. 60-65. *Culicoides haematopotus* Malloch. Female: 60, wing; 61, palpus; 62, tibial comb; 63, spermathecae. Male: 64, claspettes; 65, genitalia, claspettes removed.

nected along posterior margin of wing to form a "C"; spots present over mesal portions of vein M_1 and M_2; a small spot at base of medio-cubital fork. Macrotrichia present in distal and posterior portions of the wing. Costa extending to 0.55 (0.52-0.56; n=15) of distance to wing apex.

Abdomen: Two unequal, oval spermathecae (Fig. 62) 82 x 43 and 66 x 36 μ, with ducts sclerotized for a long distance; rudimentary spermatheca and heavily sclerotized ring present.

MALE—Genitalia (Figs. 64, 65) with ninth sternum broadly, shallowly emarginate. Ninth tergum tapering posteriorly, with short, triangular apicolateral processes. Basimere tapering posteriorly; ventral root long, curved, with pointed apex, a large boot-shaped hook on posterior margin; dosal root broad, truncate. Telomere slender with slightly swollen apex. Aedeagus with very long, straight-sided median posterior process, with serrate, truncate apex; aedeagal arms turned laterad basally, curved postero-medially to form median posterior process; prominent triangular process on apical portion of aedeagal arms. Claspette with stout base; stem sinuate, with large, laterally directed thumblike lobe approximately at mid-length; stem narrowed immediately above lobe, turned laterad to form greatly swollen apex bearing numerous spines, outermost spine largest.

DISTRIBUTION: Culicoides haematopotus is a common species occurring over most of the United States. New Mexico County Records: Catron, DeBaca, Dona Ana, Eddy, Lincoln, Quay and Socorro.

VARIATION: Two forms of this species exist in New Mexico. One has a relatively small wing and an antennal sensorial pattern of 3, 5, 7, 9-15, and is here considered typical *haematopotus*; a second form possesses a large wing and a sensorial pattern of 3, 10-15. This second form can be characterized as having a larger wing (WL=1.38 mm.), a slightly smaller antennal ratio (AR=1.37), a slightly more swollen third palpal segment (PR=2.3) and a slightly longer 11th antennal segment (9+10 to 11=0.86). In this form some of the distal wing spots are reduced in size and intensity. No perceptible difference has been found in the male genitalia of the two forms. Intermediates between these two forms exist at Glenwood, Catron County, New Mexico.

The description by Jamnback (1965) of *haematopotus* as it occurs in New York differs markedly from that of specimens identified as this species in the southwestern United States. The differences between the eastern and western forms of this species and the presence of two forms or phases mentioned above would suggest that *haematopotus* as we now understand it is a complex of very similar species. A critical study is needed of what is now understood to be *haematopotus* to determine the extent of morphological and biological variation and to determine if this variation is specific, sub-specific or infrasubspecific.

An intersex of this species was collected at Glenwood, Catron Co., New Mexico.

FEEDING HABITS: Several authors have reported this species as biting man, but only in small numbers. Others, such as Fallis and Bennett (1960, 1961) and Messersmith (1965), have presented evidence that *haematopotus* may be ornithophilic. The studies by Snow (1955) on vertical distribution of biting flies would seem to support this latter premise, since he found this species to be more common in the forest canopy than at ground level.

Subgenus *OECACTA* Poey, 1851:238 (as genus)

Type species *furens* Poey (monotype).

A rather diverse assemblage of species including those forms with the second radial cell usually in a dark area and commonly with a distinct wing pattern of pale and dark spots. Occasionally, however, the wings are more or less unicolorous and lack a pattern of spots. The females have two spermathecae, rarely one. The claspettes are separate and may or may not be modified apically. The basimere has well developed ventral roots, a boat-shaped hook may be present on the posterior margin and the dorsal root is usually long and simple. The apicolateral processes of the ninth tergum are usually prominent.

This subgenus, as currently defined, contains a heterogeneous accumulation of species groups. There exists considerable disagreement among various workers as to the contents of *Oecacta*. Many of the species groups now "lumped" into *Oecacta* will no doubt later be elevated to subgeneric status when their natural affinities become better understood.

Culicoides limai Group

This group consists of species with large pale spots more or less filling the wing cells. A pale spot is found straddling vein M_2 and occasionally a second spot over M_1. The sensorial pattern is 3, 7-10 or 3-10 and there are four tibial spines. The male genitalia may or may not possess a foot-shaped ventral root. The apex of the claspette is fringed and a lobe or blade-like process may be present.

Culicoides luglani is provisionally referred to this group, but its affinities are still not clear. The *limai* group, as outlined by Wirth and Blanton (1958) for four Panama species, possess foot-shaped ventral roots and the median posterior process lacks lateral projections. Both *luglani* and *tenuilobus,* which it closely resembles, have simple ventral roots and the median process has prominent lateral projections. In addition, all the Panama representatives have a sensorial pattern of 3, 7-10 while *luglani* has 3-10.

12. **Culicoides luglani** Jones and Wirth

(Figs. 66-70)

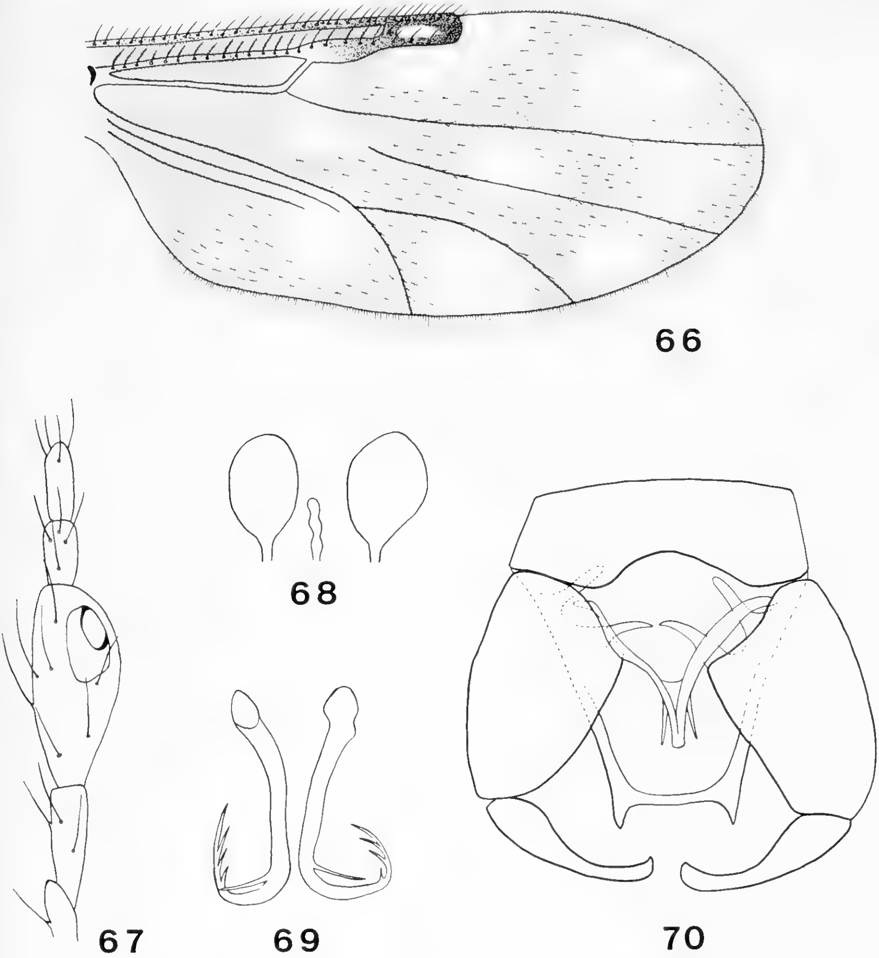
Culicoides luglani Jones and Wirth, 1958, J. Kansas Ent. Soc. 31:89-91 (male, female; Texas; fig. wing, mesonotal disc, spermathecae, palpus, male genitalia).

FEMALE—Length of wing 1.22 (1.17-1.26; n=3) mm.

Head: Eyes very narrowly separated. Antenna with flagellomeres in proportion of 10:10:10:11:11:11:12:12:15:15:18:18:21; antennal ratio 0.95 0.89-0.99; n=3); distal sensory tufts present on segments 3-10, rarely absent from 5; antennal segments 9+10 to 11 in ratio of 0.59 (0.58-0.60; n=3). Distal 4 palpal segments in proportion of 15:28:8:10; third palpal segment greatly swollen, 2.12 (2.0-2.2; n=3) times as long as greatest breadth, with a deep sense organ with a rounded opening (Fig. 67). Ratio of length of head to proboscis 1.05 (1.01-1.09; n=3). Mandible with 13-16 (n=3) teeth.

Thorax: Femora with pre-apical pale rings, tibiae with subbasal pale rings. Hind tibial comb with 4 spines.

Wing: (Fig. 66). Second radial cell in a dark area; small round pale spot over r-m crossvein, extending from anterior margin of wing to barely be-



FIGS. 66-70. *Culicoides luglani* Jones and Wirth. Female: 66, wing; 67, palpus; 68, spermathecae. Male: 69, claspettes; 70, genitalia, claspettes removed.

yond vein M_{1+2}; poststigmatic spot narrow; a large pale spot in distal portion of cell R_5; spot in distal portion of cell M_1 not attaining wing margin; pale spots in cells M_2 and M_4 both attaining wing margin; 2 small pale spots in vannal cell, neither reaching posterior edge of wing; a pale spot circumscribing vein M_2 extending anteriorly to posterior edge of vein M_1; a small spot in extreme proximal portion of cell M_2 lying just below r-m crossvein; medio-cubital fork in a dark area. Macrotrichia confined to distal and posterior portions of wing. Costa extending to 0.53 (0.52-0.56; $n=3$) of distance to wing apex.

Abdomen: Two slightly unequal spermathecae (Fig. 68) with long sclerotized necks, 73 x 50 and 66 x 46 μ. Rudimentary spermatheca and ring present.

MALE—(Figs. 69, 70). Ninth sternum with narrow, rather shallow emargination. Ninth tergum strongly tapering, with small triangular apicolateral processes. Basimere tapering distally; roots prominent, ventral root with simple, expanded base, not tapering to point, almost touching mesally. Telomere swollen basally, then narrowing to slightly swollen tip. Median posterior process of aedeagus elongate with two rather obscure lateral lobes at apex; aedeagal arms long, slender and slightly bowed mesally, bases turned laterad. Lateral lobes of median process much stouter in New Mexico specimens than pictured by Wirth and Jones. Claspette with knobbed base; stem stout basally, tapering posteriorly; mesal margin of stem relatively straight, lateral margin with slight median swelling; distal portion of stem gently recurved, bearing several small, slender spines; a large, strong, laterally directed spine arising just before lateral curve of stem.

DISTRIBUTION: Texas, Arizona, Mexico. New Mexico County Records: Catron, DeBaca, Grants and Lincoln.

VARIATION: The New Mexico material of this species differs somewhat from the original description. The proboscis of the New Mexico specimens is considerably shorter than that of Texas individuals.

DISCUSSION: Females of this species superficially resemble members of the *palmerae* group, particularly with regard to the wing pattern. The sensorial pattern will readily separate *luglani* from *novamexicanus* n. sp. With regard to *palmerae* and *utahensis,* separation can be made by the shape of the third palpal segment, the antennal ratio and eye separation. The genitalia of the males are quite distinct.

Close examination of material identified as *tenuilobus* Wirth and Blanton from Panama in the USNM shows *luglani* and *tenuilobus* not to be synonomous as previously thought (Wirth 1963).

Culicoides furens Group

The *furens* group is composed of an assemblage of species which often possess pale spots in the extreme distal portions of cells R_5 and M_1. The sensorial pattern is 3, 8-10 and there are four or five tibial spines. The spermathecae have distinct selerotized necks. The ventral root of the male genitalia is foot-shaped and the claspettes have simple bases, a ventral lobe on the stem and an apical fringe of spines.

13. **Culicoides stellifer** (Coquillett)

(Figs. 71-76)

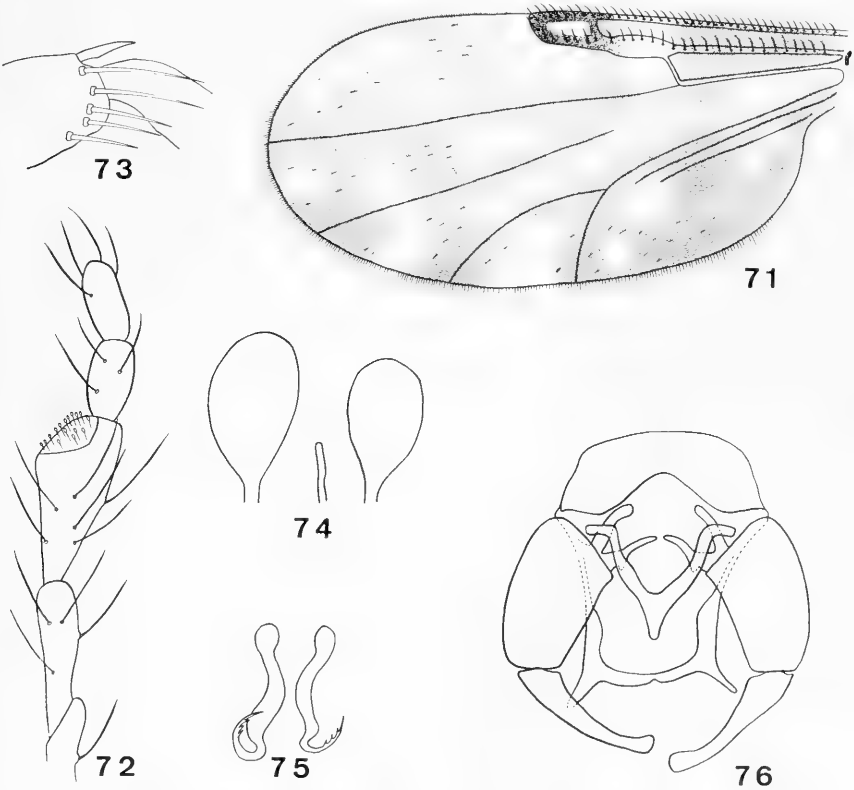
Ceratopogon stellifer Coquillett, 1901, U.S. Nat. Mus. Proc. 23:604.
Culicoides stellifer (Coquillett); Kieffer, 1906, Gen. Insectorum, fasc. 42:55.

FEMALE—Length of wing 1.24 (1.18-1.32; n=12) mm.

Head: Eyes separated less than diameter of a facet; inferior transocular suture always present. Antenna with flagellomeres in proportion of 10:10:10:10:11:11:11:11:13:16:17:17:30; antennal ratio 0.96 (0.90-1.07; n=10); distal sensory tufts on segments 3, 7-10, occasionally absent from 7, rarely present on 5 and 6; segments 9+10 to 11 in ratio of 0.62 (0.54-0.78; n=11). Distal 4 palpal segments in proportion of 17:22:8:10; third palpal segment moderately swollen, 2.47 (2.25-2.87; n=11) times as long as greatest breadth (Fig. 72). Ratio of head length to proboscis 1.22 (1.11-1.28; n=8). Mandible with 12-14 (n=10) teeth.

Thorax: Legs dark brown; fore and middle femora with pre-apical pale ring; all tibiae with subbasal pale rings; hind tibiae with long, apical pale area indistinct on fore and middle tibiae. Hind tibial comb with 5 spines (Fig. 73).

Wing: (Fig. 71). Second radial cell in a dark area; spot over r-m crossvein extending from costa to vein M_{1+2}; poststigmatic spot mesally con-



FIGS. 71-76. *Culicoides stellifer* (Coquillett). Female: 71, wing; 72, palpus; 73, tibial comb; 74, spermathecae. Male: 75, claspettes; 76, genitalia, claspettes removed.

stricted, basal portion of spot larger and extending proximally behind second radial cell; spot in cell R_5 "C" shaped, following anterior and distal margins of the wing; 2 spots in distal portion of cell M_1, apical spot and spots in cells M_2 and M_4 attaining wing margin; 2 round spots in distal part of vannal cell; an elongate triangular-shaped pale area lying at basal end of cell M_1; a long pale area in basal portion of cell M_2 beginning at arculus and extending well beyond medio-cubital fork. Macrotrichia rather sparse, occurring primarily on marginal part of wing. Costa extending 0.54 (0.50-0.58; n=12) of distance to wing apex.

Abdomen: Two unequal spermathecae (Fig. 74) 69 x 40 and 60 x 34 μ, (n=5); ducts well developed.

MALE—(Figs. 75, 76). Ninth sternum broad, with a narrow, deep caudomedial excavation. Ninth tergum tapering, with long, slender, finger-like apicolateral processes. Basimere with prominent roots; ventral roots elongate, almost touching mesally, each with a distinct hook on posterior margin; dorsal root long and slender. Telomere tapering, with slightly swollen apex. Aedeagus in shape of V; median posterior process short, posteriorly rounded; aedeagal arms widely separated anteriorly, basal ends sharply curved laterad, converging posteriorly to form median process; basal arch rounded. Claspette with knobbed base; stems stout, sinuate; apical third strongly recurved and bearing spines; stem with slightly swollen lobe located immediately anterior to narrowed recurved apex.

DISTRIBUTION: This is a common and very widespread species, having been recorded from the majority of states in the U.S. from Canada to Mexico, in addition to Trinidad and Venezuela. New Mexico County Records: DeBaca, Lincoln, Otero, San Miguel and Taos.

VARIATION: A female specimen from Taos County exhibits an atypical wing pattern in that the "C" shaped spot in cell R_5 lacks the heavier basal area and is, therefore, reduced to a curved line along the wing margin. Other specimens from Lincoln Co. have this spot divided into a mesally constricted proximal portion with its prolongation reduced to a small spot in the very distal part of the cell, reminiscent of the pattern in *C. paraensis* (Goeldi). Many specimens exhibit considerable variation in the number and position of the pale spots in cell M_1. The two distal pale spots in this cell may be separate, narrowly joined or completely fused. A female from Bonita Lake, Lincoln Co. has in cell M_1 a triangular spot in the proximal portion of the cell narrowly joined to the two completely fused distal spots.

FEEDING HABITS: This species has been reported as biting man in Utah by Rees and Bullock (1954), while Malloch (1915), Hoffman (1925), Root and Hoffman (1937) and Murray (1957) have cited man-biting records in the eastern states. Snow *et al.* (1957) found that man-biting records believed to pertain to *stellifer* in the Tennessee Valley were *paraensis* (Goeldi).

Therefore, many eastern biting records for *stellifer* may be in error. Khalaf (1966) has given characters sufficient to distinguish these two species.

Culicoides stonei Group

The *stonei* group includes species with unmarked wings, a sensorial pattern of 3-14, 3, 7-14 or 3, 9-14, pale legs without a distinct banding pattern and the spermathecal system lacks a sclerotized ring. The male genitalia possesses very long, stout, diverging apicolateral processes and the mesal margin of the ninth tergum has a row of stout spines. The aedeagus has slender basal arms and the median posterior process is broadly rounded apically . The claspettes possess slender anterior processes on the basal knob.

This group, as outlined above, includes *C. stonei* James and two apparently undescribed species in the USNM collections. The shape of the anterior process on the basal knob of the claspettes, the very prominent apicolateral processes and the absence of a sclerotized ring closely ally the *stonei* group with the *biguttatus* and *spinosus* groups.

14. **Culicoides stonei** James

(Figs. 77-81)

Culicoides stonei James, 1943, Pan-Pacific Ent. 19:149 (male, female; Colorado; fig. male genitalia).
Culicoides weesei Khalaf, 1952, Jour. Kansas Ent. Soc. 25:65.

FEMALE—Length of wing 1.17 (1.06-1.22; n=6) mm.

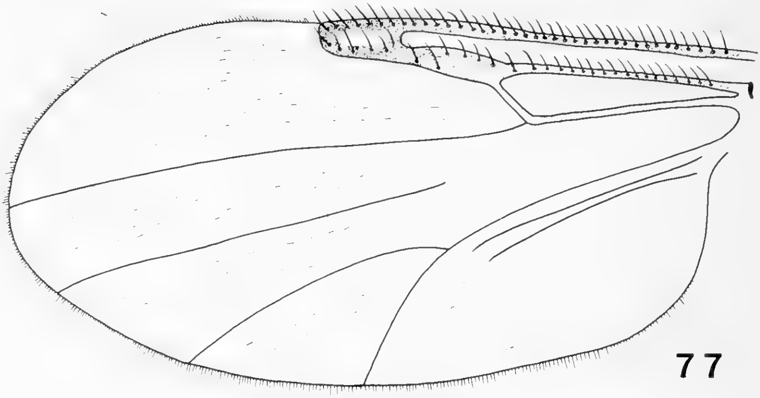
Head: Eye separation approximately half the diameter of a facet. Antenna with flagellomeres in proportion of 11:8:9:10:10:9:10:10:14:13:16:18:21; antennal ratio 1.10 (1.05-1.15; n=6); segments 9+10 to 11 in ratio 0.69 (0.65-0.72; n=5). Distal sensory tufts on segments 3-14 (15), occasionally absent from segment 4. Distal 4 palpal segments in proportion of 20:24:10:8; third palpal segment swollen, 2.3 (2.1-2.4; n=6) times as long as greatest breadth, with shallow sensory pore, from which arise numerous stalked sensillae (Fig. 78). Ratio of head length to proboscis 1.04 (1.01-1.09; n=5). Mandible with 12-13 teeth (n=7).

Thorax: Legs pale, without apparent banding pattern. Hind tibial comb with 4 spines.

Wing: (Fig. 77). Wings with no pattern of light or dark spots. Costa extending 0.56 (0.55-0.58; n=6) of entire length of wing. Macrotrichia relatively abundant.

Abdomen: Two large, heavily sclerotized, unequal spermathecae (Fig. 79); ducts well developed; rudimentary spermatheca present, ring absent.

MALE—Genitalia (Figs. 80, 81) with ninth sternum possessing narrow deep caudomedial excavation; membrane spiculate. Ninth tergum with very prominent, broad, divergent apicolateral processes; posterior portion of ninth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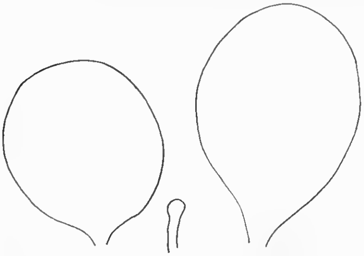
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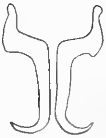
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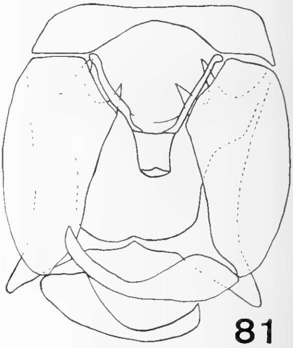
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FIGS. 77-81. *Culicoides stonei* James. Female: 77, wing; 78, palpus; 79, spermathecae. Male: 80, claspettes; 81, genitalia, claspettes removed.

tergum distinctly notched. Basimere with long, simple roots, dorsal root longer than ventral root. Aedeagus with very broad, sub-truncate median posterior process; aedeagal arms slender, straight, divergent, with slight postero-laterally directed bases. Claspette stout basally; basolateral process with tapering anterior extension; stems narrowing slightly to sickle-like apex.

DISTRIBUTION: *Culicoides stonei* has been previously reported from the western half of the United States, Texas to South Dakota, westward to California. New Mexico County Records: Chaves, DeBaca, Eddy, Quay and Roosevelt.

DISCUSSION: The unmarked wings of this species resemble those of *bottimeri* Wirth, but these two species can be separated by sensorial pattern of the females and very distinctive male genitalia. In addition, the unmarked wings of *stonei* superficially resemble various species of the subgenus *Selfia;* however, the presence of well sclerotized spermathecae in *stonei* will easily differentiate females of these species.

Culicoides spinosus Group

The females of this group have poorly marked wings lacking distal pale spots, sensoria on segments 3, 11-15 (except *usingeri*), eyes narrowly separated to contiguous, and the ring is absent. (Examination of type material of *usingeri* Wirth showed the ring not present as previously thought.) The male genitalia have prominent apicolateral processes and the claspettes, which bear marginal spines, have stems bent at almost right angles with the bases.

The *spinosus* group, as outlined above, includes *spinosus* Root and Hoffman, *loisae* Jamnback, *usingeri* Wirth and *sublettei* n. sp. These species, included in the *biguttatus* group by many authors, appear to form a closely related group because of the great similarity of the male genitalia as well as the wing pattern, sensorial pattern, etc.

15. **Culicoides sublettei** new species

(Figs. 2, 82-87)

FEMALE—Length of wing 1.19 (1.08-1.27; n=12) mm.

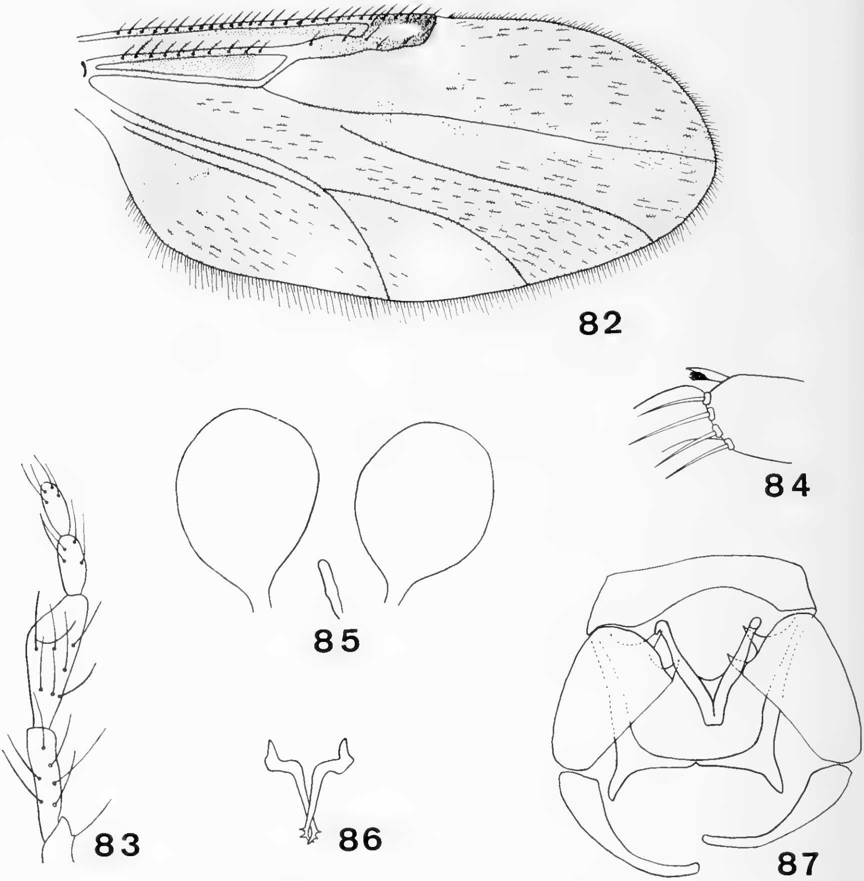
Head: Eyes separated less than diameter of a facet; inferior interocular suture present (very faint in allotype female). Antnna with flagellomeres in proportion of 10:8:8:8:10:10:11:11:15:17:18:18:25; antennal ratio 1.07 (1.03-1.13; n=3); segments 9+10 to 11 in ratio of 0.67 (0.65-0.72; n=4); distal sensory tufts on segments 3, 11-15, rarely absent from 11. Distal 4 palpal segments in proportion of 17:23:12:8; third palpal segment swollen (Fig. 83), 2.37 (2.08-2.60; n=10) times as long as greatest breadth, with moderately shallow, round sensory pore. Ratio of head length to proboscis 1.05 (0.90-1.12; n=9). Mandible with 14-16 (n=11) teeth.

Thorax: Legs brown, without distinct banding on femora or tibiae. Hind tibial comb with 4 spines (Fig. 84).

Wing: (Fig. 82). Wing with faint pattern; second radial cell in a dark area; small, round spot over r-m crossvein, extending barely beyond vein M_{1+2}; poststigmatic spot very small; pale spots in cell M_4 and distal portion of vannal cell, both attaining wing margin; a very indistinct pale spot in distal portion of cell M_2. Costa extending 0.55 (0.53-0.59; n=12) of length of wing. Macrotrichia abundant over entire wing surface.

Abdomen: Two dark equal spermathecae (Fig. 85) 66 x 43 μ (slightly unequal in one paratype), ducts sclerotized for a short distance; rudimentary spermatheca present, ring absent.

MALE—(Figs. 86, 87). Genitalia with ninth sternum having narrow, shallow posterior emargination. Ninth tergum with broad, pointed apicolateral processes. Basimere with slender, simple roots. Telomere arcuate, stout



FIGS. 82-87. *Culicoides sublettei,* new species. Female: 82, wing; 83, palpus; 84, tibial comb; 85, spermathecae. Male: 86, claspettes; 87, genitalia, claspettes removed.

basally, tapering distally, with simple apex. Aedeagus with short, broad, truncate median posterior process; aedeagal arms widely separated anteriorly, with small, postero-laterally directed bases, arms converging posteriorly to form median process; basal arch gently rounded, extending approximately half length of entire aedeagus. Claspette with basal end L-shaped, anterior process pointed; stem slender, diminishing posteriorly to slightly curved, pointed apex, bearing two small but distinct sub-apical spines.

DISTRIBUTION: New Mexico (DeBaca and Quay Counties) and Texas.

Specimens examined: Holotype male, Ft. Sumner, DeBaca County, New Mexico, 8 June 1964, at light, NMDPH. Allotype female, same data. Paratypes, 1 males, 12 females: 1 male, 7 females, Ft. Sumner, 8 June 1964; 5 females, Ft. Sumner, 15-18 June 1964. Additional specimens examined: 1 female, Balmorhea State Park, Reeves Co., Texas, 24 Aug. 1964, F. S. Blanton.

DISCUSSION: Culicoides sublettei n. sp. belongs to the *spinosus* group, being closest to *spinosus* Root and Hoffman and *loisae* Jamnback, both of which occur in the eastern United States. *C. sublettei* is very similar to the figures given by Jamnback for *loisae;* however, the females may be distinguished from this species by the presence of distinctly denticulate mandibles. The more swollen third palpal segment as well as the longer proboscis in relation to the head length will separate *sublettei* females from those of *spinosus.*

The male genitalia of *sublettei* have stouter and slightly bowed aedeagal arms with truncate tips, while in *loisae* the arms are straight. In both eastern species the apex of the aedeagus is rounded or sharply narrowed.

In the western states *sublettei* may be separated from *usingeri* Wirth by the sensorial pattern and the presence of five tibial spines in *usingeri.* Males of *usingeri* have a conical median posterior process of the adeagus and about five spines on the claspettes.

I am very happy to name this species for my good friend and former teacher, Dr. James E. Sublette, who first interested me in the study of Diptera.

Culicoides daedalus Group

The *daedalus* group, as outlined by Wirth and Blanton (1959), has females with very hairy wings. A pale spot straddles vein M_2 and sensoria are found on segments 3, 11-15 or 3, 5, 7, 9, 11-15. The pit of the third palpal segment is broad and shallow or deep and opening by a small pore. The male genitalia possess slender, unmodified ventral roots, the claspettes are pointed apically with distinct anterior processes on the basal knobs, and the aedeagus is simple.

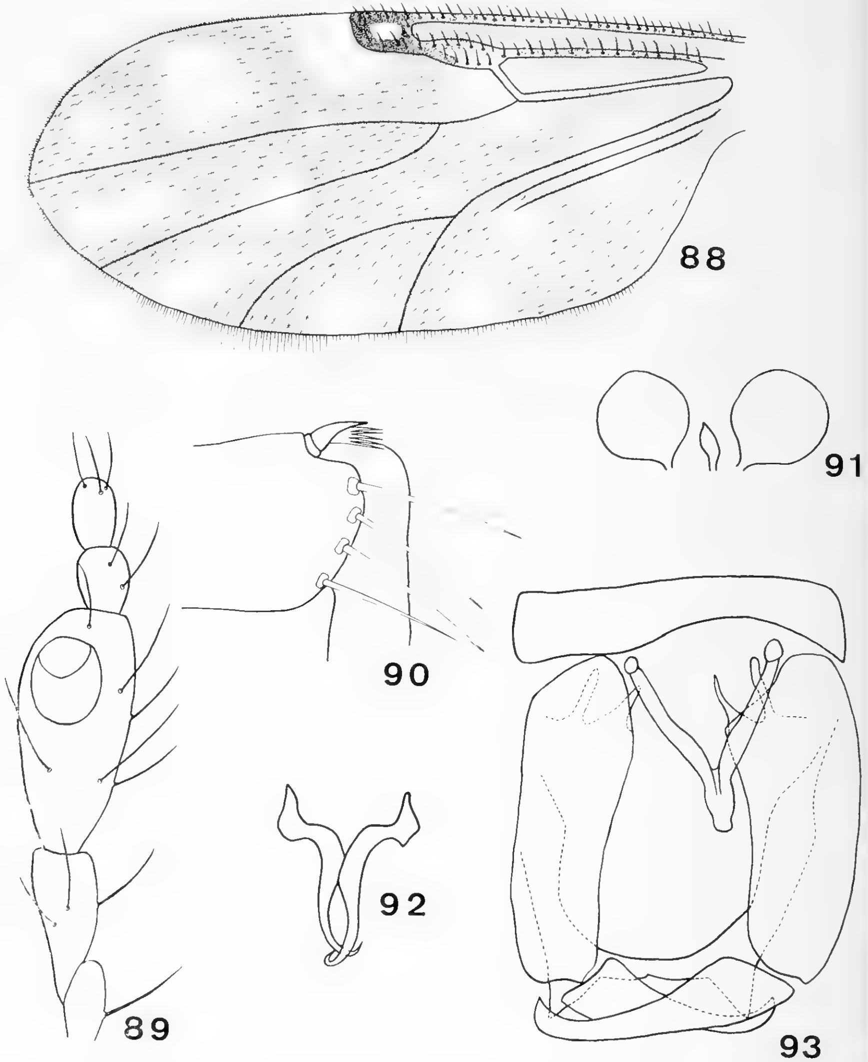
16. **Culicoides pampoikilus** Macfie

(Figs. 88-93)

Culicoides pampoikilus Macfie, 1948, Ann. Trop. Med. Parasit., 42:79 (female; Chiapas, Mexico; fig. wing).
Culicoides dominicii Ortiz, 1951, Nov. Cient. Mus. Hist. Nat. LaSalle, zool. ser., no. 5:7.

FEMALE—Length of wing 1.52 mm.

Head: Eyes contiguous. Antenna with flagellomeres in proportion of 14:12:13:12:12:12:13:14:23:24:26:27:36; antennal ratio 1.55; segments 9+10 to 11 in ratio of 0.89; distal sensory tufts present on segments 3, 5, 7, 9, 11-15, occasionally present on segments 4 and 8 (only specimen from New Mexico has sensoria on segment 4 on 1 antenna and 8 on other). Distal 4 palpal segments in proportion of 15:30:8:8; third palpal segment very swollen, 2.0 times as long as greatest breadth, with large, deep sensory pore (Fig. 89). Ratio of head length to proboscis 1.32. Mandible with 15 very small teeth.



FIGS. 88-93. *Culicoides pampoikilus* Macfie. Female: 88, wing; 89, palpus; 90, tibial comb; 91, spermathecae. Male: 92, claspettes; 93, genitalia, claspettes removed.

Thorax: Hind femora darker than middle and fore pair. Banding pattern not evident on available female specimen, described by Wirth and Blanton (1959) as follows: "fore and mid femora with subapical and all tibiae with subbasal narrow pale rings." Hind tibial comb with 4 spines (Fig. 90).

Wing: (Fig. 88). Second radial cell in a dark area; pale spot on r-m crossvein, extending posteriorly beyond vein M_{1+2}; small, narrow, poststigmatic spot; 2 pale spots in cell R_5 in addition to poststigmatic spot, a large spot located more or less in middle of cell R_5 and a small, faint spot at distal margin; pale spots in cells M_1, M_2 and M_4 all reaching wing margin; two pale spots in distal portion of vannal cell, distalmost attaining wing margin; pale spot on vein M_2; small pale spot over medio-cubital fork; large pale spot in proximal portion of wing broadly overlapping veins Cu_1, Cu_2 and 1V. Costa extending 0.54 of wing length. Macrotrichia abundant on entire surface.

Abdomen: Two small spermathecae (Fig. 91) with ducts sclerotized for a short distance (spermathecae crumpled in New Mexico specimen); rudimentary spermatheca slightly expanded.

MALE—Male genitalia described from specimen from Cartago, Navarro, Costa Rica (Figs. 92, 93). Ninth sternum with slight caudomedian excavation. Ninth tergum with prominent triangular apicolateral processes. Basimere long, slender; dorsal and ventral roots elongate, slender, subequal. Telomere tapering, with distinctly hooked apex. Aedeagus with median posterior process slightly expanded mesally, truncate; aedeagal arms long, slender, slightly sinuate, with postero-laterally directed bases; basal arch pointed, extending approximately 0.35 of entire length of aedeagus. Basal end of claspette with slender, pointed process; stem rather stout basally, tapering distally, with simple, strongly sinuate apex.

DISTRIBUTION: Culicoides pampoikilus is a tropical species, having previously been reported from Costa Rica, Mexico, Panama and Venezuela. Wirth and Blanton (1959) list *pampoikilus* as a rare species in the humid tropics of Panama. The following record of this species from the mountainous region of southern New Mexico constitutes a new United States record: Lincoln Co., Rudioso, Cedar Creek Canyon, elev. 7100 ft., 16 July 1965, at light, W. R. Atchley.

DISCUSSION: The single female specimen of this species was examined by Dr. Willis Wirth, who concluded that it was *pampoikilus.* The *daedalus* group, to which this species belongs, is most numerous in western Panama, according to Wirth and Blanton (1959). *Culicoides pampoikilus* is apparently not closely related to any other species in the New Mexico fauna.

Culicoides leoni Group

Wirth and Blanton (1959) erected the *leoni* group for a small assemblage of species possessing almost bare wings. The distal portion of the wings is marked by two transverse rows of pale spots: one in line with the poststigmatic spot, the other with the distal pale spot in cell R_5. The antennal segments of the females are in 2 series: one from 3 to 10, the other from 11 to 15. Each series gradually increases in length from the proximal segment so that segment 11 is shorter than 10. Sensoria are located on segments 3, 7 or 8 to 10, there are 4 tibial spines and one spermatheca. The male genitalia have short claspette stems which may or may not possess mesal lobes.

17. **Culicoides reevesi** Wirth

(Figs. 94-98)

Culicoides reevesi Wirth, 1952, Univ. Calif. Pub. Ent. 9:193 (female; Calif.; fig. wing).

FEMALE—Length of wing 0.85 (0.82-0.88; n=2) mm.

Head: Eyes very narrowly separated, considerably less than diameter of a facet. Antenna with flagellomeres in proportion of 10:8:8:11:12:12:10:13:8:8:13:12:18; antennal ratio 0.65 (0.64-0.66; n=2); distal sensory tufts on segments 3, 8-10; segments 9+10 to 11 in ratio of 0.33 (0.31-0.34; n=2) (Fig. 98). Distal 4 palpal segments in proportion of 12:15:6:5; third segment only slightly swollen, 2.1 times as long as greatest breadth; sensory organ very deep (Fig. 95). Ratio of head length to proboscis 1.16. Mandible with 14-16 (n=3) teeth.

Thorax: Legs pale brown; fore and middle femora with subapical pale bands; all tibiae with subbasal pale bands, hind tibia with indistinct apical pale band. Hind tibial comb with 4 spines (Fig. 96).

Wing: (Fig. 94). Second radial cell in a dark area; spot on r-m crossvein extending from costa to vein M_{1+2}; poststigmatic spot large, extending almost to vein M_1; round spot in cell R_5 and spot in cell M_1 not attaining wing margin; pale spots in cells M_2 and M_4 attaining wing margin; spot in vannal cell extending along wing margin for almost entire length of cell; small spot in distal portion of cell M_1 on proximal portion of vein M_2; elongate pale area extending proximally from approximately fork of M_{1+2} and medio-cubital fork to arculus. Macrotrichia sparse, occurring only in distalmost portions of cells R_5, M_1 and M_2. Costa extending 0.56 (0.54-0.56; n=3) of length of wing.

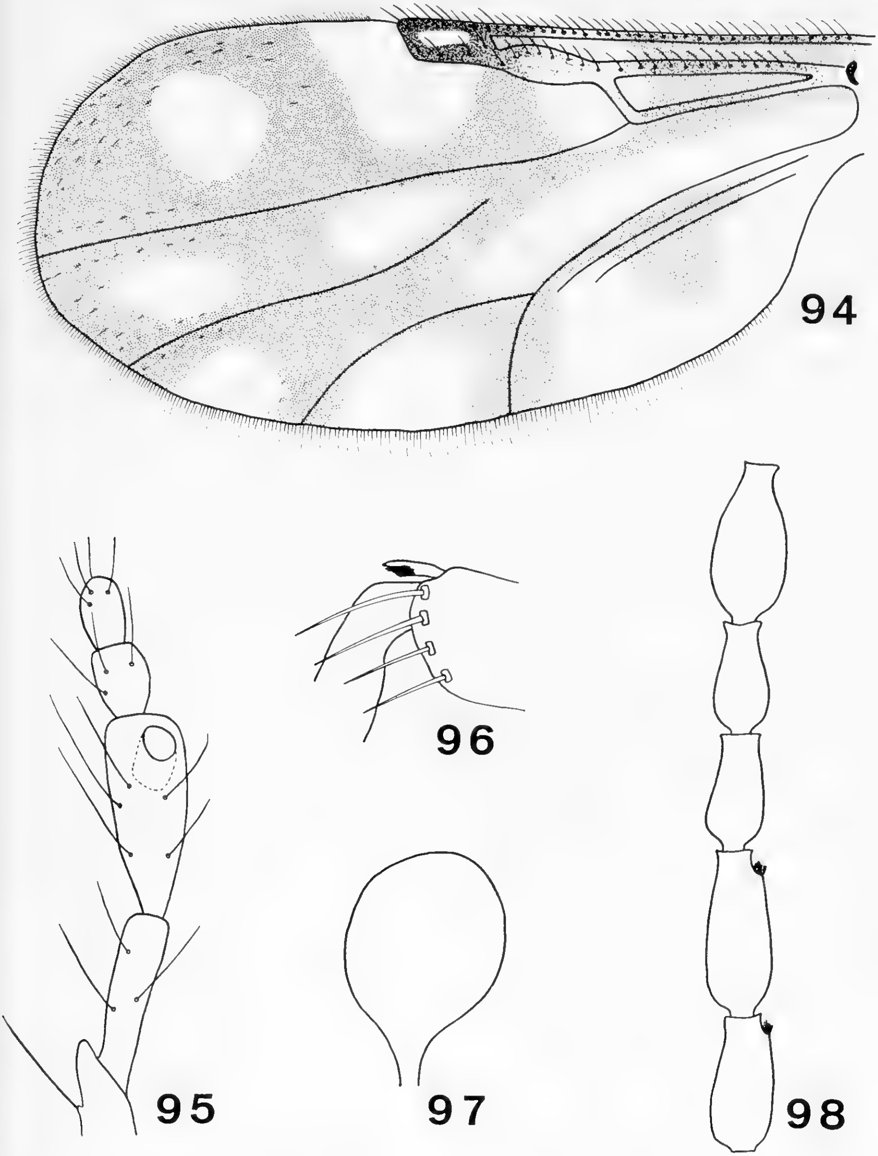
Abdomen: One subspherical spermatheca (Fig. 97) 56 x 36 μ; duct sclerotized for some distance.

MALE—Unknown.

DISTRIBUTION: This species has been reported from California, Arizona, and New Mexico. During this investigation it was taken at the following localities: Catron (5 mi. e. of Glenwood, 24 June 1953, W. W. Wirth, biting man), Grant (Cherry Creek near Pinos Altos, 22 June 1953, W. W. Wirth, biting man; Roberts Lake north of Silver City, 31 July 1965, W. R. Atchley, biting man) and Rio Arriba counties.

DISCUSSION: *Culicoides reevesi* is not closely allied to any other New Mexico species, but it is nearest to a group of neotropical taxa centered around *leoni* Barbosa.

The presence of a single spermatheca and the unusual shape of antennal segments 11 and 12 will readily separate this species.



Figs. 94-98. *Culicoides reevesi* Wirth. Female: 94, wing; 95, palpus; 96, tibial comb; 97, spermatheca; 98, antennal segments 9-13.

FEEDING HABITS: This is a man-biting species previously reported as attacking man in California. In New Mexico it has been collected biting man at three localities in the western portion of he state. My own records indicate that this species is probably crepuscular, attacking at approximately sunset.

Culicoides guttipennis Group

This group has females characterized by having the anterior half of the mesonotal disc with light markings on a dark background (except *ousairani,* which has the anterior half dull), well marked wings with macrotrichia abundant over most of the wing and 5 tibial spines. The male genitalia have basimeres with simple roots and the apicolateral processes of the ninth tergum are well developed. The claspettes are usually swollen mesally, tapering distally to more or less blunt points and lacking apical spines.

Vargas (1960) proposed the subgenus *Glaphiromyia* for this group of species.

18. **Culicoides pecosensis** Wirth

(Figs. 99-104)

Culicoides pecosensis Wirth, 1955, Wash. Acad. Sci. Jour. 45:358 (male, female; Texas; fig. wing, mesonotal disc, palp, male genitalia).

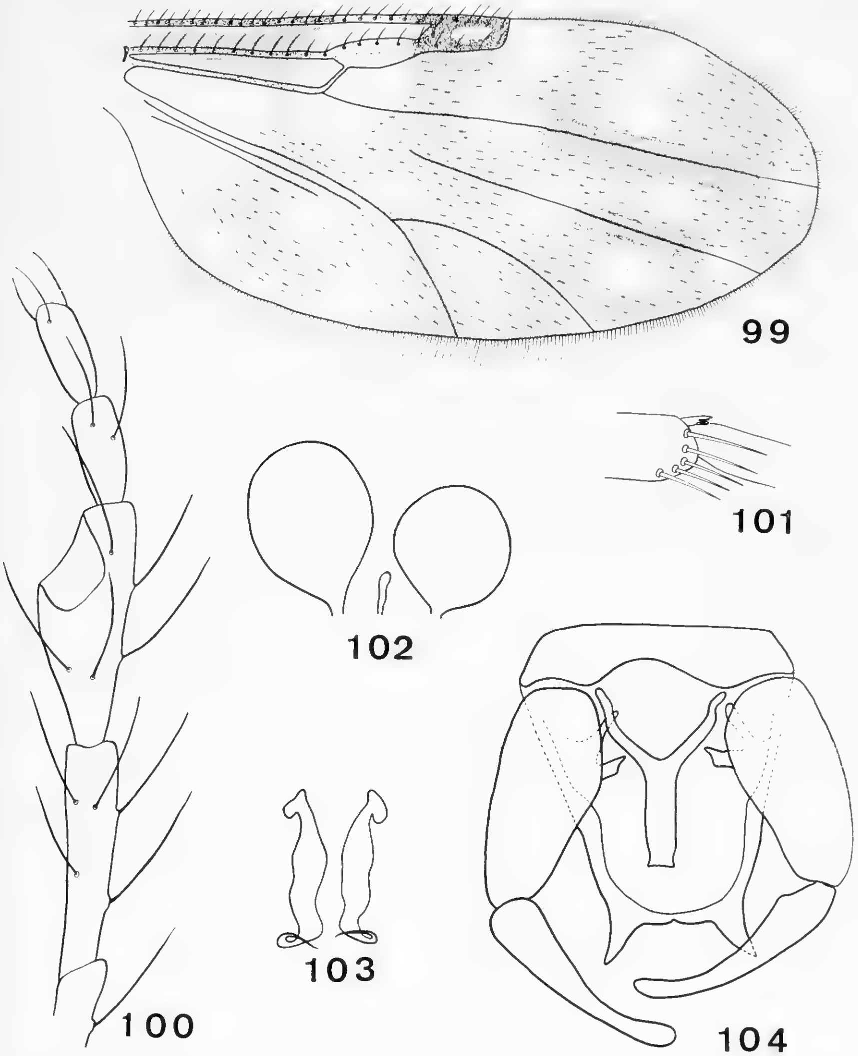
FEMALE—Length of wing 1.22 (1.17-1.34; n=6) mm.

Head: Eyes very narrowly separated to contiguous. Antenna with flagellomeres in proportion of 13:13:13:13:12:12:12:12:19:20:22:23:30; antennal ratio 1.25 (1.21-1.34; n=5); segments 9+10 to 11 in ratio of 0.81 (0.79-0.87; n=6); distal sensory tufts more or less irregular in occurrence, usually on segments 3-7, 9, 11-14. Distal 4 palpal segments in proportion of 23:26:11:10; third palpal segment moderately swollen, 2.48 (2.33-2.60; n=7) times as long as greatest breadth, with shallow sensory pore (Fig. 100). Ratio of head length to proboscis 0.93 (0.84-1.0; n=6). Mandible with 17-18 (n=6) teeth.

Thorax: Legs dark brown; femora with pre-apical pale bands; tibiae with subbasal pale bands, hind tibia with broad apical band. Hind tibial comb with 5 spines (Fig. 101).

Wing: (Fig. 99). Second radial cell in a dark area; spot over r-m crossvein large, extending from costa well beyond vein M_{1+2} where it joins another rather indefinite pale area in proximal portion of wing; poststigmatic spot small; cell R_5 with an elongate, mesally constricted spot; small round spots in distal portions of cell M_1 and M_2; pale spot extending posteriorly in M_4 from vein M_{3+4}; none of preceding spots attaining wing margin; 2 spots in distal portions on vannal cell; pale spot over vein M_1 immediately posterior of poststigmatic spot; a double spot bordering each side of mesal portion of vein M_2; a small spot over medio-cubital fork; apices of veins M_1, M_2 and M_{3+4} pale. Costa extending 0.54 (0.53-0.55; n=6) of entire wing length. Macrotrichia abundant over entire surface of wing.

Abdomen: Two slightly unequal spermathecae (Fig. 102) 57 x 42 and 47 x 35 μ; ducts sclerotized for a very short distance. Rudimentary spermatheca and ring present.



FIGS. 99-104. *Culicoides pecosensis* Wirth. Female: 99, wing; 100, palpus; 101, tibial comb; 102, spermathecae. Male: 103, claspettes; 104, genitalia, claspettes removed.

MALE—Description of genitalia based on male paratype (Figs. 103, 104). Ninth sternum with broad, shallow excavation. Ninth tergum narrowing posteriorly, with long prominent, triangular, apicolateral processes. Basimere with simple, prominent roots. Telomere slightly bowed, tapering apically. Aedeagus with extended, truncate median posterior process; aedeagal arms slender, straight but slightly sinuate basally; basal arch not markedly rounded, extending about 0.40 of entire length of aedeagus. Claspettes with strong postero-laterally directed bases; stems constricted immediately behind basal end, then greatly expanded, mesal portion of stem very stout, distal third of stem abruptly narrowed, apex contorted.

DISTRIBUTION: *Culicoides pecosensis* has been previously known only from Texas. This is the first recording of this species from New Mexico (Catron Co.).

DISCUSSION: Females of this species can be separated from the other members of the *guttipennis* group by the following characters: the anterior half of the mesonotum has a pattern of light and dark markings which are absent from *ousairani* Khalaf; a large spot on the r-m crossvein which in *pecosensis* extends well beyond vein M_{1+2}, barely extends beyond vein M_{1+2} in *villosipennis* Root and Hoffman; the pale spot which extends along vein Cu_1 posteriorly to the wing margin will distinguish *pecosensis* from *guttipennis* (Coquillett), *arboricola* Root and Hoffman and *oklahomensis* Khalaf. The male genitalia of *pecosensis* lack the subapical aedeagal processes of *villosipennis* and *oklahomensis* and the truncate aedeagus of *pecosensis* and *ousairani*, and are distinctly different from those of *guttipennis*.

19. **Culicoides oklahomensis** Khalaf

(Figs. 105-108)

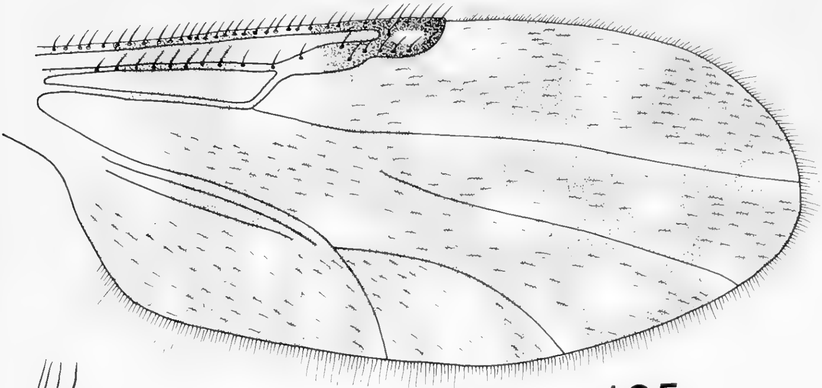
Culicoides villosipennis oklahomensis Khalaf, 1952, Ann. Ent. Soc. Amer. 45:355 (male; Oklahoma).
Culicoides oklahomensis Khalaf; Jones and Wirth, 1958, Jour. Kansas Ent. Soc. 31:82-85.

FEMALE—Length of wing 1.21 mm.

Head: Eyes narrowly separated, much less than diameter of a facet. Antenna with flagellomeres in proportion of 13:12:13:13:13:13:13:13:23:23:26:28:33, antennal ratio 1.29; distal sensory tufts present on segments 3, 5, 7, 9, 11-15; segments 9+10 to 11 in ratio of 0.82. Third palpal segment only slightly swollen (Fig. 106), 3.0 times as long as greatest breadth, with very shallow sensory pit. Ratio of length of head to proboscis 1.04. Mandible with 14 teeth.

Thorax: Fore and middle femora with broad, distinct pre-apical pale bands, hind femora with very faint pale pre-apical band, or band may be absent; all tibiae with subbasal pale bands, hind tibiae with large, distinctive pale bands. Hind tibial comb with 5 spines.

Wing: (Fig. 105). Second radial cell in a dark area; light spot on r-m crossvein large, extending from costa to slightly beyond vein M_{1+2}; poststigmatic spot small; an elongate mesally constricted spot in cell R_5; pale spots in cells M_1 and M_2 not attaining wing margin; pale spot in cell M_4 and distalmost spot in vannal cell attaining wing margin; pale spot on anterior surface of medio-cubital fork; pale spot crossing basal portion of vein M_1; pair of spots bordering vein M_2 slightly basad of its midlength; apices of veins



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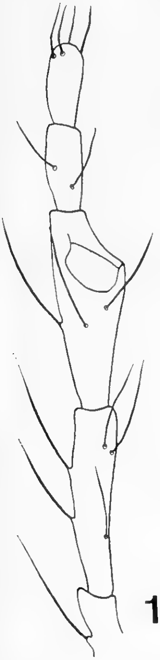

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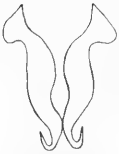

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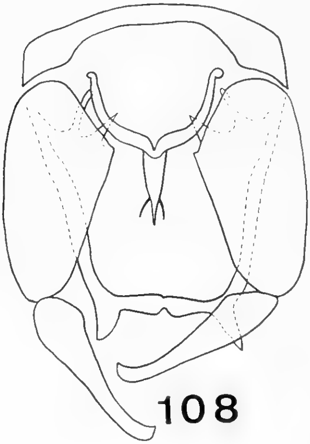

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Figs. 105-108. *Culicoides oklahomensis* Khalaf. Female: 105, wing; 106, palpus. Male: 107, claspettes; 108, genitalia, claspettes removed.

M_1, M_2, M_{3+4} and Cu_1 pale. Macrotrichia very abundant over entire surface of wing. Costa extending to 0.56 of distance to wing apex.

Abdomen: Two subequal spermathecae with very short ducts, 53 x 36 and 50 x 50 μ; rudimentary spermatheca and ring present.

MALE—Genitalia (Figs. 107, 108) with ninth sternum narrow with very broad, deep caudomedian excavation. Ninth tergum tapering, with prominent blade-like apicolateral processes; median posterior portion distinctly notched. Basimere with simple, slender, well developed roots, dorsal root longer than ventral root. Telomere tapering to a slender, slightly curved, tipped point. Median posterior process of aedeagus broad basally, extending to very narrow, pointed apex, bearing a pair of subapical filaments; aedeagal arms slender and arcuate, with small, knobbed bases; basal arch notched mesally, extending to approximately half of overall length of aedeagus. Claspette with expanded basal foot containing tapered anterior process; stem very swollen, sinuate, abruptly narrowing to slender, unmodified recurved apex.

DISTRIBUTION: Culicoides oklahomensis, originally described as a subspecies of *villosipennis*, occurs in the southwestern part of the United States and in Mexico. Within the United States it has been reported from Oklahoma, Texas and Arizona. During this investigation *oklahomensis* was collected in Catron Co., New Mexico.

DISCUSSION: Males of this species can be separated from most others of the *guttipennis* group by the presence of lateral projections of the aedeagus. The only other species of the *guttipennis* group with such projections is the eastern *villosipennis* Root and Hoffman. The male genitalia of these two species can be distinguished by the shape of the claspettes. The females of *oklahomensis* can be recognized by the sensorial pattern, the large pale spot over the r-m crossvein and the pale border of vein Cu_1.

Culicoides palmerae Group

This group, composed of *palmerae, utahensis,* and *novamexicanus,* has male genitalia characterized by very prominent apicolateral processes of the ninth tergum, strongly bent distal two-thirds of the telomere, broad aedeagus, and the well developed basal portions of the claspettes and roots of the basimeres. The females have a swollen third palpal segment, widely separated eyes, banding pattern on the legs very faint or absent and wings with dense macrotrichia.

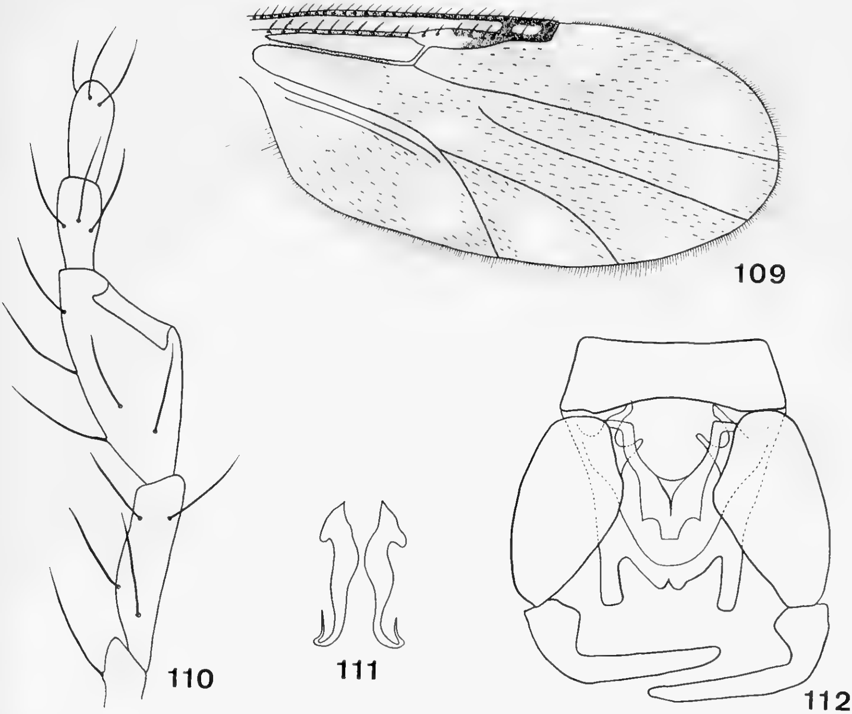
20. **Culicoides palmerae** James

(Figs. 109-112)

Culicoides palmerae James 1943, Pan-Pacific Ent. 19:151 (male, female; Colorado; fig. male genitalia).

FEMALE—Length of wing 1.48 (1.34-1.69; n=3) mm.

Head: Eye separation approximately equal to diameter of a facet. Antenna with flagellomeres in proportion of 12:9:9:9:10:10:11:12:18:18:22:23:33; antennal ratio 1.28 (1.18-1.43; n=3); distal sensory tufts on segments 3-15; segments 9+10 to 11 in ratio of 0.77 (0.75-0.78; n=2). Distal 4 palpal segments in proportion of 20:26:11:12; third palpal segment swollen (Fig. 110), 2.26 (2.07-2.45; n=3) times as long as greatest breadth, with broad, rather shallow sensory pore. Ratio of head length to proboscis 1.02 (0.89-1.15; n=4). Mandible with 14 teeth.



Figs. 109-112. *Culicoides palmerae* James. Female: 109, wing; 110, palpus. Male: 111, claspettes; 112, genitalia, claspettes removed.

Thorax: Legs brown; knees dark; tibiae with faint subbasal pale rings. Hind tibial comb with 4 spines.

Wing: (Fig. 109). Wing pattern indistinct; second radial cell in a dark area; pale spot over r-m crossvein, extending slightly posterior of vein M_{1+2}; poststigmatic spot small; an elongate, rather indistinct pale spot in distal portion of cell R_5; indistinct pale spots in cells M_1, M_2, M_4 and vannal cell, all attaining wing margin; medio-cubital fork in dark area. Costa extending 0.56 (0.55-0.57; n=3) of total length of wing. Macrotrichia abundant over entire surface of wing.

Abdomen: Two elongate, subequal spermathecae 76 x 39 and 76 x 43 μ; ducts not sclerotized; rudimentary spermatheca and ring present.

MALE—Description of male genitalia (Figs. 111, 112) based on male paratype from Ft. Collins, Colo. Ninth sternum with slight caudomedian excavation; membrane bare. Ninth tergum narrowing slightly posteriorly; posterior border very convex, with distinct mesal notch; apicolateral processes long, prominent, truncate. Basimere tapering distally; roots long, slender, subequal. Telomere strongly bent at approximate basal third, abruptly narrowed at bend, of more or less uniform width to apex. Aedeagus with median posterior process broad, with subapical lateral shoulders bearing posterior spines, apex truncate; adedeagal arms widely divergent basally, with prominent, laterally directed basal ends, arms slightly arcuate mesally, converging posteriorly; basal arch rounded, extending to about midlength of aedeagus. Claspettes with swollen bases; stems swollen basally, tapering posteriorly, apex strongly bent laterad then cephalad; apex with a few microscopic hairs.

DISTRIBUTION: Culicoides palmerae has previously been reported from the northwestern portions of the United States. Its range extends from Nebraska southwestward to California and northwestward to British Columbia. These first records from Sandoval and Taos counties in New Mexico constitute its southernmost known occurrence.

DISCUSSION: This species is very similar to *utahensis* Fox but may be separated from it by a moderately swollen third palpal segment with a broad pit. The wing pattern of *palmerae* is distinctly marked, as opposed to the poorly marked wing of *utahensis*. The presence of lateral shoulders on the aedeagus and slender claspettes will readily distinguish the males. For separation from *novamexicanus* n. sp., see discussion of that species.

21. **Culicoides utahensis** Fox

(Figs. 113-115)

Culicoides utahensis Fox, 1946, Ent. Soc. Wash. Proc. 48:246 (male; Utah; fig. male genitalia).

FEMALE*—Length of wing 1.43 mm.

Head: Eyes widely separated. Antenna with flagellomeres in proportion of 13:10:10:10:10:11:11:12:18:18:20:21:25; antennal ratio 1.12; distal sensory tufts present on segments 3-15; segments 9+10 to 11 in ratio of 0.75. Distal 4 palpal segments in proportion of 12:26:9:12; third palpal segment greatly swollen (Fig. 113), 1.85 times as long as greatest breadth, with deep sensory pit. Ratio of head length to proboscis 1.30. Mandible with 14 teeth.

Thorax: Legs dark brown. Hind tibial comb with 4 spines.

Wing: The following description is taken from Wirth (1952): "Wings grayish hyaline, anterior radial cells in a very dark spot, distinct light costal spots at r-m crossvein and at apex of second anterior radial cell, other light spots variable and indistinct, in well marked specimens with large light spots at tips of cells R_5, M_1, M_2, M_4 and anal cells, and large light areas at base of anal cell and in middle of wing between veins M_{1+2} and Cu_1. Wings with abundant long yellowish macrotrichia over entire surface." Costa extending 0.55 of total length of wing.

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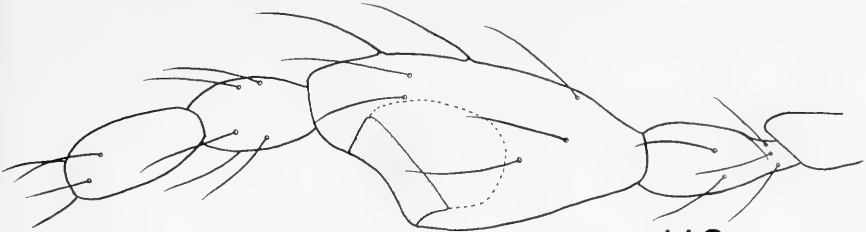
* No females of this species were collected during this study. The description was based on specimens collected from ears of rabbits at Battle Mountain, Nevada.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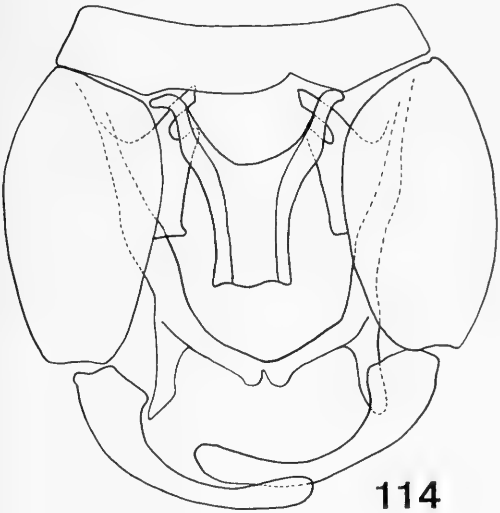
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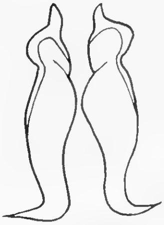
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FIGS. 113-115. *Culicoides utahensis* Fox. Female: 113, palpus. Male: 114, genitalia, claspettes removed; 115, claspettes.

Abdomen: Two subequal spermathecae 59 x 49 and 66 x 43 μ; ducts sclerotized for a very short distance. Rudimentary spermatheca and ring present.

MALE—(Figs. 114, 115). Genitalia very large. Ninth sternum with slight caudomedian excavation, membrane bare. Ninth tergum only slightly tapering posteriorly; caudal portion convex, with prominent mesal notch; apicolateral processes long and distinct, of uniform width for most of length. Basimere rather short, slightly tapering posteriorly with large distinct mesal shelf on basal half, shelf more or less flat posteriorly; short ventral root and long, slender, mesally blunt dorsal root. Telomere swollen basally, sharply bent at basal third, apical two-thirds narrowed, approximately uniform width for remainder of length. Aedeagus very stout; median posterior process broad, truncate, with slightly sinuate apex; aedeagal arms short, with laterally directed bases; basal arch rounded, extending only about 0.35 of length of aedeagus. Expanded base of claspette with curved anterior process; stem strongly swollen basally, tapering to laterally turned, lancolate apex.

DISTRIBUTION: Previous records of *utahensis* indicate that it is limited to far western portions of the United States, having been reported from Utah, Nevada and California. The discovery of this species in the mountainous region of southern New Mexico (Lincoln Co., male) represents its easternmost record.

DISCUSSION: The high incidence of males with female head parts in this species has prompted considerable discussion. Downes (1958) discussed this phenomenon at some length and suggested the possibility of more than one species being included under the name *utahensis.* Both sexes of this species have been taken from the ears of jackrabbits on numerous occasions, and the males taken in this fashion have antennae and palps of the female type. This modification is assumed to assist the males in locating the host of the female and thereby facilitate mating. Copulation is probably initiated by contact. The modification of the head structures of the males of this species may represent evolution toward parasitism, instead of the predatory behavior exhibited by most other species of *Culicoides.*

So far as known all male representatives of this species from New Mexico have female head parts.

See discussion of *palmerae* and *novamexicanus* n. sp. for characteristics sufficient to distinguish these species.

22. **Culicoides novamexicanus** new species

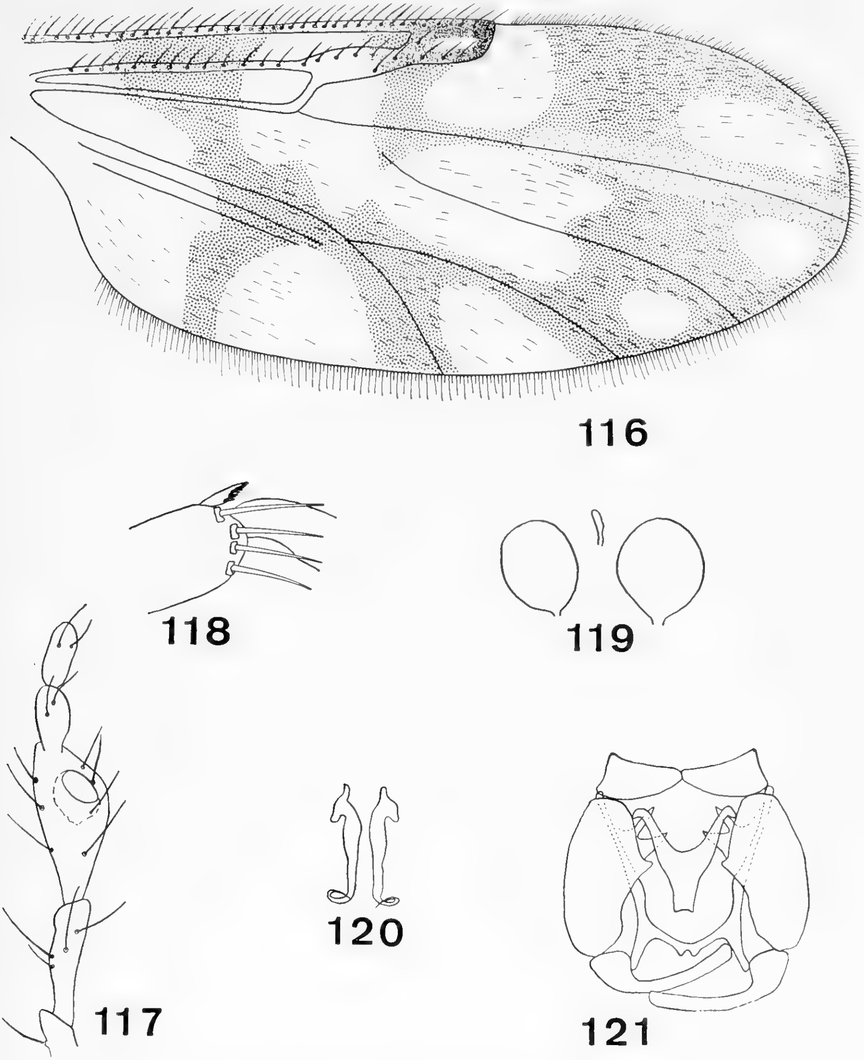
(Figs. 116-121)

FEMALE—Length of wing 1.23 (1.13-1.36; n=3) mm.

Head: Eyes separated about diameter of a facet. Antenna with flagellomeres in proportion of 13:10:10:10:10:10:11:12:15:16:18:18:25; antennal ratio 1.02 (0.98-1.05; n=3); distal sensory tufts on segments 3-5, 7, 9, 11, 13-15, occasionally absent on segment 4 or present on 6 or 12; segments 9+10 to 11 in ratio of 0.58 (0.55-0.60; n=3). Distal 4 palpal segments in proportion of 21:28:12:13; third palpal segment swollen (Fig. 114), 2.12 (2.0-2.2; n=3) times as long as greatest breadth; sensory pit moderately deep. Ratio of head length to proboscis 1.04 (1.01-1.06; n= 3). Mandible with 14-16 (n=3) teeth.

Thorax: Legs brown; tibiae with very faint, narrow subbasal pale rings. Hind tibial comb with 4 spines (Fig. 118).

Wing: (Fig. 116). Second radial cell in a dark area; poststigmatic spot large, bounded posteriorly by vein M_1; pale spot on r-m crossvein large, extending from anterior wing margin well beyond vein M_{1+2}, connecting with large pale area in proximal portions of cells M_1 and M_2; pale spot in cell M_4 and distalmost spot in vannal cell broadly joining wing margin; 2 large pale spots in proximal portions of cells M_1 and M_2 broadly encompassing basal half of vein M_2; basal portion of vannal cell and extreme basal area



FIGS. 116-121. *Culicoides novamexicanus*, new species. Female: 116, wing; 117, palpus; 118, tibial comb; 119, spermathecae. Male: 120, claspettes; 121, genitalia, claspettes removed.

of cell M_2 in pale area; mediocubital fork in dark area; distal ends of veins M_1, M_2 M_{3+4} and Cu_1 dark. Macrotrichia abundant over entire surface of wing. Costa extending 0.56 (0.55-0.57; n=3) of length of wing.

Abdomen: Two subequal spermathecae (Fig. 119) 69 x 46 and 56 x 43 μ; ducts sclerotized for a very short distance; rudimentary spermatheca present. MALE—(Figs. 120, 121). Genitalia with ninth sternum divided; narrow, shallow, pointed caudomedian emargination. Ninth tergum tapering;

postero-medial portion convex, with prominent notch; apicolateral processes distinctly long and fingerlike. Basimere with dorsal and ventral roots subequal in size, without processes; dorsal root more slender than stout ventral root. Telomere swollen basally, abruptly bent and narrowed at approximately one-third of length from base, continuing at more or less uniform width to apex. Aedeagus stout; median posterior process conical, truncate; aedeagal arms strong, diverging anteriorly, basal portion of each turned posterolaterally to give footlike appearance; basal arch rounded, extending to approximately half length of aedeagus. Claspette with prominent foot-shaped base, with microscopic fringe of lateral spines on anterior "toe" portion; stem stout basally but tapering to slender, helical apex.

DISTRIBUTION: Chaves County, New Mexico.

Specimens examined: Holotype male, Pecos River, 7 mi. e. of Roswell, New Mexico, 14 June 1965, W. R. Atchley, at light. Allotype female and 3 female paratypes, same data.

DISCUSSION: *Culicoides novamexicanus* can be separated from *palmerae* by the sensorial pattern, smaller antennal ratio, lack of lateral projections on the aedeagus and the slender, simple claspettes; and from *utahensis* by the widely separated eyes, sensorial pattern, more extensive pale markings on the wings, the slender aedeagus and aedeagal arms and the characteristic claspettes.

Culicoides piliferus Group

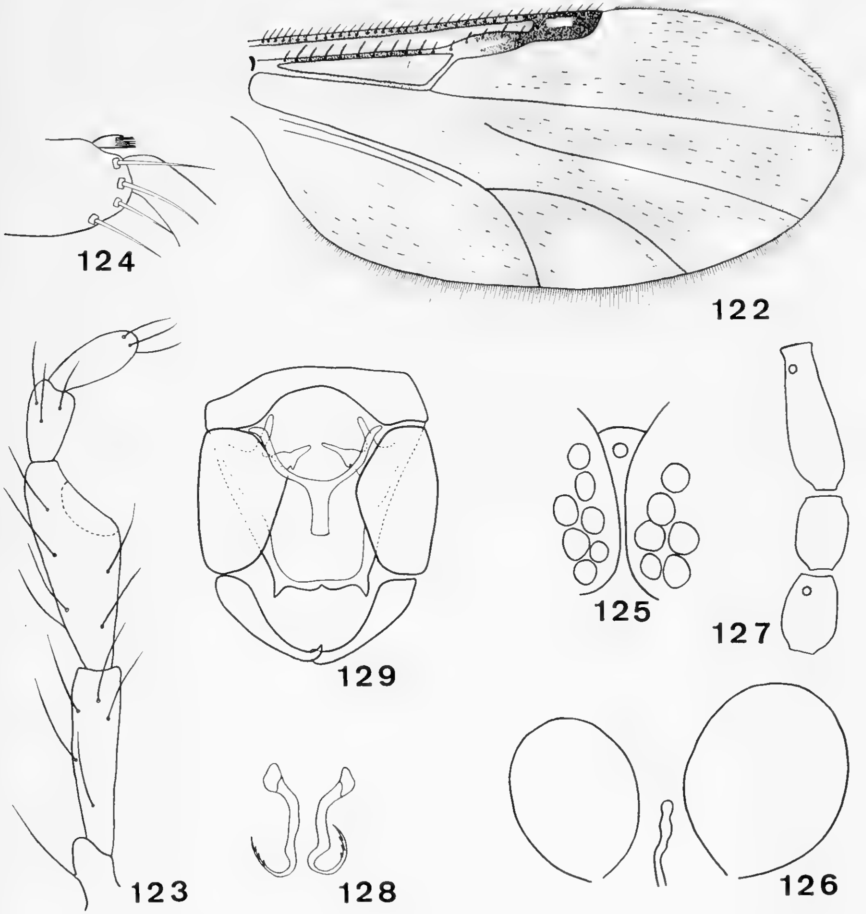
The wings of the females of the *piliferus* group usually have pale spots straddling the midportions of veins M_1 and M_2; however, the pattern is sometimes very reduced. The sensoria are found on segments 3, 5, 7, 9, 11-15 in the generalized condition, but may be reduced to the distal flagellomeres in some species. The eyes are contiguous to moderately separated and hind tibial comb possesses 4, occasionally 5, spines. The spermathecae are subequal to very unequal in size and usually lack necks. The ventral root of basimere is foot-shaped and the claspettes taper to a fine tip with a lateral fringe of spines.

23. **Culicoides doeringae** new species

(Figs. 122-129)

FEMALE—Length of wing 1.24 (1.13-1.34; n=14) mm.

Head: Eyes narrowly separated (Fig. 129); in holotype, separation approximately equal to width of median hair socket. Antenna with flagellomeres in proportion of 13:8:8:8:8:8:9:9:22:23:23:23:35; antennal ratio 1.63 (1.48-1.73; n=14), segments 9+10 to 11 in ratio of 1.11 (1.0-1.27; n=14) (Fig. 126); distal sensory tufts on segments 3, 5, 7, 9, 11, 13-15, occasionally also on 12. Distal 4 palpal segments in proportion of 22:23:10:9; third segment moderately broad (Fig. 123), 2.61 (2.3-2.87; n=12) times as long as



FIGS. 122-129. *Culicoides doeringae,* new species. Female: 122, wing; 123, palpus; 124, tbial comb; 125, spermathecae; 126, antennal segments 9-11; 127, interocular space. Male: 128. claspettes; 129, genitalia, claspettes removed.

greatest breadth, with shallow sensory pit. Ratio of head length to proboscis 1.12 (1.03-1.20; n=12). Mandible with 12-15 (n=12) teeth.

Thorax: Legs brown; fore and middle femora with pre-apical pale bands, all tibiae with subbasal pale bands. Hind tibial comb with 4 spines (Fig. 124).

Wing: (Fig. 122). Second radial cell in a dark area; small round spot over r-m crossvein barely extending beyond vein M_{1+2}; poststigmatic spot small; pale spot in distal portion of cell R_5; pale spots in distal portions of cells M_1, M_2 and M_4 all attaining wing margin; spot in distal portion of vannal cell variable, usually large, round anteriorly, mesally constricted in many specimens, with posterior portion either expanded or, as in holotype, extended to wing margin in same width as mesal constriction; pale spot on vein M_1 immediately behind poststigmatic spot; pale spot near mid-length of vein M_2; a rather elongate pale area bounded posteriorly by mediocubital fork extending anteriorly almost to veins M_{1+2} and M_2. Costa extending 0.58 (0.56-0.59; n=14) of wing length. Macrotrichia abundant over entire surface of wing.

Abdomen: Two very unequal spermathecae (Fig. 125) 76 x 56 and 56 x 39 μ, ducts unsclerotized; rudimentary spermatheca and ring present.

MALE—Genitalia (Figs. 128, 129) with ninth sternum possessing deep caudomedian excavation. Ninth tergum with small, triangular apicolateral processes, mesal notch distinct. Basimere tapering slightly; ventral root triangular, with definite "heel-like" process on mesal margin; dorsal root long, slender. Telomere with swollen base, narrowing distally to mesally tipped apex. Aedeagus with long, parallel-sided, truncate median posterior process; aedeagal arms slightly knobbed basally, arcuate mesally; basal arch gently rounded, extending approximately 0.45 length of aedeagus. Claspettes distinctly knobbed basally; stems sinuate, gradually diminishing toward tip, with a fringe of apical spines.

DISTRIBUTION: New Mexico (Catron, Lincoln and Otero Counties) and Arizona.

Specimens examined: Holotype female, Catron Co., Glenwood Fish Hatchery, 2 Aug. 1965, W. R. Atchley, at light. Allotype male, Lincoln Co., Alto Reservoir, 16 June 1965, W. R. Atchley, at light. Paratypes: 18 females, same data as holotype; 1 male, 2 females, same data as allotype; 4 males, 9 females, Lincoln Co., Ruidoso, Cedar Creek Canyon, 16 June 1965, W. R. Atchley, at light; 5 females, Otero Co., Silver Creek Canyon, 28 July 1965, W. R. Atchley, at light. Additional specimens examined: 2 females, Coconino Co., Oak Creek Canyon, Arizona, 22 July 1959, C. W. O'Brien; 1 female, Cochise Co., Southwest Research Station, Arizona, 1 Aug. 1964, D. R. Davis; 1 female, Cochise Co., Chiricahua Mts., 2 mi. n. of Paradise, Arizona, 6 July 1964, D. R. Davis.

DISCUSSION: Culicoides doeringae belongs to the *piliferus* group and is probably most closely related to the eastern *piliferus* Root and Hoffman. These two species may be differentiated by the slightly smaller antennal ratio, the greater ratio of antennal segments 9+10 to 11 and the sensoria pattern 3, 5, 7, 9, 11, 13-15 in *doeringae*.

Atchley and Wirth (1967) have given characters sufficient to distinguish *doeringae* from *riggsi* Khalaf, another southwestern species of the *piliferus* group.

It gives me great pleasure to name this species for Dr. Kathleen C. Doering, Professor Emerita of insect morphology at the University of Kansas.

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ERRATUM

In the paper by F. J. Rohlf and R. R. Sokal, "Coefficients of correlation and distance in numerical taxonomy," *University of Kansas Science Bulletin,* vol. XLV, No. 1, pp. 3 to 27, Figures 9 and 10 were inadvertently interchanged. Thus Figure 9 is above the legend of Figure 10, while Figure 10 appears above the legend for Figure 9.

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