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VOL. 134

"Every man is a valuable member of society who, by his observations, researches, and experiments, procures knowledge for men"—James Smithson

(Publication 4311)

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Leonard Carmichael,
Secretary, Smithsonian Institution.

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VOLUME 134, NUMBER 1

Roebling Fund

PERIODS RELATED TO 273 MONTHS OR 22-3/4 YEARS

By
C. G. ABBOT
Research Associate, Smithsonian Institution

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PERIODS RELATED TO 273 MONTHS OR 22¾ YEARS

By C. G. ABBOT
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This period was discovered in the variation of the measures of the solar constant of radiation, made daily by the Smithsonian Astrophysical Observatory from 1920 to 1952. It was first glimpsed in 1935,[1] and noted in various terrestrial phenomena, such as temperatures, precipitation, width of tree rings, and levels of lakes. The level of Lake Huron, since 1837, has followed related periods of about 23, 46, and 91 years. I ventured, in 1938, to predict droughts during the 1950's, the 1970's, and the 2020's, based on recurring periodic depressions of the level of Lake Huron. The first of these predictions is now verified.

1. PERIODS FOUND IN SOLAR-CONSTANT MEASUREMENTS

The "solar constant of radiation" is the term in use to describe quantitatively the intensity of the sun's radiation, as it would reach points in space outside the earth's atmosphere, at the earth's mean distance from the sun.

Smithsonian measurements over many years, made at stations ranging from sea level to 14,400 feet altitude, and supplemented by automatic records at 15 miles of elevation from sounding balloons, yield as the value of the solar constant 1.946 calories per square centimeter per minute. A recent revision by F. S. Johnson,[2] in which he used the latest data from high rocket flights to improve the Smithsonian estimates in the extreme ultraviolet spectrum, yielded the value 2.00 cal. ± 0.04 cal. His value differs from the Smithsonian value by little beyond the probable error of either one. For purposes of estimating solar periodic variations, this small difference as to the basic value is inconsequential.

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[1] C. G. Abbot, Solar radiation and weather studies, Smithsonian Misc. Coll., vol. 94, No. 10, 1935.

[2] Journ. Meteorol., vol. 11, No. 6, December 1954.

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What is important for the proof of variation is the accidental error of Smithsonian daily observations of the solar constant. There are several determinations of it. From volume 6 of the Annals of the Smithsonian Observatory, page 163, I quote the differences, in thousandths of a calorie, between daily values of the solar constant obtained at Smithsonian stations in the Northern and the Southern Hemispheres, respectively. This comparison covered all days observed in both hemispheres for the years 1932 to 1936, numbering 616.

TABLE 1.—*Numbers of daily differences in solar-constant measures, 1932 to 1936, having different amplitudes.*

Amplitudes in thousandths of a calorie.

Amplitudes	22–28	20–22	18–20	16–18	15	14	12	11	10
No. of days	17	12	10	35	13	15	20	22	27
Product	391	252	190	595	195	210	240	242	270

Amplitudes	9	8	7	6	5	4	3	2	1	0
No. of days	34	30	35	43	51	55	55	37	48	35
Product	306	240	245	258	255	220	165	74	48	0

Total days 616. Total of products 4,682.
Weighted mean daily difference, 7.60 thousandths of a calorie.

Mrs. Hill has made for me similar tables for more recent differences between daily solar-constant results, where measures at Montezuma, Chile, are compared to those of Table Mountain and Tyrone in the United States, and those at Table Mountain, Calif., to those at Tyrone, N. Mex. For these three cases the weighted mean differences are 7.68, 7.96, and 7.79 thousandths of a calorie. These results cover all days measured at both stations from 1940 to 1952. They number, respectively, 891, 283, and 202 days. The weighted mean difference is 7.75 thousandths calorie. As the results of these recent years differ but slightly from those of 1932 to 1936 shown in table 1, we may adopt 7.7 thousandths of a calorie as the weighted mean average daily accidental difference between results of widely separated stations observing the solar constant. Assuming the stations to be of equal accuracy, that gives for the percentage accidental error of a solar-constant measure of one day at one station:

$100 \times 0.00385 \times 0.84 \div 1.946 = 0.166$, or ⅙ percent of the solar constant.

I use 10-day and monthly solar-constant values in my investigations. For these the percentage probable error (if all days of these intervals were observed) becomes $\frac{1}{6} \div \sqrt{10}$ and $\frac{1}{6} \div \sqrt{30}$, or $\frac{1}{19}$ and $\frac{1}{33}$ percent of the solar constant.

A single supposed periodic appearance from mean monthly data, with an amplitude four times as great, or $\frac{4}{33}$ percent, would have some claim to veridity. Using monthly means from 1924 to 1952, 348 in number, all periods shorter than 45 months would have 8 or more repetitions. The criterion for probable veridity would be a percentage range exceeding $\frac{4}{33} \div \sqrt{8} = \frac{1}{23}$ percent of the solar constant for a 45-month period. The requirement decreases as the square root of the number of repetitions increases. Thus for a period of $4\frac{1}{3}$ months, my shortest used in syntheses, it would be $\frac{1}{72}$ percent. The $\frac{1}{23}$ percent of the solar constant is 0.0008 calories.

RANGES OF PERIODS IN SOLAR-CONSTANT MEASURES, WHICH ARE ALIQUOT PARTS OF 273 MONTHS

In my paper "Periodic Solar Variation,"[3] I list in table 2 64 periods. They range in amplitude as follows:

TABLE 2.—*Ranges of periods discovered, in percentage of the solar constant*

Periods in months	136.5–45	39–25	23–15	14–10	10–6	5–4.5
Number	5	5	5	5	5	5
Amplitudes, %	0.09–0.18	0.05–0.21	0.03–0.08	0.02–0.11	0.06–0.13	0.02–0.08
Periods in months	4.4–3.7	3.5–2.9	2.7–2.4	2.1–1.7	1.7–1.3	<1.3
Number	5	5	5	5	5	9
Amplitudes, %	0.03–0.06	0.03–0.04	0.02–0.08	0.02–0.04	0.02–0.04	>0.02

All these 64 periods, so far as ranges of amplitude indicate, fall within the criterion for veridity based on accidental error of observation.

OTHER EVIDENCES OF VERIDITY

Referring again to the last-cited paper, figures 1 and 2 therein show how the curves of observed periods which are aliquot parts of 273 months stand out more and more plainly, as superriding periods whose lengths are also aliquot parts of 273 months are removed. Figure 3 of that paper shows how strongly the smoothed curves resemble sine curves when cleared of such superriders.

Still more convincing indications of the veridity of a large number of the periods found in solar-constant measures will appear in following sections, as we note how periods in quite different phenomena are identical with them.

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[3] Smithsonian Misc. Coll., vol. 128, No. 4, 1955.

2. PERIODS RELATED TO 273 MONTHS FOUND IN WEATHER

In an important paper published in 1947,[4] I discovered, both in solar variation and in Washington temperature departure from normal, a period of 6.6456 days. This solar periodic variation recurred with perfect regularity in its phases from 1923 to 1944. The Washington periodic variation in temperature departures, though frequently out of phase, yet for any single month of the 12 months of the year in the entire interval from 1910 to 1945 averaged exactly the same length as the sun's variation, namely 6.6456 days. I did not then understand why phase changes occurred from time to time in Washington temperature departure. It is now quite clear to me, as will appear below.

Not until 1953 did I perceive that this period of 6.6456 days, so strongly evidenced, belongs to the family of submultiples of 22¾ years. For 22¾ × 365.2564 days = 8309.5831 days. Dividing by 6.6456, we have 1250.38, or within 1/30 percent of 1250. So it is probably an exact submultiple of 273 months, to an accuracy far beyond the precision of the data.

In the years 1952 to 1955 I published eight papers on the control of weather by the family of periods related to 273 months.[5]

Before particularizing these weather investigations, I wish to emphasize that they stand entirely on meteorological records. Meteorologists are apt to say that the variations of the sun are too small to influence terrestrial weather appreciably. But solar-variation measures play no part in my studies just cited. The periodicities in weather which relate to 273 months are to be found in weather records themselves. No further reference to solar measures is required. Periodic variations in precipitation are large. They range from 5 to 25 percent of normal for the individual periodicities. In temperature departures they range up to 5° F.

These large periodic changes of weather related to 273 months lie buried in the published records and may be demonstrated from them. No reference to solar variation is required to find them.

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[4] The sun's regular variation and its large effect on terrestrial temperatures, Smithsonian Misc. Coll., vol. 107, No. 4, 1947.

[5] Periodicities in the solar-constant measures, Smithsonian Misc. Coll., vol. 117, No. 10, 1952; Important interferences with normals in weather records, associated with sunspot frequency, ibid., No. 11, 1952; Solar variation and precipitation at Peoria, Illinois, ibid., No. 16, 1952; Solar variation and precipitation at Albany, N. Y., ibid., vol. 121, No. 5, 1953; Long-range effects of the sun's variation on the temperature of Washington, D. C., ibid., vol. 122, No. 1, 1953; Solar variation, a leading weather element, ibid., No. 4, 1953; Sixty-year weather forecasts, ibid., vol. 128, No. 3, 1955; Periodic solar variation, ibid., No. 4, 1955.

These periodicities in weather cannot be satisfactorily demonstrated without attending to several steps made necessary by changes of the atmosphere.

1. Normals and departures must be separately tabulated for times of high Wolf sunspot numbers, and of low Wolf numbers. I am accustomed to drawing the line at 20 Wolf numbers.

2. For all the shorter periods (i.e., <15 months) the months of the year must be used in several separate groups because atmospheric conditions differ. I am accustomed to dividing the year into three groups: January-April, May-August, September-December. I omit this grouping after periods of 15 months. Beyond that, too few columns would generally be available in a tabulation, and the division of the year into several groups is less important compared to the length of periods. The division of data into three groups mentioned above indeed leaves the tables with too few columns to yield satisfactory means. Therefore I make the assumption that the form and amplitude of periods in different seasons will be sufficiently similar to permit combination of six separate tables for the three seasons and two ranges of Wolf numbers into one by shifting them all to a common phase. But when such a combined table is used in a synthesis its general mean must always be restored to the proper phase in the synthesis.

3. As the earth is copiously bombarded with solar ions when sunspots are numerous, and these ions act to produce haze in the atmosphere, it is also necessary to separate tabulations for high and low Wolf numbers. I am accustomed to drawing the line at 20 Wolf numbers.

4. As the growth and shifting of populations and the invention of new devices, such as automobiles and airplanes, operate to alter the atmosphere, it is necessary to make a division of data for this. I am accustomed to drawing the line at the year 1900. That is not really adequate, but perfection is beyond reach, for with 23 periods to be synthesized, the precautionary measures mentioned above require 186 tables to be used.

5. As there are many periods, all exact aliquot parts of 273 months, it follows that most tabulations for a selected period are encumbered by shorter periods, exact aliquot parts of the period tabulated. I am accustomed to plotting the mean result of such a tabulation, scanning the graph for superriders, and, one after another, computing form and amplitude of these superriding periods, and removing them by subtraction till the wanted period stands out alone.

SOME RESULTS OF STUDIES OF WEATHER PERIODS

"Sixty-year Weather Forecasts," my Saint Louis precipitation paper, may be thought to have a sensational title. Critics are apt to say that when I use all the monthly mean values of precipitation at Saint Louis from 1854 to 1939 as a basis to determine the form and amplitude of 23 periods, no part of the synthesis of them between these dates is a forecast. On the contrary, 1,032 months are used to determine the features of these periods. No year has more than 12 months. Hence the form and amplitude of the curve representing the march of precipitation in any one year between 1854 and 1939 can have no more than $\frac{12}{1032} = 1.2$ percent influence on that year's curve. Therefore, each year's march of precipitation between 1854 and 1939 is *practically* an *independent* forecast. After 1939, up to 1957 when my synthesis ends, all years are *completely independent* forecasts. As the halfway point between 1854 and 1939 is the year 1897, forecasts may be regarded as made from 1897.

Thus, speaking approximately, every year from 1854 to 1957 is forecasted as if from 1897. As a fair specimen of such forecasts, I cite from "Sixty-year Weather Forecasts": figure 1 (here fig. 1), a facsimile of the 5-year Saint Louis forecast, 1875-1879; figures 2, 3, and 4 (here fig. 2), comparing forecasts with events for 6-year intervals, 1934-1939 in percentages of normal in the precipitation at Peoria and Saint Louis, and in the temperature departures from the normal at Washington, D. C.; and figure 5 (here fig. 3), comparing synthesis and event for Saint Louis precipitation, 1860-1887. Finally, I cite figure 6 (here fig. 4), comparing predictions for 1952-1957 of precipitation at Saint Louis and Peoria, prepared, of course, from wholly independent data. The predictions are in effect based on the year 1897, the halfway point between 1854 and 1939, which were the extremities of the basic interval employed. These two stations, Saint Louis and Peoria, are about 100 miles apart. Their 60-year forecasts run almost parallel. Both indicate the approach in 1952, waxing, maximum severity in 1956, and probable end of the drought in 1957.

The tabulation of Saint Louis precipitation for 104 years (1,248 months) is preserved at my home in a roll 25 columns wide, 1,248 lines long, and about 20 feet from end to end. Comparing its two curves of synthesis and event for 100 years, 1854-1954, 70 of the 100 years were of the same degree of similarity in time, form, and amplitude of range, shown by figure 3 of the present paper. In the other 30 years the features of the parallel curves were similar, but

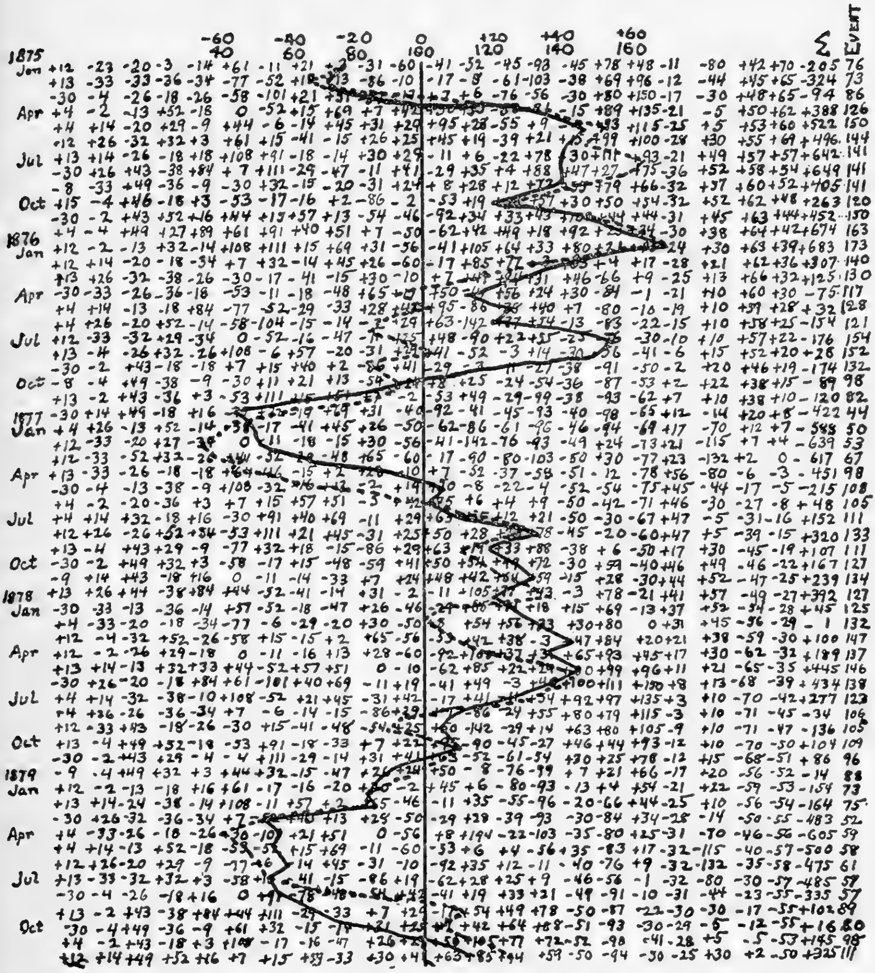

FIG. 1.—Facsimile of computation of St. Louis precipitation, 1875-1879, compared with the observed precipitation as percentage of normal. Data from monthly mean precipitation smoothed by 5-month running means. Dotted curve from summation of 22 regular periodicities, determined as averages over the 84-year epoch, 1854-1939. Full curve, the event.

displaced one or more months. These displacements seemed generally to follow either great volcanic eruptions, such as Krakatoa, Colima, and Katmai, or great bombing periods, as in the war years 1916-1918 and 1940-1945, and recent tests of atomic bombs.

The results, though subject to such blemishes, seem to offer a useful means of mapping countries for decades in advance to exhibit probable precipitation in percentages of the normal. Suppose 50

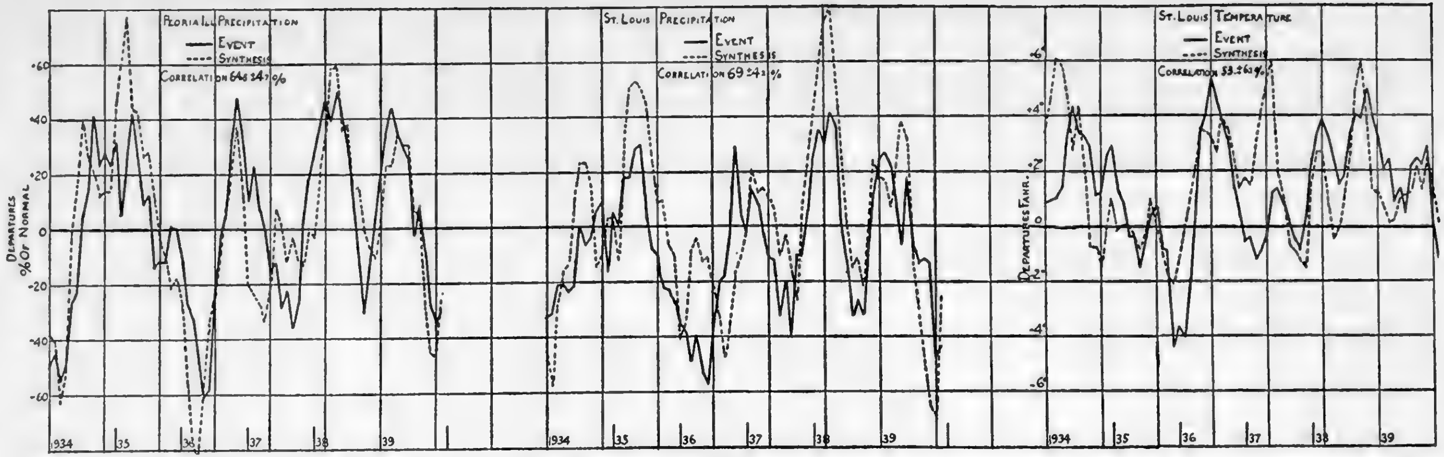

FIG. 2.—Three 6-year predictions 40 years in advance. Precipitation (Peoria and St. Louis) and temperature (St. Louis) computations 1934-1939 compared to the events. Precipitation, percentages of normal; temperature, departures from normal. Dotted curves, computed; full curves, events. All from 5-month smoothed running means.

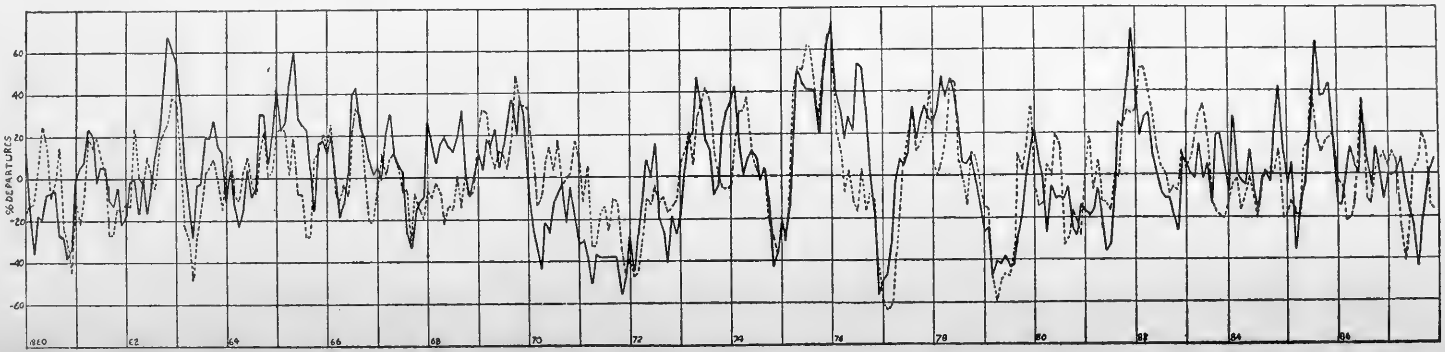

FIG. 3.—Synthesis of computations, 1860-1887, of St. Louis precipitation compared to the event. Dotted curve, computed; full curve, the event.

stations east of the Rocky Mountains in the United States were treated as I have done at Saint Louis, Peoria, and Albany. Lines of equal probable percentage of normal precipitation could be drawn for each season of the year for 10 years in advance. A success of 70 percent, as in Saint Louis, would be a boon to industry, and moderate phase displacements in 30 percent would be no serious failure. After all, it is *seasonal* weather that is most desired to be known. Three-month averages would remove most of the blemishes.

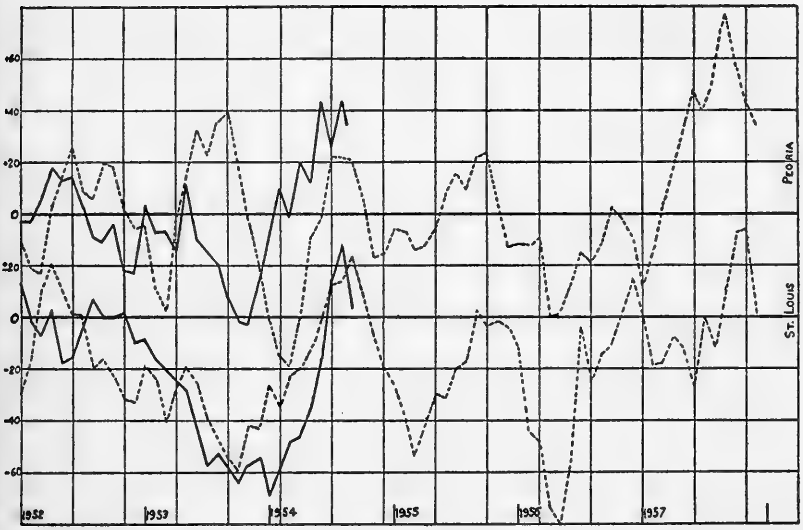

FIG. 4.—Predicted precipitation, Peoria (upper) and St. Louis (lower), 1952-1957, from mean forms of 22 periodicities over the epoch 1854-1939. End of prediction 18 years after 1939 and 60 years after middle of base, 1897. Dotted curves, prediction; full curves, event. Horizontal lines represent normal precipitation. Drought indicated ending 1957.

3. SNOW-COVERED DATES AT TOKYO, JAPAN

My friend Dr. H. Arakawa recently published [6] dates of the earliest wintry snow coverage for Tokyo since 1632. Many years are missing, but about 200 years are included. Dr. Arakawa treats the data very interestingly, but in large groupings. It occurred to me to plot all the dates of first coverage, reckoned after November 30, in days for each year given. I plotted blank years in the same regular order as the rest. Though the long plot showed many breaks, I seemed to see in it a tendency to a period of 45½ years, twice 273 months.

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[6] Quart. Journ. Roy. Meteorol. Soc., vol. 82, No. 352, p. 222, April 1956.

I then tabulated all the data. The mean march of them is shown in curve A, figure 5. A period of $45\frac{1}{2} \div 3$, equaling $15\frac{1}{6}$ years, seemed indicated, as shown in curve B. Subtracting its smoother ordinates ($42 + \text{smooth}\triangle$), the final column of the mean table, $\triangle$, results, and is plotted in curve C. Though rough, a period of 45½ years, with an amplitude of 8 days, is found. The smoothed curve B for 15⅙ years has the amplitude of 7 days. From curve C, one would expect a snow coverage at Tokyo averaging a week earlier for the years 1955-1970 than the average which prevailed from 1930-1945.

Casting the eye along any of the 45 lines of the table (fig. 5), one sees no well-marked tendency for a change in amplitude at any phase of the 45½-year period from the seventeenth to the twentieth century.

GLACIAL ADVANCES RELATED TO 273 MONTHS

I recently received from the author, Herbert Grünhagen of Stadtoldendorf, Germany, a paper entitled "Die Klimawellen der Eiszeit." [7] He refers to a beautifully printed small book by W. Soergel, professor of geology and paleontology at the University of Freiburg, entitled "Die Vereisungskurve." [8] In this paper Soergel gives a curve to represent the fluctuation of latitudes of ice penetration in central Europe as glaciation advanced and receded from the direction of Sweden.

Grünhagen smooths Soergel's curve by using mean values for each successive 65,000 years. The curve thus treated he plots in 102 points, covering the interval from minus 565,000 to minus 30 years earlier than the year 1800 of our era.

Grünhagen's prior researches had disclosed to him periodic variations related to various phenomena. He had noted that when such a period was found, the double of it was also apt to be a recognizable period in the phenomena.

In these circumstances, a copy of my paper "Sixty-year Weather Forecasts" came to him, and some of the solar periods I used agreed closely with some periods he had found. He calls attention to families among my solar periods, in one of which the periods go in the order 1, ½, ¼, ⅛; and another in which the order 1, ⅓, ⅙, 1/12 is found.

It occurred to Grünhagen to see if longer periods than mine, increasing by powers of 2, might perhaps be found in the smoothed Soergel curve. He puts forward six such periods as follows: 15 years multiplying by 2^{12}, 2^{13}, 2^{14}, yielding 61,440, 122,880, and 245,760

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[7] Separate from Niedersachsen, a periodical for home and culture, Heft 1, 1956.

[8] Published by Borntraeger Brothers, Berlin, 1937.

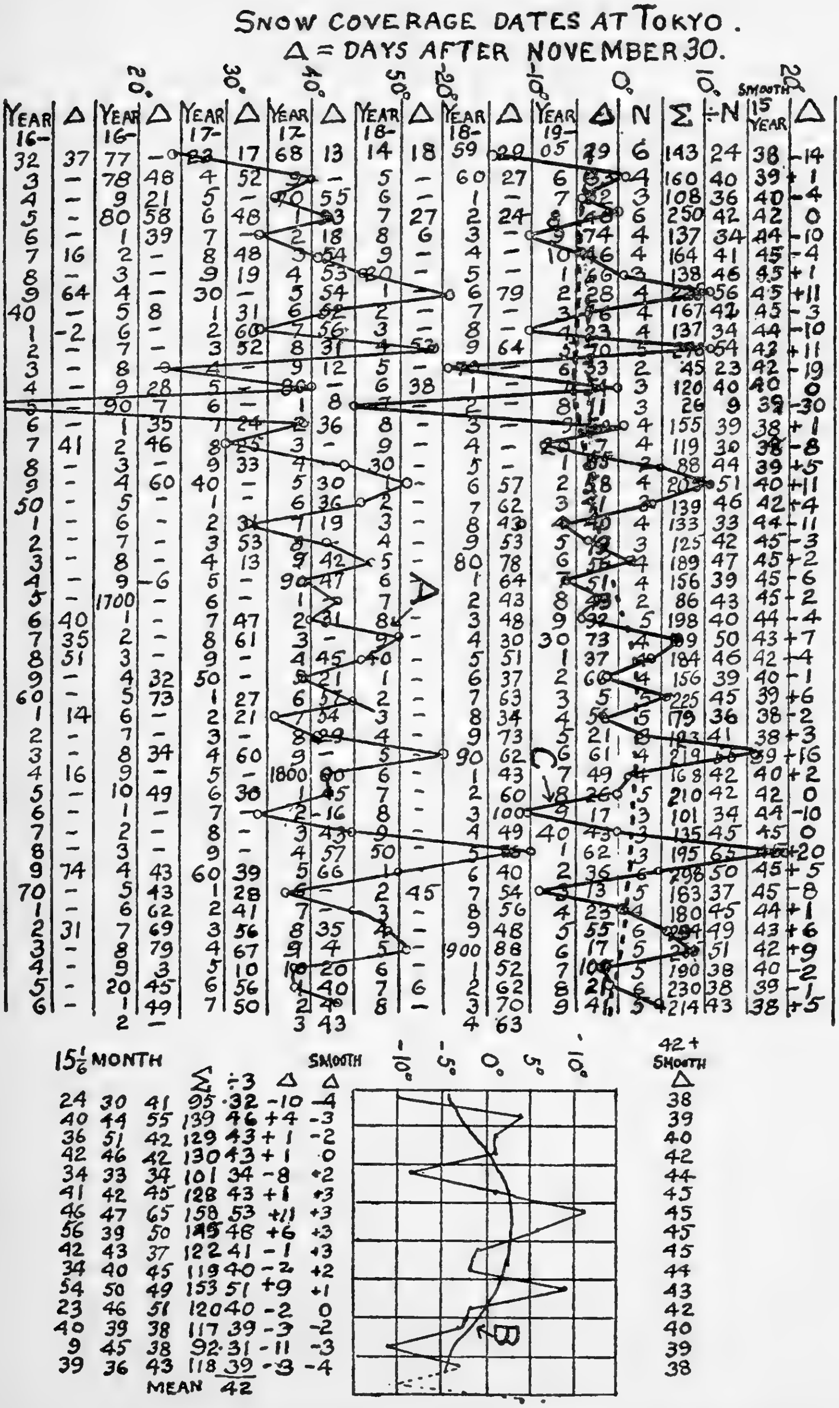

FIG. 5.—Snow coverage of Tokyo (Arakawa). The periods of 15⅙ and 45½ years are multiples of 273 months.

years; also 11.25 years multiplied by 2^{14}, 2^{15}, 2^{16} yielding 184,320, 368,640, and 737,280 years.

Grünhagen publishes, along with Soergel's smoothed curve of latitudes of penetration, another curve made up, as he states, from these six periods. The parallelism is striking.

I could not interpret from Grünhagen's paper how he obtained the phases, forms, and amplitudes in which he combined the six periods which he formed out of my 273-month solar period. I therefore read off 102 points of his smoothed Soergel curve. I computed from them the mean forms, phases, and amplitudes of the four shortest of Grünhagen's six periods. The longer two were not repeated enough times to compute good mean values. However, as I have found all my solar periods to be exact submultiples of 22¾ years, I used for these four Grünhagen periods 7½ × (2^{13}, 2^{14}, 2^{15}) and 22¾ × (2^{13}, 2^{14}, 2^{15}). This gives for my first three periods the same values as his first three, but for my last three 186.4, 372.7, and 745.5 in thousands of years, instead of the value which he based on 11.25 years.

In the following table I give the mean latitudes computed from the smoothed Soergel curve to suit periods of 61.4, 122.9, 186.4, and

TABLE 3.—*Glacial periods synthesized*

Periods in years	61,400		122,900		186,400		245,800		ΣΔ+56°8		Soergel smooth curve	0.7ΣΔ+56°8	
	Mean	Δ	Mean	Δ	Mean	Δ	Mean	Δ					
1	57°0	0°2	55°9	—0°8	55°3	—1°3	58°7	1°7	—0°2	56°6	59°4	—0°1	56°7
2	56.8	0.0	56.0	—0.7	55.4	—1.2	59.0	2.0	0.1	56.9	59.3	0.1	56.9
3	57.1	0.3	56.2	—0.5	55.6	—1.0	59.3	2.3	1.1	57.9	59.4	0.8	57.6
4	57.0	0.2	56.2	—0.3	56.0	—0.6	60.0	3.0	2.3	59.1	60.5	1.6	58.4
5	57.0	0.2	56.6	—0.1	56.4	—0.2	60.6	3.6	3.5	60.3	61.2	2.4	59.2
6	56.8	0.0	56.7	0.0	56.7	0.1	60.5	3.5	3.6	60.4	61.4	2.5	59.3
7	56.7	—0.1	56.7	0.0	57.1	0.5	60.5	3.5	3.9	60.7	61.3	2.7	59.5
8	56.7	—0.1	57.0	0.3	57.4	0.8	60.5	3.5	4.5	61.3	61.3	3.1	59.9
9	56.7	—0.1	57.6	0.9	58.0	1.4	61.5	4.1	6.3	63.1	61.8	4.4	61.2
10	56.7	—0.1	57.9	1.2	58.3	1.7	61.5	4.5	7.3	64.1	62.1	5.1	61.9
11	56.6	—0.2	58.2	1.5	58.4	1.8	62.1	5.1	8.2	65.0	62.5	5.7	62.5
12	56.8	0.0	58.2	1.5	58.6	2.0	62.7	5.7	9.2	66.0	63.0	6.4	63.2
13	....	0.2	58.2	1.7	59.0	2.4	62.7	5.7	10.0	66.8	63.6	7.0	63.8
14	....	0.0	58.4	1.4	59.3	2.7	62.0	5.0	9.1	65.9	63.3	6.4	63.2
15	....	0.3	58.1	0.8	59.4	2.8	61.1	4.1	8.0	64.8	62.7	5.6	62.4
16	....	0.2	57.5	1.0	59.1	2.5	60.7	3.7	7.4	64.2	61.6	5.2	62.0
17	....	0.2	57.4	0.7	58.8	2.2	59.7	2.7	5.8	62.6	60.8	4.1	60.9
18	....	0.0	56.9	0.2	58.2	1.6	59.0	2.0	3.8	60.6	60.0	2.7	59.5
19	....	—0.1	56.7	0.0	57.5	0.9	58.2	1.2	2.0	58.8	59.0	1.4	58.2
20	....	—0.1	56.5	—0.2	57.4	0.8	57.8	0.8	1.3	58.1	58.6	0.9	57.7
21	....	—0.1	56.0	—0.7	57.3	0.7	57.0	0.0	—0.1	56.7	57.4	—0.1	56.7
22	....	—0.1	55.7	—1.0	57.3	0.7	56.0	—1.0	—1.4	55.4	56.8	—1.0	55.8
23	....	—0.2	55.1	—1.6	57.2	0.6	54.9	—2.1	—3.3	53.5	55.4	—2.3	54.5
24	....	0.0	54.7	—2.0	57.0	0.4	53.8	—3.2	—4.8	52.0	54.6	—3.4	53.4
25	....	0.2	54.3	—2.4	56.1	—0.5	52.9	—4.1	—6.8	50.0	53.2	—4.8	52.0
26	....	0.0	....	—0.7	55.6	—1.0	52.7	—4.3	—6.0	50.8	52.7	—4.2	52.6
27	....	0.3	....	—0.5	55.6	—1.0	52.8	—4.2	—5.4	51.4	52.7	—3.8	53.0
28	....	0.2	....	—0.3	55.6	—1.0	52.8	—4.2	—5.3	51.5	52.7	—3.7	53.1
29	....	0.2	....	—0.1	55.6	—1.0	52.8	—4.2	—5.1	51.7	52.7	—3.6	53.2
30	....	0.0	....	0.0	55.3	—1.7	52.8	—4.2	—5.9	50.9	52.7	—4.1	52.7
31	....	—0.1	....	0.0	54.8	—1.6	52.8	—4.2	—5.7	51.1	52.6	—4.0	52.8
32	....	—0.1	....	0.3	54.7	—1.9	52.9	—4.1	—5.8	51.0	52.6	—4.1	52.7
33	....	—0.1	....	0.9	54.5	—2.1	53.2	—3.8	—5.1	51.7	52.5	—3.6	53.2
34	....	—0.1	....	1.2	54.6	—2.0	53.1	—3.9	—4.8	52.0	52.5	—3.4	53.4
35	....	—0.2	....	1.5	55.0	—1.6	53.9	—3.1	—3.4	53.4	52.6	—2.4	54.4
36	....	0.0	....	1.5	55.4	—1.2	54.0	—3.0	—2.7	54.1	53.0	—1.9	54.9
37	....	0.1	....	1.7	55.6	—1.0	54.1	—2.9	—2.1	54.7	53.2	—1.5	55.3

TABLE 3.—Continued

Periods n years	61,400		122,900		186,400		245,800		ΣΔ+56°.8		Soergel smooth curve	0.7ΣΔ+56°.8	
	Mean	Δ	Mean	Δ	Mean	Δ	Mean	Δ					
38	....	0.2	....	1.4	....	—1.3	54.5	—2.5	—2.2	54.6	53.8	—1.5	55.3
39	....	0.0	....	0.8	....	—1.2	54.8	—2.2	—2.6	54.2	54.0	—1.8	55.0
40	....	0.3	....	1.0	....	—1.0	55.3	—1.7	—1.4	55.4	54.4	—1.0	55.8
41	....	0.2	....	0.7	....	—0.6	55.3	—1.8	—1.5	55.3	54.6	—1.1	55.7
42	....	0.2	....	0.2	....	—0.2	55.3	—1.7	—1.5	55.3	55.0	—1.1	55.7
43	....	0.0	....	0.0	....	0.1	55.1	—1.9	—2.0	54.8	55.5	—1.4	55.4
44	....	—0.1	....	—0.2	....	0.5	55.3	—1.7	—1.5	55.3	56.7	—1.1	55.7
45	....	—0.1	....	—0.7	....	0.8	55.4	—1.6	—1.6	55.2	57.0	—1.1	55.7
46	....	—0.1	....	—1.0	....	1.4	55.6	—1.4	—1.1	55.7	57.2	—0.8	56.0
47	....	—0.1	....	—1.6	....	1.7	55.9	—1.1	—1.1	55.7	57.6	—0.8	56.0
48	....	—0.2	....	—2.0	....	1.8	55.9	—1.1	—1.5	55.3	57.7	—1.1	55.7
49	....	0.0	....	—2.4	....	2.0	56.1	—0.9	—1.3	55.5	57.7	—0.9	57.7
50	....	0.2	....	—0.8	....	2.4	....	1.7	3.5	60.3	58.0	2.4	59.2
51	....	0.0	....	—0.7	....	2.7	....	2.0	4.0	60.8	58.8	2.8	59.6
52	....	0.3	....	—0.5	....	2.8	....	2.3	4.9	61.7	59.2	3.4	60.2
53	....	0.2	....	—0.3	....	2.5	....	3.0	5.4	62.2	59.6	3.8	60.6
54	....	0.2	....	—0.1	....	2.2	....	3.6	5.9	62.7	59.9	4.1	60.9
55	....	0.0	....	0.0	....	1.6	....	3.5	5.1	61.9	59.7	3.6	60.4
56	....	—0.1	....	0.0	....	0.9	....	3.5	4.3	61.1	59.6	3.0	59.8
57	....	—0.1	....	0.3	....	0.8	....	3.5	4.5	61.3	59.7	3.2	60.0
58	....	—0.1	....	0.9	....	0.7	....	4.1	5.6	62.4	60.9	3.9	60.7
59	....	—0.1	....	1.2	....	0.7	....	4.5	6.3	63.1	60.9	4.4	61.2
60	....	—0.2	....	1.5	....	0.6	....	5.1	7.0	63.8	61.7	4.9	61.7
61	....	0.0	....	1.5	....	0.4	....	5.7	7.6	64.4	62.4	5.3	62.1
62	....	0.2	....	1.7	....	—0.5	....	5.7	7.1	63.9	61.7	5.0	61.8
63	....	0.0	....	1.4	....	—1.0	....	5.0	5.4	62.2	60.6	3.8	60.6
64	....	0.3	....	0.8	....	—1.0	....	4.1	4.2	61.0	59.5	2.9	59.7
65	....	0.2	....	1.0	....	—1.0	....	3.7	3.9	60.7	58.8	2.7	59.5
66	....	0.2	....	0.7	....	—1.0	....	2.7	2.6	59.4	58.5	1.8	58.6
67	....	0.0	....	0.2	....	—1.7	....	2.0	0.5	57.3	58.0	0.4	57.2
68	....	—0.1	....	0.0	....	—1.6	....	1.2	—0.5	56.3	57.5	—0.4	56.4
69	....	—0.1	....	—0.2	....	—1.9	....	0.8	—1.4	55.4	57.1	—1.0	55.8
70	....	—0.1	....	—0.7	....	—2.1	....	0.0	—2.9	53.9	56.6	—2.0	54.8
71	....	—0.1	....	—1.0	....	—2.0	....	—1.0	—4.1	52.7	55.3	—2.9	53.9
72	....	—0.2	....	—1.6	....	—1.6	....	—2.1	—5.5	51.3	54.4	—3.8	53.0
73	....	0.0	....	—2.0	....	—1.2	....	—3.2	—6.4	50.4	53.0	—4.5	52.3
74	....	0.1	....	—2.4	....	—1.0	....	—4.1	—7.4	49.4	52.6	—5.2	51.6
75	....	0.2	....	—0.8	....	—1.1	....	—4.3	—6.0	50.8	52.7	—4.2	52.6
76	....	0.0	....	—0.7	....	—1.3	....	—4.2	—6.2	50.6	52.9	—4.3	52.5
77	....	0.3	....	—0.5	....	—1.2	....	—4.2	—5.6	51.2	53.0	—3.9	52.9
78	....	0.2	....	—0.3	....	—1.0	....	—4.2	—5.3	51.5	52.9	—3.7	52.1
79	....	0.2	....	—0.1	....	—0.6	....	—4.2	—4.7	52.1	52.9	—3.5	53.3
80	....	0.0	....	0.0	....	—0.2	....	—4.2	—4.4	52.4	53.1	—3.1	53.7
81	....	—0.1	....	0.0	....	—0.1	....	—4.1	—4.3	52.5	53.2	—3.0	53.8
82	....	—0.1	....	0.3	....	0.5	....	—3.8	—3.1	53.7	54.0	—2.2	54.6
83	....	—0.1	....	0.9	....	0.8	....	—3.9	—2.3	54.5	55.1	—1.6	55.2
84	....	—0.1	....	1.2	....	1.4	....	—3.1	—0.6	56.2	55.2	—0.4	55.4
85	....	—0.2	....	1.5	....	1.7	....	—3.0	0.0	56.8	55.1	0.0	56.8
86	....	0.0	....	1.5	....	1.8	....	—2.9	0.4	57.2	55.0	0.3	57.1
87	....	0.2	....	1.7	....	2.0	....	—2.5	1.4	58.2	55.3	1.0	57.8
88	....	0.0	....	1.4	....	2.4	....	—2.2	1.6	58.4	55.7	1.1	57.9
89	....	0.3	....	0.8	....	2.7	....	—1.7	2.1	58.9	56.3	1.5	58.3
90	....	0.2	....	1.0	....	2.8	....	—1.8	2.2	59.0	56.0	1.5	58.3
91	....	0.2	....	0.7	....	2.5	....	—1.7	1.7	58.5	55.7	1.2	58.0
92	....	0.0	....	0.2	....	2.2	....	—1.9	0.5	57.3	54.8	0.3	57.1
93	....	—0.1	....	0.0	....	1.6	....	—1.7	—0.2	56.6	54.0	—0.1	56.7
94	....	—0.1	....	—0.2	....	0.9	....	—1.6	—1.0	55.8	53.9	—0.7	56.1
95	....	—0.1	....	—0.7	....	0.8	....	—1.4	—1.4	55.4	54.2	—1.0	55.8
96	....	—0.1	....	—1.0	....	0.7	....	—1.1	—1.5	55.3	54.2	—1.1	55.7
97	....	—0.2	....	—1.6	....	0.7	....	—1.1	—2.2	54.6	54.5	—1.5	55.3
98	....	0.0	....	—2.0	....	0.6	....	—0.9	—2.3	54.5	54.0	—1.6	55.2
99	....	0.2	....	—0.8	....	0.4	....	1.7	1.5	58.3	53.3	1.1	57.9
100	....	0.0	....	—0.7	....	—0.5	....	2.0	0.8	57.6	53.4	0.6	57.4
101	....	0.3	....	—0.5	....	—1.0	....	2.3	1.1	57.9	54.5	0.8	57.6
102	....	0.2	....	—0.3	....	—1.0	....	3.0	1.9	58.7	55.4	1.3	58.1
										Mean	56.8°		

245.8 thousands of years, and the departures of each of these mean curves from the general mean for each.

In figure 6 I plot the smoothed Soergel curve A; then curve B, which is the synthesis of my four long periods plus 56.8°; and finally

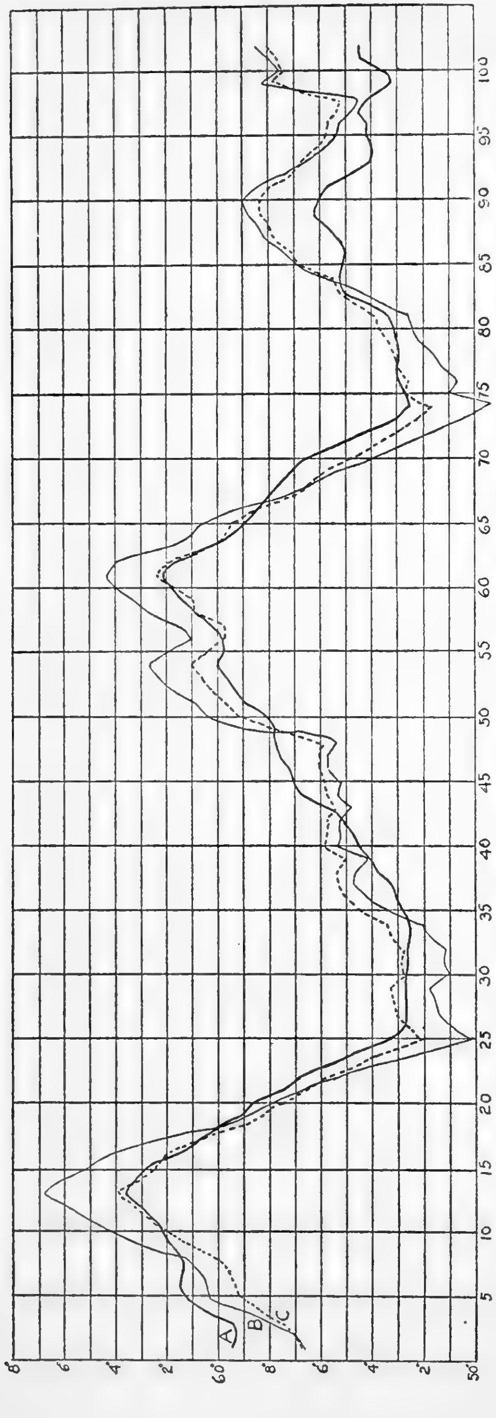

FIG. 6.—Glacial penetration in Germany. A, Soergel's curve as smoothed by Grünhagen. B, Synthesis of four periods, multiples of 273 months. C, Curve B reduced to 7/10 in ordinates.

curve C, which is my synthesis multiplied by 7/10 plus 56.8°. It is plain that the principal features and even most details of the smoothed Soergel curve are closely duplicated in my curve C. As Grünhagen used 6 periods, and I used but 4, the scale difference, 10 to 7, may be for lack of the others.

I do not fully understand how Soergel derived the time scale for these very ancient events. Doubtless he used several disciplines, including paleontology and stratigraphy. It is extraordinary how closely my *exact* time scale fits with his time scale, which must have been built up from rather *loosely timed* data.

4. MAGNETIC AND ELECTRICAL RELATIONS TO THE PERIOD OF 273 MONTHS

Nearly 50 years ago Dr. G. E. Hale discovered magnetism in sunspots. When this phenomenon had been followed long enough, the well-known remarkable reversal of polarities at intervals of double the sunspot period of 11⅜ years was found. So the 273-month period is surely a magnetic period in the sun.

When, about 1935, the ionosphere became systematically observed, the fluctuation of these electrical phenomena proved to be closely associated with sunspot frequency. But later I discovered that ionospheric changes were also associated with the variations of measures of the solar constant. I will merely refer here to publications on this relationship.[9]

5. THE HUMAN PULSE RATE

In a former publication[10] I mentioned that my friend Dr. F. P. Marshall had kept a record of her pulse rate for three years, which indicated a regular period of 212 days and submultiples thereof. The observations were made every day before rising, and form a continuous record for 1,095 days of basal pulse rates.

Dr. Marshall has kindly permitted me to use this evidence, which is unpublished. It shows clearly a period of 212 days and six periods, aliquot parts thereof (fig. 7), and others which I have not investigated.

Dr. Marshall was familiar with my first studies on the solar constant of radiation, about 1935. She followed much the same course with the pulse observations. However, as the 15-year record of solar-

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[9] Smithsonian Misc. Coll., vol. 107, No. 4, pp. 24-26, 1947; ibid., vol. 122, No. 4, pp. 9-11, 1953.

[10] Periodic solar variation, Smithsonian Misc. Coll., vol. 128, No. 4, pp. 3, 6, 1955.

constant measures then available had many breaks in the continuity of the daily observations, I was constrained to use 10-day and monthly mean values in my work. As she had an unbroken daily record of almost 1,100 days, she employed daily values of pulse.

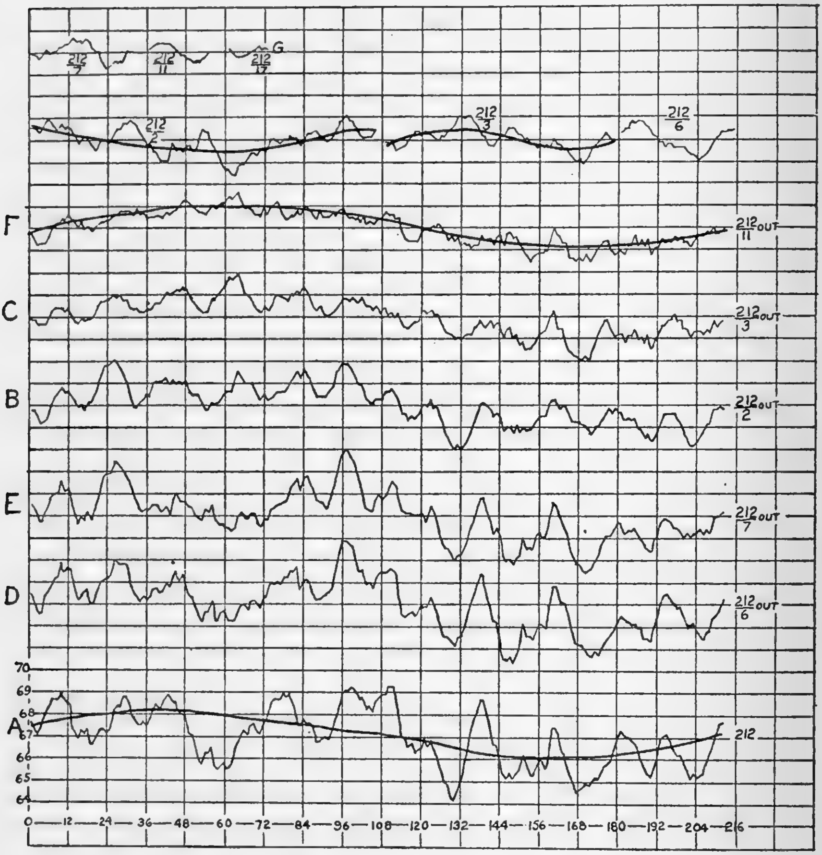

FIG. 7.—Basal pulse rates (Marshall). A, Mean march of 212-day period for 3 years. D, Period of $^{212}/_{6}$ removed. E, Period of $^{212}/_{7}$ removed. B, Period of $^{212}/_{2}$ removed. C, Period of $^{212}/_{3}$ removed. F, Period of $^{212}/_{11}$ removed. G, Remaining period of $^{212}/_{17}$, not removed. Seven months, $^{1}/_{39}$ × 273 months, is 213.07 days. Therefore all seven periods found are submultiples of 273 months.

Plotting these in their complete continuity, her figure, like my solar-constant figure, resembled a wide ribbon, with its many closely lying ups and downs. But the pulse values, not being subject to accidental errors, were more satisfactory to investigate than the solar-constant values in which accidental errors were of about the same magnitude as real variations of the sun. Still her ribbon plot was so wide that it was found desirable to smooth the record. This she did by taking 7-day overlapping means. The range of pulse remaining after smoothing was approximately from 60 to 70 pulses per minute.

Scanning the smoothed pulse record, it appeared to present a recurring period of 106 days. The range of that period seemed to show alternately maxima and minima. So a period of 212 days was sought for by tabulation. With five repetitions of the 212-day tabulation, their mean was as represented by the line A in figure 7. It is easy to see that, though loaded with many irregularities, the line A is fairly indicative of an approximate sine curve, with a range of two pulses, as shown by the smooth line.

Following the procedure of my weather-variation papers, the curve A was cleared successively of five periods, which are aliquot parts of 212 days, respectively ½, ⅓, ⅙, ⅐, and 1/11 of 212 days. These are shown in the upper part of figure 7. The successive removals of them show the successive smoothing of curve A, in curves D, E, B, C, and F. There still remains, as shown in curve G, a period of $\frac{212}{17}$ days, or 12½ days, and doubtless others. But curve F is so smooth that little doubt remains that the smooth line upon curve F is the veritable period of 212 days, as relieved of superriders. This smooth line is almost exactly the same in form and amplitude as that drawn free-hand on curve A. It has a range of two pulses or about 3 percent of the average pulse rate per minute.

In the solar variation, a 7-month period is one of the stronger ones. Reduced to days, a 7-month period is $\frac{1}{39} \times 22\frac{3}{4}$ years, which is $\frac{22.75 \times 365.2564}{39} = 213.07$ days. This, of course, to well within the probable error, is the same as Dr. Marshall's 212 days. Hence I conclude that Dr. Marshall's physiological period and its exact submultiples are all aliquot parts of my master solar period of 273 months. Doubtless this relationship is not accidental, and physiologists will, I am sure, note it with interest.

SUMMARY

The author shows that weather, glaciation, dates of snow coverage in Japan, magnetism in the sun, variations of the ionosphere, and human pulse rates all present regular periods which are exact multiples or submultiples of the master period of 273 months in the variation of the sun's emission of radiation.

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THE ASIATIC SPECIES OF BIRDS OF THE GENUS CRINIGER (PYCNONOTIDAE)

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Among the birds of tropical Asia, few groups can have been the subject of so many revisions with such diverse results as the forms of the pycnonotine genus *Criniger*. In the course of studies made in connection with work on the bulbuls for the continuation of the late J. L. Peters's "Check-list of Birds of the World," I have found that there has been no agreement among the several authors even as to the number of species involved, and it has frequently proved quite impossible for me to decide which form was meant by a name used in a particular instance. In the circumstances, I have been compelled to make a wholly new study based upon personal examination of hundreds of specimens and of many of the pertinent types, and here present a new arrangement that will, I believe, settle most of the previously doubtful points of relationship within the group. Six species (five of them polytypic) are accepted, each of which appears to be somewhere sympatric with one or more of the others, but in the pages to follow will be found no comment on the two uncontroversial species, *finschii* Salvadori, 1871, and *phaeocephalus* (Hartlaub), 1844.

CRINIGER FLAVEOLUS (Gould), 1836

Criniger flaveolus flaveolus (GOULD).

Trichophorus flaveolus GOULD, Proc. Zool. Soc. London, pt. 4, No. 37, April 9, 1836, p. 6 (" in montibus Himalayensibus, in Nepaliâ, &c."; type locality restricted to Nepal, by Koelz, Contr. Inst. Reg. Expl., No. 1, 1954, p. 10).

Trichophorus xanthogaster HODGSON, *in* J. E. Gray, Zoological Miscellany, No. 3, "June" 1844, p. 83 (Nepal). *Nomen nudum.*

Lanixus xanthogaster "Hodgs." BOWDLER SHARPE, Catalogue of the Birds in the British Museum, vol. 6, 1881, p. 77 (Nepal). In synonymy with *Criniger flaveolus* (Gould), not *Criniger xanthogaster* Cassin, 1855.

Trichophorus xanthogaster "Hodgs." BOWDLER SHARPE, Catalogue of the Birds in the British Museum, vol. 6, 1881, p. 77 (Nepal). In synonymy with *Criniger flaveolus* (Gould), not *Criniger xanthogaster* Cassin, 1855.

Criniger flaveolus viridulus KOELZ, Contr. Inst. Reg. Expl., No. 1, September 24, 1954, p. 10 (Sangau, Lushai Hills, Assam State, India).

Criniger flaveolus aureolus KOELZ, Contr. Inst. Reg. Expl., No. 1, September 24, 1954, p. 10 (Kohima, Naga Hills, Assam State, India).

Range.—The sub-Himalayas from Garhwal to easternmost Assam, south through Assam to Arakan, the Chin Hills, central and northeastern Burma.

Criniger flaveolus burmanicus OATES.

Criniger burmanicus OATES, Fauna of British India, Birds, vol. 1, December 1889, p. 256 ("Toungngoo; the Karen hills; Karennee; Tenasserim, as far south as Meetan at the base of Muleyit mountain, and throughout the Thoungyeen valley"; type locality commonly restricted to Toungoo District, Pegu Division, Burma).

Range.—Southeastern Burma (the valley of the Salween from the Northern Shan States to its mouth in the Amherst District of Tenasserim) and western Thailand (valleys of the Mae Moei [Thaungyin] and the Mae Klong).

Remarks.—*Criniger flaveolus burmanicus* seems to be sympatric in central Tenasserim with *Criniger pallidus robinsoni* and *Criniger ochraceus ochraceus,* and in southwestern Thailand with *Criniger ochraceus ochraceus.*

CRINIGER PALLIDUS Swinhoe, 1870

Criniger pallidus pallidus SWINHOE.

Criniger pallidus SWINHOE, Ibis, ser. 2, vol. 6, No. 22, April 1870, p. 252 (Hainan).

Pinarocichla schmackeri STYAN, Bull. Brit. Orn. Club, vol. [1], No. 2, November 1, 1892, p. vi (Hainan).

Range.—Hainan.

Criniger pallidus henrici OUSTALET.

Criniger Henrici OUSTALET, Bull. Mus. Hist. Nat. [Paris], vol. 2, No. 5, June 22, 1896, p. 185 ("entre Manhao et Se-mao [Yunnan], sur les bords de la Rivière-Noire . . . à Nam-Xong, Ban-Moi et Hat-Hoa [Tonkin]").

Criniger pallida grandis STUART BAKER, Bull. Brit. Orn. Club, vol. 38, No. 228, December 4, 1917, p. 15 (Yunnan Province, China; type specimens from Yuankiang [lat. 23°37′ N., long. 102°01′ E.]).

Range.—Southern Yunnan (valleys of the Red and Black Rivers), Tongking, northernmost Annam, northwestern Laos, Southern Shan States (valley of the Mae Khong), and northern Thailand.

Criniger pallidus robinsoni TICEHURST.

Criniger tephrogenys robinsoni TICEHURST, Bull. Brit. Orn. Club, vol. 53, No. 362, October 31, 1932, p. 19 (Ye, Amherst District, Tenasserim Division, Burma).

Range.—Southern Burma (the Amherst District of Tenasserim) and (probably) northwestern Thailand.

Remarks.—This form was based upon three faded specimens in London, collected in the Amherst District during the 1870's; two of them, including the type, are apparently immature, differing from an obvious adult by paler, bright, and more gold-suffused coloration above and below, and by the slight development of the gular feathers.

The length of crest feathers and tail of the adult show that it belongs rather with *pallidus* than with *bres* (*"tephrogenys"* of Ticehurst), and making allowances for its quite serious fading, it appears to represent a population intermediate between *henrici* and *griseiceps*.

An apparent difficulty arises from the fact that *griseiceps* is until now reported only from the Pegu Yomas, *robinsoni* only from the Amherst District of Tenasserim, and *henrici* from nowhere south and west of Doi Ang Ka (lat. 18°35′ N., long. 98°30′ E.) in northwestern Thailand; thus the three populations seem to be quite isolated from each other. Yet it is difficult to believe that the intervening territory, so suitable for the species, should wholly lack some representative of the group, and the suspicion that the vacuum is more imaginary than real is supported by the existence of a unique skin (M.C.Z. No. 196535) from Doi Ang Ka that can be separated from *griseiceps* only by having the crest feathers colored quite as in *henrici,* without the least grayish wash. A second indication of probable intergradation between the two, and one further strengthening the view that *robinsoni* is an intergradient population, is the fact that, of the two faded paratypes of *robinsoni* now before me in Washington, while the adult has the crest faintly washed with gray (as if approaching *griseiceps*), the immature has it red-brown (as if approaching *henrici*).

For the present, I consider *griseiceps* a geographically and chromatically extreme representative of *Criniger pallidus,* with which it is connected in conventional fashion through *robinsoni.*

Criniger pallidus robinsoni seems to be sympatric in the Amherst District with *Cringer flaveolus burmanicus* and *Criniger ochraceus ochraceus.*

Criniger pallidus griseiceps Hume.

Criniger griseiceps Hume, Stray Feathers, vol. 1, No. 6, December 1873, p. 478 ("Upper Pegu," Burma).

Range.—Southern Burma (Pegu Yomas).

Remarks.—This race is very strongly marked compared with others of the species. Its mantle is greener (but wholly lacking the golden tone appearing in *Criniger fl. burmanicus*) ; its crest is strongly suffused with gray, although basically a dull red-brown as in the rest.

Another peculiarity is its suffusion of pinkish buff, which affects the throat, the ground color of the under parts, and the tones of the crest and upper parts, but a similar suffusion appears in slight degree also in some skins of *henrici* from western Thailand. In the circumstances, and because of the specimen from Doi Ang Ka discussed above, *griseiceps* seems to be properly placed in the species *pallidus*.

Criniger pallidus isani, subsp. nov.

Type.—U.S.N.M. No. 459700, adult male, collected at Ban Muang Khai (lat. 17°30′ N., long. 101°20′ E.), Loei Province, Thailand, on January 14, 1955, by Robert E. Elbel; original number RE 4470.

Diagnosis.—Nearest *Criniger pallidus henrici,* from which it is separable by having the olivaceous brown of the mantle decidedly paler and grayer.

Range.—Eastern Thailand (Loei and Phetchabun Provinces).

Remarks.—Although no representative of the genus had previously been reported from the Phaya Dong Fai Mountains, I have recently acquired no fewer than 24 specimens of this new race from several localities in the northwestern portion of the eastern plateau of Thailand, and the bird will certainly be found to possess a much more extensive range.

Criniger pallidus annamensis DELACOUR AND JABOUILLE.

Criniger tephogenys annamensis DELACOUR AND JABOUILLE, Bull. Brit. Orn. Club, vol. 45, No. 291, December 5, 1924, p. 32 (Lao Bao, Quangtri Province, Annam).

Range.—Central Annam, intergrading in northern Annam (Phu Qui) with *henrici,* and in south-central Annam (Dak To, Kontoum) with the next following race; central Laos, from Chiang Khwang southeastward to Lao Bao.

Criniger pallidus khmerensis, subsp. nov.

Type.—U.S.N.M. No. 360999, adult male, collected at Banteai Srei (lat. 13°16′ N., long. 104°07′ E.), Siem Reap Province, Cambodia, in January 1940, by Joseph F. C. Rock; original number 1292A.

Diagnosis.—Nearest *Criniger pallidus annamensis,* but separable by the brighter, more purely yellow (less buff-suffused) under parts and the much more golden-olive (less brownish-olive) mantle.

Range.—Southern Annam (Phanrang and Haut-Donai Provinces), Cambodia, and southern Laos (Saravane Province).

Remarks.—*Criniger pallidus khmerensis* seems to be sympatric in southern Annam with *Criniger ochraceus* subsp. nov. (named just below).

CRINIGER OCHRACEUS Moore, 1854

Criniger ochraceus hallae, subsp. nov.

Type.—Brit. Mus. Reg. No. 1928.6.26.834, adult male, collected at Tay Ninh (lat. 11°18′ N., long. 106°07′ E.), Tay Ninh Province, Cochin-China, on January 15, 1928, by Jean Delacour and Willoughby P. Lowe (Franco-British Indo-China Fourth Expedition); original number 1767.

Diagnosis.—Nearest *Criniger ochraceus cambodianus,* from which it differs by having the mantle less grayish, more strongly suffused with olivaceous, and the under parts much brighter, strongly suffused with creamy- or yellow-buff.

Range.—Southern Annam (Haut-Donai Province) and Cochin-China (Bien Hoa and Tay Ninh Provinces).

Remarks.—This isolated population (named for Mrs. B. P. Hall of the British Museum, Nat. Hist.) has until now been placed with the nominate race of Tenasserim, from which it is of course quite distinct.

It is apparently sympatric in southern Annam with *Criniger pallidus khmerensis.*

Criniger ochraceus cambodianus DELACOUR AND JABOUILLE.

Criniger gutturalis cambodianus DELACOUR AND JABOUILLE, Bull. Brit. Orn. Club, vol. 48, No. 325, July 10, 1928, p. 130 (Le Boc Kor [lat. 10°37′ N., long. 104°03′ E.], Kampot Province, Cambodia).

Range.—Southwestern Cambodia (Chaîne de l'Éléphant) and southeastern Thailand.

Criniger ochraceus ochraceus MOORE.

Criniger ochraceus MOORE, *in* Horsfield and Moore, Catalogue of the Birds in the Museum of the Hon. East-India Company, vol. 1, 1854, pp. xv [*nomen nudum*], 252 (Tenasserim Division, Burma; type locality here restricted to Mergui [lat. 12°26′ N., long. 98°36′ E.], Mergui District).

Criniger ochraceus crinitus DEIGNAN, Journ. Washington Acad. Sci., vol. 44, No. 4, May 3, 1954, p. 125 (Ban Hin Laem [lat. 14°40′ N., long. 98°40′ E.], Kanchanaburi Province, Thailand).

Range.—Tenasserim from the Amherst District (Ye) south to the Mergui District (Tenasserim Town), and southwestern Thailand (valley of the Mae Klong and south in the forest to Prachuap Khiri Khan Province [Khao Luang]).

Remarks.—Since two races of *ochraceus* appear in Tenasserim, it has been necessary to restrict Moore's type locality. Comparison of the type specimen in London with others has shown that nominate *ochraceus* occurs as far south as Tenasserim Town, and one specimen from that place is even very like the type itself in its deep coloration.

Accordingly, Mergui, still farther north and the provenience of a number of Helfer's skins, may be considered a suitable *terra typica.*

Criniger ochraceus ochraceus seems to be sympatric in central Tenasserim with *Cringer pallidus robinsoni* and *Criniger flaveolus burmanicus,* and in southwestern Thailand with *Criniger flaveolus burmanicus.*

Criniger ochraceus sordidus RICHMOND.

?Criniger Cabanisi A. MÜLLER, Die Ornis der Insel Salanga, [*ante* October 4] 1882, p. 32 (Phuket [lat. 7°55′ N., long. 98°25′ E.], Phuket Province, Thailand).

?Criniger Cabanisi A. MÜLLER, Journ. für Orn., Jahrg. 30, No. 160, November 1882, p. 384 (Phuket, Phuket Province, Thailand).

Criniger sordidus RICHMOND, Proc. U.S. Nat. Mus., vol. 22, No. 1201, May 12, 1900, p. 320 (Khao Soi Dao [lat. 7°20′ N., long. 99°50′ E.], Trang Province, Thailand).

?[*Criniger*] *salangæ* BOWDLER SHARPE, Hand-list of the Genera and Species of Birds, vol. 3, 1901, p. 316. New name for *Criniger Cabanisi* A. Müller, Journ. für Orn., Jahrg. 30, No. 160, November 1882, p. 384 (Phuket, Phuket Province, Thailand), not *Criniger cabanisi* Bowdler Sharpe, "1881" [1882].

Range.—The Mergui Archipelago (Ross, Sullivan, and St. Matthew's Islands) and mainland Tenasserim from the head of Pak Chan Estuary to Victoria Point; Thailand from Sathani Map Ammarit (lat. 10°50′ N., long. 99°20′ E.) south through the Malay Peninsula into northwestern Malaya (Perlis State and the Langkawi Islands).

Remarks.—*Criniger ochraceus sordidus* has lain in synonymy with the nominate race for many years, but it is readily distinguished in series by its darker upper parts and more ochraceus, less buffy, under parts. Most discussion of this form has been based upon skins from the Merguis and Tenasserim and from the Siamese side of the Isthmus of Kra, all of which are, strictly speaking, *sordidus*>*ochraceus,* and therefore misleading for taxonomic purposes.

This form is apparently sympatric in southernmost Tenasserim, peninsular Thailand, and northwestern Malaya with *Criniger bres tephrogenys.*

Criniger ochraceus sacculatus ROBINSON.

Criniger ochraceus sacculatus ROBINSON, *in* Robinson and Boden Kloss, Ibis, ser. 10, vol. 3, No. 4, October 8, 1915, p. 746 (Ginting Bidei [lat. 3°18′ N., long. 101°50′ E.], Selangor State, Malaya).

Range.—Malaya, from northern Perak south to Negri Sembilan and Pahang.

Remarks.—*Criniger ochraceus sacculatus* is apparently sympatric in Malaya with *Criniger bres tephrogenys.* It is frequently stated that the former is a hill form, while the latter is one of the lowlands, but it should be noted that *sacculatus* ranges principally between 2,500 and 4,500 feet, while *tephrogenys* "is met with on the hills of Negri Sembilan, and on Kedah Peak, and also on the hills of Patani up to about 3000 feet" (Robinson, Birds of the Malay Peninsula, vol. 2, 1928, p. 163). Both forms have been taken at Ginting Bidei at an elevation of 2,300 feet.

Criniger ochraceus sumatranus WARDLAW RAMSAY.

Criniger sumatranus WARDLAW RAMSAY, Ann. and Mag. Nat. Hist., ser. 5, vol. 10, No. 60, December 1882, p. 431 ("M[ount]. Sago" [*ca.* 70 miles northeast of Padang, which lies at lat. 0°58′ S., long. 100°21′ E.], Sumatra).

Range.—Highlands of western Sumatra.

Criniger ochraceus ruficrissus BOWDLER SHARPE.

Criniger ruficrissus BOWDLER SHARPE, Proc. Zool. Soc. London, for 1879, pt. 2, August 1879, p. 248 (Kina Balu [lat. 6°05′ N., long. 116°30′ E.], North Borneo).

Range.—Highlands of northern Borneo.

Remarks.—Although some authorities prefer to treat *ruficrissus* as a monotypic species, I look upon it as merely a strongly marked geographical representative of *ochraceus.* It is apparently sympatric in northern Borneo with *Criniger bres gutturalis* (see Finsch, Notes from the Leyden Museum, vol. 26, 1905, p. 106).

CRINIGER BRES (Lesson), 1832

Criniger bres tephrogenys (JARDINE AND SELBY).

Trichophorus tephrogenys JARDINE AND SELBY, Illustrations of Ornithology, ser. 1, vol. 3, pt. 9, February 1833, pl. 127 and text (". . . though we are uncertain of its locality, we suspect it to be Indian"; type locality corrected to Malacca, by Hartert, Nov. Zool., vol. 9, 1902, p. 558).

Range.—Southern Tenasserim (one specimen from the Mergui District in Liverpool, *ex* Coll. Tristram); peninsular Thailand southward from the Isthmus of Kra; Malaya; lowlands of eastern Sumatra.

Remarks.—Criniger bres tephrogenys is apparently sympatric in southern Tenasserim and peninsular Thailand with *Criniger ochraceus sordidus,* and in Malaya with *Criniger ochraceus sacculatus.*

Criniger bres gutturalis (BONAPARTE).

T[*richophorus*]. *gutturalis* "Müll. Mus. Lugd." BONAPARTE, Consp. Gen. Av., vol. 1, 1850 or 1851, p. 262 (Borneo type specimen from Banjermasin [lat. 3°20′ S., long. 114°35′ E.], *fide* Finsch, Notes from the Leyden Musuem, vol. 26, 1905, p. 105).

Range.—Borneo.

Remarks.—This form is apparently sympatric in northern Borneo with *Criniger ochraceus ruficrissus* (see Finsch, *loc. cit.,* p. 106).

Criniger bres frater BOWDLER SHARPE.

Criniger frater BOWDLER SHARPE, Trans. Linn. Soc. London, ser. 2, vol. 1, pt. 6, November 1877, p. 334 (Puerto Princesa, Paláwan Island, Philippine Islands).

Range.—Paláwan.

Criniger bres bres (LESSON).

Turdus gularis HORSFIELD, Trans. Linn. Soc. London, vol. 13, pt. 1, May 1821, p. 150 (Java).

Lanius Bres LESSON, *in* Bélanger, Voyage aux Indes-Orientales, pt. 4, August 1832, p. 255 (Java; type locality here restricted to Bogor [Buitenzorg]). New name for *Turdus gularis* Horsfield, Trans. Linn. Soc. London, vol. 13, pt. 1, May 1821, p. 150 (Java), not *T*[*urdus*]. *gularis* Latham, 1801.

Trichophorus xanthizurus OBERHOLSER, Smithsonian Misc. Coll., Quarterly Issue, vol. 48, No. 2, July 1, 1905, p. 152. New name for *Turdus gularis* Horsfield (*vide supra*), not *T*[*urdus*]. *gularis* Latham, 1801.

Criniger balicus bartelsi COLLIN AND HARTERT, Nov. Zool., vol. 34, No. 1, August 10, 1927, p. 51. New name for *Turdus gularis* Horsfield (*vide supra*), not *T*[*urdus*]. *gularis* Latham, 1801.

Range.—Western and central Java.

Remarks.—Since two forms of the species are known from Java, it is important to know which one is represented by Lesson's type specimen. Bélanger (Voyage, pp. xxix-xxx) says: ". . . j'entrepris, . . . un nouveau voyage aux îles de la Sonde. Le détroit de ce nom, une partie de la côte orientale de Java, les districts de Bantam et de Buitenzorg dans cette île, furent les lieux principaux soumis à mes recherches." In short, Bélanger's collections were made within the ranges of *both* races.

It is no longer possible to solve the problem by examination of Bélanger's material. In reply to my query, Professor Berlioz has written: "I am sorry to say definitely that we do not possess this type of Lesson nor any bird which might be eventually considered as such. In fact there are extremely few birds here originated in Bélanger's travel—and in very bad condition—and if ever this bird came to our Museum it is not impossible that it would have been destroyed, as there is no trace of it even in our old register."

In the circumstances, I am justified in fixing a type locality for Lesson's *bres,* and have chosen Bogor (Buitenzorg) as a place visited by Bélanger and one at which commonly occur birds clearly assignable to the more western race.

Criniger bres balicus STRESEMANN.

Criniger gularis balicus STRESEMANN, Nov. Zool., vol. 20, No.2, June 17, 1913, p. 358 (Gitgit, Bali Island).

Range.—Eastern Java and Bali.

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LOOP DEVELOPMENT OF THE PENNSYLVANIAN TEREBRATULID CRYPTACANTHIA

(With 2 Plates)

By

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The silicified specimens forming the subject of this discussion are unusual in preserving parts or all of the internal skeleton in youthful individuals as well as adults. They were dissolved from Magdalena limestone taken from a ledge on the north side of an arroyo just east of the Grapevine Canyon road one-eighth mile south of Old Juniper and a cattle tank, about in the center of the W$\frac{1}{2}$SE$\frac{1}{4}$SW$\frac{1}{4}$ sec. 25, T. 19 S., R. 11 E., Escondido Canyon (15′) Quadrangle, Otero County, N. Mex. These fossils and others described earlier from the same place (Cooper, 1956) are from 30 to 40 feet below the top of the Magdalena formation.

The bed containing these fossils is a gray, fine-grained limestone containing a large amount of light-gray insoluble material and numerous other brachiopods, among which are: *Cleiothyridina, Punctospirifer, Stenoscisma, Dielasma,* and smaller forms still to be identified. Immature forms of several of the genera are very abundant and some small specimens appear to be adults of an undescribed genus. Gastropods and pelecypods are fairly common but their preservation is poor.

One of the most abundant brachiopods in this limestone is the hitherto poorly known and extremely rare genus *Cryptacanthia.* Although this genus has been identified in many areas of Pennsylvanian rocks, it is one of the rarest of all Pennsylvanian fossils. The original specimens on which the genus was based come from Iowa but it is known in adjacent Illinois and Missouri. It occurs in the Gaptank formation in west Texas and is known elsewhere in New Mexico and Kansas besides the occurrences mentioned above. The genus was described by White and St. John (1867) but little has been written about it since then. Dunbar and Condra (1932) redescribed the genus and added another species from the early Permian. Study of the specimens described herein and of another preparation of the loop of *Cryptacanthia* from Madison County, Iowa, shows that this structure was improperly restored by Dunbar and Condra.

About a dozen blocks of various sizes were collected at the locality in Grapevine Canyon. These yielded about 4,000 specimens of *Cryptacanthia,* including many with almost perfect interiors and some with the loop preserved to perfection. These specimens permit a nearly complete description of the development of the loop and other details of the interior. This is the first Paleozoic long-looped brachiopod in which the stages of loop development have been described.

In comparing the New Mexico specimens with those from Iowa, which are topotypes, it was discovered that the ones from the Southwest are clearly a new species for which the name *Cryptacanthia prolifica* Cooper is here proposed.

CRYPTACANTHIA PROLIFICA Cooper, new species

Small, pentagonal in outline, length and width nearly equal but varying from an oval outline in the young to subpentagonal in the adult; inequivalve, the pedicle valve having the greater depth, posterolateral margins nearly straight forming an angle at the beak of 105° to 110°; sides narrowly rounded; anterolateral margins gently concave to straight; anterior margin truncated to gently emarginate; greatest width at about midvalve but variable with age; anterior commissure strongly sulcate; surface smooth.

Pedicle valve evenly and strongly convex, with the maximum convexity at the middle; anterior profile narrowly domed with steep, concave sides; beak small, incurved, suberect to erect; foramen elongate-elliptical, mesothyrid to submesothyrid; deltidial plates conjunct; umbo narrow, moderately convex; fold originating on anterior side of umbo, widening anteriorly to front margin, somewhat flat-topped and with a sulcus originating at about midvalve; umbonal slopes gentle, anterolateral slopes precipitate.

Brachial valve shallow, evenly and gently convex in lateral profile; anterior profile nearly flat but with a shallow median depression; umbo gently swollen; sulcus originating just anterior to the umbo, widening and deepening anteriorly to the front margin; sulcus in many specimens with a low, indistinct fold originating just anterior to midvalve and extending to the front margin; flanks bounding sulcus gently convex.

Interior.—See Internal Morphology, below.

MEASUREMENTS IN MILLIMETERS

	Length	Brachial length	Maximum width	Thickness
Holotype	7.0	6.3	7.4	4.5
Paratype 127067a	8.9	7.8	8.9	5.1
“ 127067b	8.5	7.5	8.7	4.9
“ 127067c	8.0	7.1	7.9	5.0
“ 127067d	7.5	6.7	8.2	4.7
“ 127067e	7.5	6.9	7.4	3.7
“ 127067f	7.0	6.2	6.5	3.8
“ 127067g	6.5	5.8	6.4	3.8
“ 127067h	6.0	5.5	5.9	3.2
“ 127202a	5.6	4.8	5.3	2.6
“ 127202b	5.0	4.6	4.5	2.4
“ 127202c	4.5	3.9	3.8	1.9
“ 127202d	4.0	3.5	3.6	1.6
“ 127202e	3.5	3.0	3.0	1.2
“ 127202f	3.0	2.5	2.5	1.1
“ 127202g	2.5	2,4	2.4	0.8
“ 127202h	2.0	1.7	1.7	0.75
“ 127202i	1.5	1.25	1.3	0.56
“ 127202j	1.1	0.87	0.94	0.44

Types.—Holotype, U.S.N.M. No. 127066; figured paratypes, U.S.N.M. Nos. 127202j, k, s, u, w, z; 127203h, i, l; 127204c, h, l, n, o, q, s, t; 127205h-j, l, m-q, s, t; 127206k, r; 127207p; measured paratypes, U.S.N.M. Nos. 127202a-j; 127067a-h; unfigured paratypes, U.S.N.M. Nos. 127202l-r, t, v, x; 127203a-g, j, k, m-z; 127204a, b, d-g, i-k, m, p, r, u-z; 127205a-g, k, r, u-z; 127206a-j, l-q, s-z; 127207a-o, q-z; 127208a-z; 127209.

Discussion.—The New Mexico specimens differ from *Cryptacanthia compacta* White and St. John in details of the interior as well as of the exterior. The Iowa species is much more robust and is much thicker than *C. prolifica.* In lateral profile the extremely deep pedicle valve of *C. compacta* has a pronounced bulge in it about a third the length from the anterior margin. This is a prominent feature of the species. A similar bulge occurs in *C. prolifica* but it is not so strongly marked as in the Iowa species. Furthermore *C. prolifica* is somewhat squarer in outline, especially when seen from the dorsal side, and has very distinct posterolateral shoulders. These features are not so prominent in the Iowa species which has much more rounded contours especially in the adult form. The New Mexico species is thus a more slender one, even the largest specimens never attaining the great thickness of *C. compacta.*

The differences between the loops of the two species is very pronounced and is described below in connection with the loop of *C. prolifica.* (See text figure 1.)

EXTERNAL MORPHOLOGY OF *CRYPTACANTHIA PROLIFICA*

The abundant material on hand from the Magdalena limestone permits a detailed account of this species. Although the preservation is poor in many instances it is, nevertheless, possible to determine most of the features of the shell.

Growth.—The smallest specimen (pl. 1, D, fig. 7) that could be identified with certainty as *Cryptacanthia prolifica* is paratype U.S.N.M. No. 127202j which is 1.1 mm. long, length of brachial valve 0.87 mm., maximum width 0.94 mm., and thickness 0.44 mm. The specimen is oval in outline and has the maximum width at about the middle. The brachial valve is deeper than the pedicle valve, a condition opposite to the adult, and the anterior commissure is uniplicate. The beak is straight, blunt, and has an open delthyrium.

The pedicle valve of this specimen is nearly flat in lateral profile but with gentle curvature at the umbo. The anterior profile is broadly and gently convex. The umbonal and medial regions are gently swollen.

The brachial valve of this small specimen is gently convex in lateral profile but with the posterior half more convex than the front half which is somewhat flattened. The anterior profile is broadly and moderately convex, most convex in the middle and with long sloping sides. The umbo is somewhat narrowly swollen.

The smallest specimens are distinctly elongate-oval in outline and do not have the angularity so characteristic of the adult specimen. Sulcation of the anterior commissure starts at about the 2 mm. stage. At this stage, too, the shell begins to widen somewhat and develops some of the shouldered appearance of the adult. The young specimens remain distinctly elongate-oval until they reach about 6 mm. After 6 mm., specimens appear that have length and width equal, but no specimen smaller than 5.9 mm. was measured with length and width equal. The larger specimens generally have length and width more nearly equal than those less than 6 mm. long. All the specimens measured above 8 mm. have the length and width equal or the length slightly less than the width.

After sulcation appears at 2 mm., the sulcus becomes deeper and deeper with age. In old adults the fold becomes sulcate anteriorly. This produces emargination at the front. This is usually not strong, but a few specimens appear that are fairly deeply emarginate.

From the earliest stage seen to about 3 mm. the delthyrium acts as the foramen. After about 3 mm., small triangular deltidial plates appear in the lower angles of the delthyrium. These gradually grow to restrict that opening. After about 3.5 mm., the deltidial plates become conjunct and in late adult stages may develop an incipient reflected lip on the posterior margin. The deltidial plates never seal the line of junction to produce a symphytium.

INTERNAL MORPHOLOGY OF *CRYPTACANTHIA PROLIFICA*

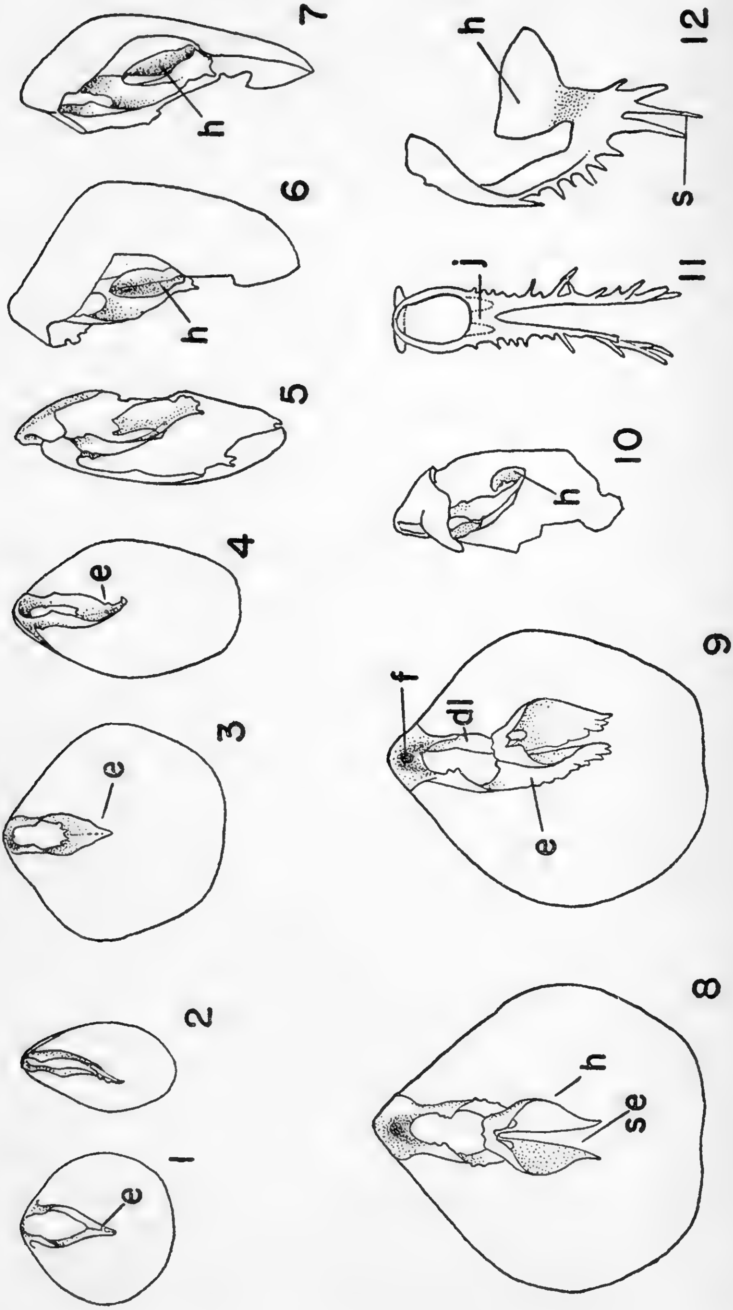
Changes of great interest and importance take place in certain structures inside *C. prolifica,* especially in the development of the loop and the hinge plate.

Interior of the pedicle valve.—The valves are firmly articulated and the processes of silicification have added to the difficulties of separating the shells. Consequently the teeth have not been seen except in the articulated state where they appear to be long, slender, and somewhat curved.

Dental plates were seen in one of the smallest stages, 1.5 to 2 mm., and it is therefore inferred that they would appear also in earlier stages. In the youngest stage seen they are receding but vertical. In the large adult they are no longer receding, are still vertical but quite stout. They are actually slightly advancing at their anterior ends and the floor of the delthyrial chamber is somewhat thickened. No details of the musculature could be determined. The valves are generally thin-shelled and the inner surfaces are not well preserved.

Interior of the brachial valve.—The most important part of the brachial valve is the cardinalia consisting of the hinge plates and the loop. Like the brachial valve no trace of the muscle scars could be determined. The median septum, or ridge, is not a conspicuous feature of this genus.

DEVELOPMENT OF THE HINGE PLATE: In the earliest stage, 1.6 to 2.0 mm. (U.S.N.M. No. 127202k), in which the cardinalia are clearly visible (pl. 2, A, fig. 1), the socket plate is a subtriangular ridge fused with the crural base on the inner wall of the valve. Buttressing the crural base is a small plate, barely visible and converging medially to join the floor. These supporting plates do not unite on the floor of the valve. Little change could be noticed in any of these plates in the next succeeding stages to the 3.1 to 3.5 mm. stage.



FIGS. 1-12
(See legend on opposite page.)

In the 3.0 to 3.5 mm. stage the buttress plates unite on the floor of the posterior chamber and in the succeeding stage (3.6 to 4.0 mm.) gradually are raised as a distinct plate above the floor at the rear of the valve. A specimen 3.4 mm. long (U.S.N.M. No. 127202l) has a complete inner hinge plate with the anterior margin free but the posterior sessile and imperforate. After the 4.0 mm. stage the hinge plate consists of a single piece, commonly with a slight, or even pronounced, convex flexure but with a round or longitudinally oval foramen at the rear (pl. 1, E, fig. 22). A few specimens have no foramen but the adult generally is so provided.

DEVELOPMENT OF THE LOOP: The collection here described does not include the complete development of the loop because no specimens smaller than 1 mm. were hollow and none of this size showed the loop. The earliest stages (0 to 1 mm.) must therefore be inferred.

FIGS. 1-12

All drawings by Lawrence B. Isham, scientific illustrator.

ABBREVIATIONS

dl—descending lamella
e —echmidium
f —foramen in hinge plate
h—hood
j —jugum
s—spines
se—split in echmidium

Figs. 1-10, *Cryptacanthia prolifica* Cooper, new species:

1. Specimen in the 2.1-2.5 mm. stage showing slender lamellae and echmidium, × 10. (See pl. 2, B, fig. 3.) Margin restored. Paratype U.S.N.M. No. 127202s.
2. Same as above seen from the side and showing long point of echmidium, × 10.
3. Specimen in the 3.1-3.5 mm. stage showing a stouter echmidium, × 10. Paratype U.S.N.M. No. 127203g.
4. Same as preceding but turned to side to show point of echmidium, × 10.
5. Specimen in the 4.1-4.5 mm. stage showing a small but well-formed hood on the point of the echmidium, × 8. (See pl. 2, F, fig. 10,) U.S.N.M. No. 127204h.
6. Same specimen as preceding but turned to show elliptical opening of the early-formed hood, × 8.
7. Same specimen as preceding, only slightly turned to the side but showing the small cuplike hood, × 8. (See pl. 2, F, fig. 11.)
8. Specimen in the 4.6-5.0 mm. stage showing fully formed and notched hood, × 8. Paratype U.S.N.M. No. 127204t. (See pl. 1, I, fig. 27.)
9. Same as preceding but loop seen partially from side, × 8.
10. Specimen in the 3.1-3.5 mm. stage showing incipient hood on tip of echmidium, × 10. Paratype U.S.N.M. No. 127203i. (See pl. 2, D, fig. 7.)

Figs. 11, 12, *Cryptacanthia compacta:*

11. Dorsal view of the loop of *Cryptacanthia compacta* showing the long spines, deep cleft, jugum, and short descending lamellae. Dotted lines indicate where part of loop was dissolved away but jugum is intact. (Compare pl. 1, A, fig. 1.) Hypotype U.S.N.M. No. 9382a.
12. Same as preceding but showing loop from side with its long spines, prominent erect hood, and long descending lamellae. (Contrast with profile of loop of *C. prolifica*, pl. 2, H, fig. 16.)

Stages 1.1 to 1.5 mm.: The smallest specimen (U.S.N.M. No. 127202m) showing traces of the loop is a brachial valve 1.25 mm. long and had a pedicle valve estimated to be 1.50 mm. long. In this specimen only the descending lamella on one side is visible as a thin and delicate ribbon with an angular bend medially at about midvalve (0.4 mm. anterior to the brachial beak). The fact that the descending branch bends medially suggests that at this stage the anterior ends of the loop were united. It is probable that in stages below 1.0 mm. only the initial stages of the descending lamellae are present and are not bent medially at their distal ends.

Stages 1.6 to 2.0 mm.: Two specimens (U.S.N.M. Nos. 127202k, 127202n) measuring between 1.5 and 2.0 mm. in length exhibit the loop. Specimen U.S.N.M. No. 127202n is exactly 2.0 mm. long and 1.68 mm. wide. The entire loop is not visible but the pointed anterior can be seen and indicates a loop of about 0.8 mm. in length. The loop of the other specimen (U.S.N.M. No. 127202k) is broken on one side (pl. 2, A, fig. 1) but the descending branches are thin and delicate and bent medially about 0.4 mm. anterior to the beak. These two specimens thus indicate a loop of about 0.8 mm. in length, the lateral branches of which bend medially and unite distally in a sharp point.

Stages 2.1 to 2.5 mm.: Information on these stages is based on 5 specimens (U.S.N.M. Nos. 127202-o, p, q, r, s). Three of the specimens are 2.4 mm. long and 2.0 mm. wide, but two are 2.3 mm. long and 2.0 mm. wide. The loop varies in length from 1.0 to 1.2 mm. The loop is much stouter than in the preceding stage and the crural processes are visible as blunt points. The angular bend of the descending lamellae is present and the two branches unite distally to form a sharp, angular, pointed plate not greatly extended anteriorly. The line of junction between the descending branches varies from 0.3 to 0.4 mm. The descending lamellae thus unite to form a spear-shaped plate here called the *echmidium*.[1] This name is introduced because, in the development of the loop, the spear-shaped plate becomes increasingly prominent and ultimately is the site on which grow the ascending elements of the loop. At the 2.1 to 2.5 mm. stages no ascending elements or their beginnings were seen in any of the specimens.

Stages 2.6 to 3.0 mm.: Thirteen specimens with this range, having the loops preserved, appear in the collection (U.S.N.M. Nos. 127202t-z, 127203a-f). The length of the loop averages 1.33 mm. and

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[1] Echmidium is derived from *aichmidion,* diminutive of *aichme,* point of a spear. The *ai* is transliterated *e.*

the length of the echmidium averages 0.55 mm. The descending lamellae are thicker and broader than in the previous stages and the bend medially is less pronounced, but the form of the loop is essentially the same. The echmidium is broader and longer and now has a long, sharp point. The crural processes are somewhat more pronounced and have sharper points than in the preceding stages. Some variation exists in the stoutness of all the elements, but generally they are stronger than the preceding. No ascending elements appear in these stages but traces of them are suspected. In two instances (U.S.N.M. Nos. 127202s, w) a ridge along the center of the echmidium is suggestive of an incipient development of the hood.

Stages 3.1 to 3.5 mm.: Seven specimens in this range preserve the loop (U.S.N.M. Nos. 127202l, 127203g-k, 127206k). In these the loop averages 1.48 mm. in length and the echmidium averages 0.65 mm. long. The shortest loop is 1.4 mm. long in a specimen 3.1 mm. long and is 1.6 mm. long in a specimen 3.5 mm. long. This interval sees the appearance of the hood. The best specimen (U.S.N.M. No. 127203i) to show this is about 3.2 mm. long with a loop 1.5 mm. long and with an echmidium 0.8 mm. long which is remarkable for the attenuation of the anterior point and the presence on this point of the first bud of the hood (pl. 2, D, fig. 7). This is 0.56 mm. long measured in the direction of shell length and is 0.24 mm. in height measured at right angles to the length. The line of contact with the echmidium is 0.24 mm. long and is located at the very end of the attenuated tip. The delicacy of this structure and its flimsy contact with the echmidium evidently account for the rarity of its preservation. The ventral face of the hood cannot be directly seen but the hood from the dorsal side appears to be elliptical and must therefore form an elliptical opening on the ventral side. From the dorsal side the echmidium shows well the suture between the two descending elements at the line of junction. At the anterior tip of the echmidium a faint trace of divergence laterally of the joined descending and ascending elements foreshadows the deep cleft in later stages.

Stages 3.6 to 4.0 mm.: Five specimens (U.S.N.M. Nos. 127203l, m, n, o, p) exhibit these stages of the loop, which has become stout, and the echmidium long, wide, and pointed but still undivided. The loop varies in length from 1.6 to 1.8 mm. and the echmidium is 0.88 to 1.0 mm. long. In two specimens (U.S.N.M. Nos. 127203n, 127203-o) the latter plate is 0.60 mm. wide but is still undivided at its anterior tip. Two specimens (U.S.N.M. Nos. 127203l, m) show the hood, the former showing the posterior half (pl. 2, E, fig. 9) and the latter the anterior half. The attachment of the hood to the echmidium is 0.7 mm. long and the hood varies from 0.35 to 0.5 mm. in width. The conical hood tapers rapidly in a posterodorsal direction.

Stages 4.1 to 5.0 mm.: Twelve specimens (U.S.N.M. Nos. 127203r-z, 127204c, d, h) in this size range exhibit the loop in various stages of completeness. The loop varies in length from 2.2 to 2.9 mm. but averages about 2.4 mm. The echmidium varies from 0.8 to 1.8 mm. in length and has a maximum width of 0.64 mm. Specimen U.S.N.M. No. 127204h is 4.8 mm. long and has one of the best preserved loops in this interval (pl. 2, F, figs. 10, 11). The descending lamellae are broad and flatten anteriorly on the echmidium and become nearly vertical. At the anterior end they flare laterally and unite with the lateral walls of the hood. The ventral margin of the hood slopes rapidly posterodorsally, the hood narrowing in that direction. The posterior surface of the hood is short and narrowly convex. Thus in ventral view it expands laterally but with a deep reentrant dorsally. The lateral flaring of the outer walls of the hood is the beginning of the anterior cleft of the echmidium so prominent in succeeding stages. In this specimen the cleft is 0.5 mm. long. The loop at this 4.1 to 5.0 mm. stage is thus an adult one but the anterior cleft is short. The cleft in the anterior point of the echmidium in a smaller specimen (U.S.N.M. No. 127203r) in this range is small and is noticeable only in the hood. The cleavage of the echmidium is thus initiated when the shell has attained slightly more than 4 mm. of length. Specimens of 5 mm. length show a deep cleft in the hood, about 1 mm. deep in specimen U.S.N.M. No. 127203z. The hood in this specimen is 1.5 mm. long and 1 mm. wide.

Stages 5.1 to 6.0 mm.: Four specimens (U.S.N.M. Nos. 127204k, m, t, u) in this group preserve the loop in most of its details. It is substantially the same as that of the late stages of the previous group but some modifications are evident. The cleft in the echmidium is now deeper, almost half the length of the loop which varies from 3.1 mm. to 3.6 mm. in length. The junction of the lateral branches is short and the reentrant in the hood on the posterior side is deeper in most instances but this appears to be a variable feature. The spines on the anterodorsal side of the loop are long and in two rows anterior to the junction of the lateral branches. The longest spine measures 0.4 mm. in length. The hinge plate in all members of this group is complete and usually perforate. In specimen U.S.N.M. No. 127204t, the loop is 3.6 mm. long, the hood is 1.9 mm. long, the cleft is 1.3 mm. deep, and the hood is 1.2 mm. wide (pl. 1, I, figs. 26, 27; pl. 2, G, figs. 13, 14).

Stages 6.1 to 7.0 mm.: Five specimens (U.S.N.M. Nos. 127204-o, q, u-w) with loops represent this stage. Anteriorly the lateral branches of the loop are distinctly separated. The hood is 1.6 mm. wide and the posterior surface is long, broadly rounded, and only moderately reentrant. The anterodorsal edge is marked by a double row of fairly strong spines. The loop varies in length from 3.6 mm. to 4.4 mm. and the maximum length of the hood is 2.8 mm. (pl. 2, H, figs. 16-18).

Stages 7.1 to 8.0 mm.: One specimen only (U.S.N.M. No. 127204l) in this range shows the loop (pl. 2, I, fig. 19). The specimen is 7.5 mm. long and 7.2 mm. wide and its loop measures 4.4 mm. in length and the hood is 2.8 mm. long. The anterior spines are long. It is appropriate that at this place the adult loop be described because only one other change in it takes place.

The loop of these stages has the crural bases hidden by the complete hinge plate which is buttressed against them. The descending branches are short and stout, only 0.7 mm. of broad, flat ribbon intervening between the hinge plate and the echmidium. The crural processes are given off just anterior to the hinge plate and are short, bluntly pointed projections of 0.1 to 0.2 mm. The descending lamellae are about 0.5 mm. wide. The echmidium is broad and deeply cleft anteriorly, 1.9 mm. in a loop 4.6 mm. long. The junction or jugum between the descending lamellae is 0.62 mm. long in the above loop, or less in others, and is a narrow plate. The descending lamellae posteriorly face each other and their narrow edge is perpendicular to the inner surfaces of the valves. Anteriorly these ribbons turn about 90° to become parallel with the inner valve surfaces and at the same time become fairly deeply concave and narrow distally. The hood rests on the inner ventrally curved edge of the descending lamellae. Anteriorly the hood is a widely flaring cone, expanded above but narrowing dorsally. It also narrows posterodorsally with an opening half or less of the anterior dimensions. The base of the hood is continued posteriorly beyond its narrow termination as two converging septa which unite to form a low ridge at the proximal end of the echmidium (pl. 2, I, fig. 20). The posterior side of the hood varies from round to nearly flat and with its anterior deeply notched (pl. 1, I, fig. 26) or with only a slight trace of indentation (pl. 2, I, fig. 20). The notch is a variable feature which appears to be more prominent and more uniform in smaller stages. Seen from the side the descending lamella forms a keel along the dorsal side of the loop, the base of the hood is deeply concave and the hood itself bulges prominently in a lateral direction. The ventral surfaces of the descending lamellae are convex and spinose, one set of spines on the outer edge and the other coming off the inner convex face.

A single specimen (U.S.N.M. No. 127205h) measuring 7.9 mm. in length and 8.3 mm. wide is unique in showing unequivocally the two descending branches free of each other (pl. 2, I, fig. 21). In this specimen the jugum has been resorbed because no evidence of breakage on the descending ribbons can be seen. This is the ultimate state in the development of the loop.

Stages 8.1 to 9.0 mm.: A single specimen with loop (U.S.N.M. No. 127204e, not figured) representing these stages measures 8.6 mm. long by 8.4 mm. wide and is one of the largest specimens in the collection. The loop is 5.6 mm. long and the hood is 3.7 mm. long by 1.9 mm. wide. The hood is only moderately notched on the posterior side. The descending lamellae lie very close together but the jugum has been resorbed and the descending branches are free, the ultimate condition for the loop. If larger specimens exist it is likely that the only further change in the loop would be gradual lateral migration of the descending lamellae so that they would be more distantly spaced and subparallel.

Median septum (or ridge): No distinct septum or median ridge was seen in specimens from 1.0 mm. to 3.5 mm. After the latter length is attained a median ridge is discernible but even in large adults it is not a conspicuous feature of the shell. It is apparent that the ridge or septum never shared in the development of the loop as it does in so many modern long-looped brachiopods.

Summary of loop development of *Cryptacanthia.*—The development of the loop in stages below 1 mm. can only be inferred from the early stage in the loop development of other brachiopods. In the earliest stages it is postulated that the loop originated as two processes growing anteriorly from the hinge region, the descending branches developing an angular bend medially and finally uniting distally at about the 1 mm. stage. The descending lamellae in these stages would be thin and delicate and no echmidium would have been formed (precentronelliform stage).

After the 1 mm. stage the loop begins to thicken and at the place of junction of the distal ends of the descending lamellae the joined elements widen and flatten to form a plate having the shape of a spearhead and here called the echmidium (centronelliform stage). After the formation of the central echmidium the loop continues to strengthen, but at the anterior tip of the echmidium a bud appears in the form of a small elliptical cup. This is the incipient hood (early cryptacanthiform stage). In succeeding stages this structure expands and elongates with the growing loop. After the appearance of the hood the echmidium cleaves medially, the split lengthening and widening with growth of the loop (cryptacanthiform stage). In the final stage of development the anterior cleft is completed and the descending branches of the loop become freed of each other (early glossothyropsiform stage).

THE LOOP OF *CRYPTACANTHIA COMPACTA* WHITE AND ST. JOHN

Cryptacanthia compacta is the type species of the genus and for many years was the only known species. It is important therefore that the loop of the type species be clearly understood. As presently described and figured (Dunbar and Condra, 1932, pp. 307-309) the loop is depicted as a sort of cryptonelliform loop with long descending lamellae and long but fairly broad ascending elements. The figure of the loop given by Dunbar and Condra was reconstructed from serial sections. Study of the figured serial sections suggests that the ascending element is not properly restored and a new preparation of a loop inspired by this suspicion shows that it is entirely wrong.

The new preparation of the loop was made on a specimen from Madison County, Iowa, essentially a topotype. The preparation was not made by the usual sectioning method although it was my intention when I started the work to make serial sections. The first cut showed that the specimen was filled with clear calcite in two layers, an outer somewhat granular one and a solid inner layer of transparent light-brown calcite. On discovering this condition I scraped away the granular layer and part of the more solid mass beneath, washing frequently with acid to eliminate the needle marks. Soon a perfect loop was revealed which, however, was etched slightly too far on the dorsal side. This too liberal etching removed the bulging part of the echmidium but left the jugum joining the descending lamellae. Study of the photographs makes it clear that these descending lamellae were joined like those from New Mexico. The preparation also reveals the numerous and long spines on the dorsal side of the descending lamellae which inspired White and St. John to name the genus *Cryptacanthia*.

The specimen prepared was 5.3 mm. long and the loop measures exactly 4 mm. in length. On the dorsal side the descending lamellae are posteriorly distant but swing toward each other to be joined by a broad jugum 0.4 mm. long. Anteriorly from the jugum the descending lamellae are long and slender and diverge at a small angle. Their dorsal surface, from the posterior end of the jugum to the anterior tip, is provided with long, slender, needle-like spines, the longest one measuring 0.8 mm. in length. The descending lamellae anterior to the jugum diverge at a low angle and curve strongly in an anteroventral direction. At their distal end they bear an unusually large hood with very short attachment to the descending lamellae. The hood is greatly enlarged posteriorly where it measures 1.7 mm. in length but narrows to its base of attachment where it is only 0.5 mm. long. The hood is not attached posteriorly to the descending elements. In ventral view the hood flares widely, 1.4 mm. wide, and the posterior edge is deeply notched.

Comparison of the loop of C. compacta *with that of* C. prolifica.—The loops of these two species are strikingly different. Posteriorly, that of *C. compacta* has more widely spaced descending lamellae and the jugum attaching these lamellae is longer and wider. The striking difference however is in the hoods. That of *C. prolifica* in the adult form has a long attachment and the posterior part is often extended as converging septa posteriorly along the inner edges of the descending lamellae. The hood of *C. compacta* on the other hand is greatly expanded posteriorly and its attachment to the distal ends of the descending lamellae is very short. Only one loop of *C. compacta* was studied, but when this is compared with the many specimens of *C. prolifica* it seems evident that the loop of the Iowa species was provided with more and longer spines than that of the New Mexico species.

COMPARISON OF THE LOOP OF *CRYPTACANTHIA* WITH LOOPS OF OTHER PALEOZOIC GENERA

The best-known long-looped Paleozoic brachiopod is *Cryptonella* whose loop typifies one major type of Paleozoic loop. It is like the end stage of both types of modern terebratellid loops. In *Cryptonella* the loop is simple in form and very slender in both ascending and descending elements. The development of this loop is not yet known but it is one of the most ancient of terebratulid loops as it occurs in the early Devonian. It is an odd fact that one of the most highly specialized loops is actually one of the earliest. The loop of *Cryptacanthia* is not cryptonelliform although it simulates that loop in its late stages.

The loop most like that of *Cryptacanthia* is that of *Glossothyropsis*. Although the loop of the type species of *Glossothyropsis* is yet unknown, other species have been taken from the Monos formation of Mexico and the Word formation of Texas which show well-preserved loops. The loop approaches the cryptonelliform loop in form, but the ascending elements are usually fairly broad and suggest the origin of the *Glossothyropsis* loop from that of *Cryptacanthia*. Elimination of the jugum joining the descending elements of *Cryptacanthia* and narrowing of the ascending elements will produce the loop of *Glossothyropsis.*

The development of the external form of the two genera is also similar. *Glossothyropsis* is cryptacanthiform in its profiles and the disproportionate size of the two valves. The brachial valve of both genera is shallow. *Glossothyropsis* usually has a fairly strong median septum whereas that of *Cryptacanthia* is less well developed but far better developed than indicated by Girty. It is thus probable that *Glossothyropsis* is the ultimate stage of development of the cryptacanthiform loop. It is probable that the geologically youngest species of *Glossothyropsis* will be found with a loop advanced to the cryptonelliform condition by narrowing of the ascending elements.

COMPARISON OF THE LOOP STAGE OF *CRYPTACANTHIA* WITH LOOP STAGES OF OTHER TEREBRATULIDS

The only known long-looped late Paleozoic brachiopods are *Cryptacanthia, Glossothyropsis, Heterelasma,* and an unnamed genus with cryptonelliform loop. The loop development of only the first one is now known. As described here *Cryptacanthia* passes first through a centronelliform stage (stages 1.5 to 3.5 mm.). The centronelliform stage characterizes a number of the earlier Paleozoic genera, such as *Centronella, Nanothyris, Beachia, Oriskania, Rensselaeria* and a few others (Cloud, 1942). No other adult loop is now known which represents the stages between 3.0 mm. and the point at which the jugum is completely absorbed. These stages of development of the hood are here called the cryptacanthiform loop. When the descending lamellae are free and the hood is represented by a broad ascending element with a broad transverse ribbon the loop is similar to that of *Glossothyropsis* and is called the glossothyropsiform stage.

Comparison of these loop stages with the dallinid and terebratellid loops shows fundamental differences (Elliott, 1953). Both of the terebratellid families differ from *Cryptacanthia* in loop development in possessing a median septal pillar or septum in the initial stages. *Cryptacanthia* has only a modest median septum, and as revealed by *C. prolifica* this does not develop until the late stages of the ontogeny. Furthermore, the septum of *Cryptacanthia* is independent of the loop. In the terebratellids the median pillar is important because it is the site of development of the hood and median ring which produce the ascending elements of the adult loop.

The loop-development stages of the Paleozoic *Cryptacanthia* thus bear little resemblance to the stages of development of the terebratellid genera even though the glossothyropsiform loop is similar to the loop of *Dallina* or *Magellania.* The cryptonelliform loop, which consists of long, slender descending branches, slender ascending elements, and a slender transverse band, may be the ultimate stage in the development of the cryptacanthiform loop and is thus a parallel development of the ultimate terebratellid loop.

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EXPLANATION OF PLATES

Plate 1

Unless otherwise stated all specimens are from Grapevine Canyon locality.

A. *Cryptacanthia prolifica* Cooper, new species.

Figs. 1-3. Dorsal, ventral, and side views, respectively, of a complete loop, × 6, showing the rows of spines. From a specimen in the 7 to 9 mm. stage. Paratype U.S.N.M. No. 127205l.

B. *Glossothyropsis* sp.

Figs. 4, 5. Ventral and side views of the loop of a specimen from the Word formation, Glass Mountains, Tex., showing the narrow ascending elements and the free descending branches, × 2. Figured specimen U.S.N.M. No. 127254.

C. *Cryptacanthia prolifica* Cooper, new species.

Fig. 6. Side view of a specimen 7.5 mm. long showing aberrant hood with cavity in its attachment to the descending branches, × 6. Paratype U.S.N.M. No. 127204n.

D. *Cryptacanthia prolifica* Cooper, new species.

Figs. 7-21. 7, View of the pedicle valve of the smallest specimen recognized as *C. prolifica,* × 8, paratype U.S.N.M. No. 127202j. 8-12, A series of 5 specimens showing juvenile forms with their open delthyrium, × 4, paratypes U.S.N.M. Nos. 127205m-q, respectively. 13, View of the brachial valve of a complete specimen, × 1, showing size and form, paratype U.S.N.M. No. 127208z. 14, 15, Brachial views of two individuals more slender than normal, × 3, paratypes U.S.N.M. Nos. 127208y and 127205s. 16-20, Anterior, posterior, side, pedicle, and brachial views, respectively, × 3, of the holotype U.S.N.M. No. 127066. 21, Posterior half of a large adult showing the oval foramen and deltidial plates, × 6, paratype U.S.N.M. No. 127205t.

E. *Cryptacanthia prolifica* Cooper, new species.

Fig. 22. Posterior part of a brachial valve showing the cardinalia with the convex inner plate and its foramen, × 6, paratype U.S.N.M. No. 127205i.

F. *Cryptacanthia prolifica* Cooper, new species.

Fig. 23. Imperfect loop, × 6, with hood broken away to show the posterior extensions of the hood attachment and the jugum, paratype U.S.N.M. No. 127207p.

G. *Cryptacanthia prolifica* Cooper, new species.

Fig. 24. Partial side view of a small specimen, about 5 mm. long, showing small hood, spiny descending branches, and crural processes, × 6, paratype U.S.N.M. No. 127204s.

H. *Cryptacanthia compacta* White and St. John.

Fig. 25. Side view of a lump of calcite containing a complete loop, × 10, showing the small erect hood, hypotype U.S.N.M. No. 9382a. Specimen from Pennsylvanian, Madison County, Iowa. Photograph taken under water. Note long spines in lower left.

I. *Cryptacanthia prolifica* Cooper, new species.

Figs. 26, 27. Posterior and ventral views, respectively, of a perfect loop showing the anterior notch in the hood, anterior cleft, and the crural processes, ca. × 10, paratype U.S.N.M. No. 127204t. (For additional views see pl. 2, G, figs. 13, 14.)

PLATE 2

All figures of *Cryptacanthia prolifica* Cooper, new species, and all from Grapevine Canyon locality.

A. Stage 1.6-2.0 mm. (precentronelliform stage?).

Fig. 1. Early loop stage showing very slender and delicate loop, ca. × 15, paratype U.S.N.M. No. 127202k.

B. Stages 2.1-2.5 mm. (centronelliform stage).

Fig. 2. Specimen showing stouter descending branches than the preceding which unite to form an echmidium, × 8, paratype U.S.N.M. No. 127206r.

Fig. 3. Another brachial valve with well-preserved loop showing long, pointed echmidium, × 10, paratype U.S.N.M. No. 127202s.

C. Stages 2.6-3.0 mm. (centronelliform stage or possibly early cryptacanthiform stage).

Fig. 4. Brachial valve showing loop with echmidium and incipient bud (?) of the hood, × 10, paratype U.S.N.M. No. 127202u.

Fig. 5. The loop of another specimen, × 20, showing the elbow in the descending lamellae and the echmidium with a thickening, possibly the bud of the hood, paratype U.S.N.M. No. 127202w.

D. Stages 3.1-3.5 mm. (early cryptacanthiform stage).

Fig. 6. Specimen with pedicle valve partially removed to show loop and the small hood seen from the ventral side, × 8, paratype U.S.N.M. No. 127206k.

Fig. 7. Partial view from the dorsal side showing loop with small early hood, × 8, paratype U.S.N.M. No. 127203i.

Fig. 8. Another specimen showing trace of early hood, × 8, paratype U.S.N.M. No. 127203h.

E. Stages 3.6-4.0 mm. (cryptacanthiform stage).

Fig. 9. Specimen with part of brachial valve stripped off to show upper part of hood, × 8, paratype U.S.N.M. No. 127203l.

F. Stages 4.1-4.5 mm. (cryptacanthiform stage).

Figs. 10, 11. Side and partial side views of a specimen showing the small early hood and its slender attachment to the descending branches, × 8, paratype U.S.N.M. No. 127204h.

Fig. 12. Side view of another specimen showing hood with long posterior extension, × 6, paratype U.S.N.M. No. 127204c.

G. Stages 4.6-5.0 mm. (cryptacanthiform stage).

Figs. 13, 14. Ventral and side views of an exceptionally well-preserved adult loop, × 6, paratype U.S.N.M. No. 127204t. (For additional views of this specimen see pl. 1, I, figs. 26 and 27.)

Fig. 15. Imperfect loop from dorsal side, × 6, showing jugum, paratype U.S.N.M. No. 127203x.

H. Stages 5.0-6.0 mm. (late cryptacanthiform stage).

Fig. 16. Loop seen in side view and showing long attachment to descending branches and septumlike extensions posteriorly, × 6, paratype U.S.N.M. No. 127204q.

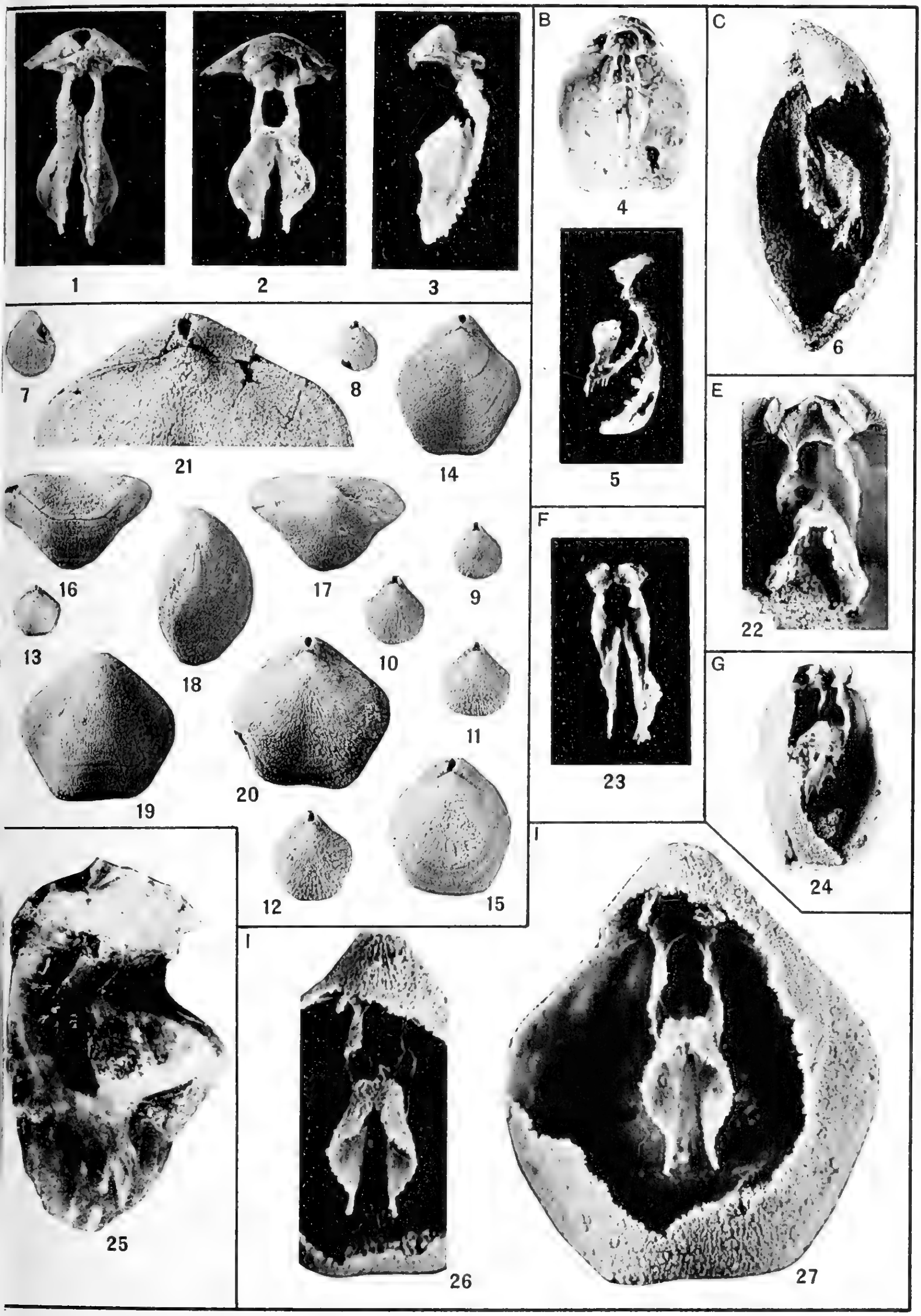
Figs. 17, 18. Two anterior views of a specimen showing the expanded hood, × 6, paratype U.S.N.M. No. 127204-o.

I. Stages 7.1-9.0 mm. (late cryptacanthiform to early glossothyropsiform stages).

Fig. 19. Adult loop seen from the laterodorsal view and showing the jugum, and the descending lamellae with their rows of spines, × 6, paratype U.S.N.M. No. 127204l.

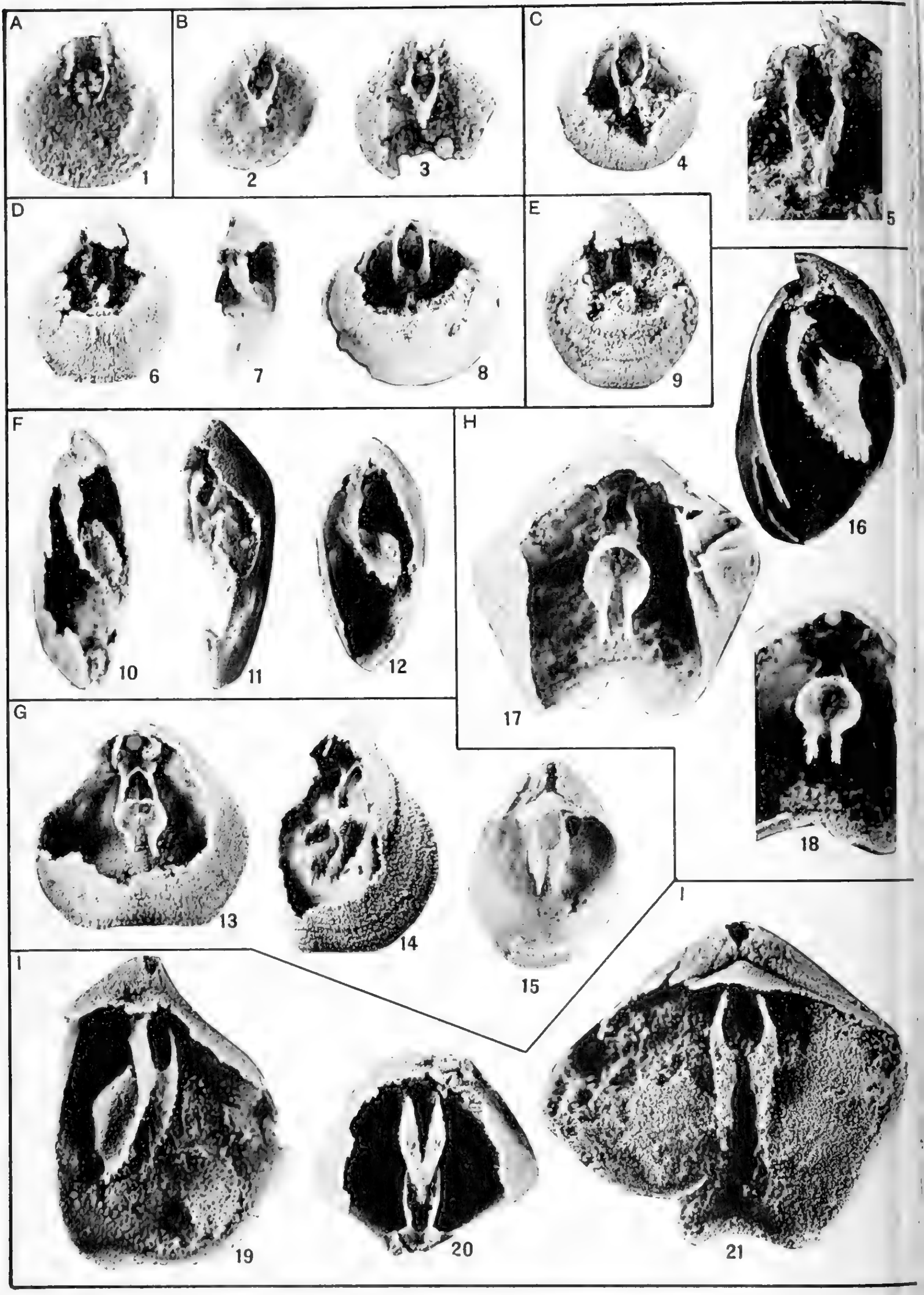
Fig. 20. Specimen seen from the posterior to show the posterior side of the hood, × 4, paratype U.S.N.M. No. 127205j.

Fig. 21. One of the largest specimens in the collection showing the descending lamellae from the dorsal side and absence of a jugum tying the branches together, × 6, paratype U.S.N.M. No. 127205h.



Cryptacanthia prolifica Cooper, new species, and Glossothyropsis sp.

(See explanation at end of text.)



CRYPTACANTHIA PROLIFICA COOPER, NEW SPECIES

(SEE EXPLANATION AT END OF TEXT.)

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THE GEOLOGY AND VERTEBRATE PALEONTOLOGY OF UPPER EOCENE STRATA IN THE NORTHEASTERN PART OF THE WIND RIVER BASIN, WYOMING

PART 1. GEOLOGY

(WITH 1 PLATE)

BY
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Geologist
United States Geological Survey

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Charles D. and Mary Vaux Walcott Research Fund

GEOLOGY AND VERTEBRATE PALEONTOLOGY OF UPPER EOCENE STRATA IN THE NORTHEASTERN PART OF THE WIND RIVER BASIN, WYOMING[1]

PART 1. GEOLOGY[2]

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(WITH 1 PLATE)

INTRODUCTION

GENERAL SETTING OF THE AREA

The northeastern part of the Wind River Basin described in this report includes the lower lands of the basin and parts of the bordering mountain ranges, which are the eastern part of the Owl Creek Mountains and the southern end of the Big Horn Mountains in Hot Springs, Fremont, and Natrona Counties, Wyoming (figs. 1 and 2). Lost Cabin and Lysite are the only towns within the area. Lysite is a station on the Chicago, Burlington, and Quincy Railroad and is about 8 miles north of Moneta, a town on U. S. Highway 20.

The Owl Creek and Big Horn Mountains are folded and faulted mountain ranges arranged in echelon and made up of pre-Cambrian and Paleozoic rocks with minor amounts of Mesozoic rocks along the outer flanks. The bordering part of the Wind River Basin is underlain by Tertiary strata of both early and late Eocene age. The younger Eocene strata consist of resedimented andesitic volcanic rocks and form a narrow belt adjacent to the mountains, and in part within them. These volcanic-rich strata are separated from the Wind River

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[1] Part 2 of this paper, "The Mammalian Fauna of the Badwater Area," by C. Lewis Gazin, appeared in Smithsonian Misc. Coll., vol. 131, No. 8, Oct. 30, 1956.

[2] Publication authorized by the Director, U. S. Geological Survey.

formation of early Eocene age on the south by a normal fault of large displacement.

The Wind River formation is a thick clastic one composed of the debris eroded from the Owl Creek and Big Horn Mountains during at least the later part of their structural deformation and growth. The Wind River formation is exceedingly coarse grained in the area of its outcrop closest to the mountains and finer grained away from the mountains. The strata of younger Eocene age are conspicuously different in appearance and composition, consisting of andesitic volcanic material derived from the volcanic centers in the Absaroka Range 70 miles to the west-northwest. Although some of the volcanic material probably was carried to the northeastern part of the Wind River Basin by streams, much of the material may have been transported aerially. The rocks include relatively little material eroded from the Owl Creek and Big Horn Mountains, which had their present form and very nearly their present topography at the time the rocks of middle(?) and late Eocene age were deposited.

HISTORY OF INVESTIGATION

The geology of the northeastern part of the Wind River Basin (fig. 1) has long been of interest because of the large faunas of vertebrate fossils that have been found in the Eocene strata there. J. L. Wortman, collecting in 1880 for E. D. Cope (Osborn, 1929, p. 160), appears to have been the first collector to enter the northeastern part of the basin. During the following years, classic collections were made from the Wind River formation in exposures along Cottonwood Creek and in a broad area east of Lost Cabin, and along Alkali Creek, just south of the map area shown in figure 2. These collections later provided the basis for the faunal definition of the latter part of early Eocene time. No fossils of younger Eocene age were found in early investigations although the younger strata are markedly different in lithology from the Wind River formation. Granger saw some of the strata now known to be of late[3] and probably middle(?) Eocene age and considered them to be a lower part of the Wind River sequence that is exposed on Cottonwood Creek (Sinclair and Granger, 1911, p. 105). The large fault that separates these two units was not recognized.

Granger's mention of the "dull-colored, deeply disintegrated clays

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[3] As used by the U. S. Geological Survey, late Eocene is equivalent to the Uintan age of most vertebrate paleontologists. The next younger age, Duchesnean, is classified by the Survey as Eocene or Oligocene.

with some feldspathic sandstone and much gypsum" is the only recognition of the younger Eocene rocks until Wood, Seton, and Hares (1936) announced the discovery of fossil mammals of late Eocene age from a locality on Badwater Creek (loc. 3, fig. 2). Love (1939, p. 78) compared the strata here with the Tepee Trail formation of late Eocene age in the Absaroka Range, where the formation consists of flows, breccias, and tuffs. Wood, Seton, and Hares recognized the fault that separates the strata of middle(?) and late Eocene age on the north from the Wind River formation on the south. In 1944, investigations of the geology of the area were begun by the U. S. Geological Survey to establish the structural relations between the Wind River Basin and the bordering Owl Creek and Big Horn Mountains and to map the geology of the area (Tourtelot, 1946, 1948, 1953).[4] Considerable emphasis was placed in these investigations on the Tertiary stratigraphy as a basis for interpreting the geologic history of the area. The fauna described by C. L. Gazin in Part 2 of this report was discovered during this work. The fauna was enlarged by collections made by A. E. Wood (1949) and by C. L. Gazin and Franklin Pearce in 1946 and 1953.

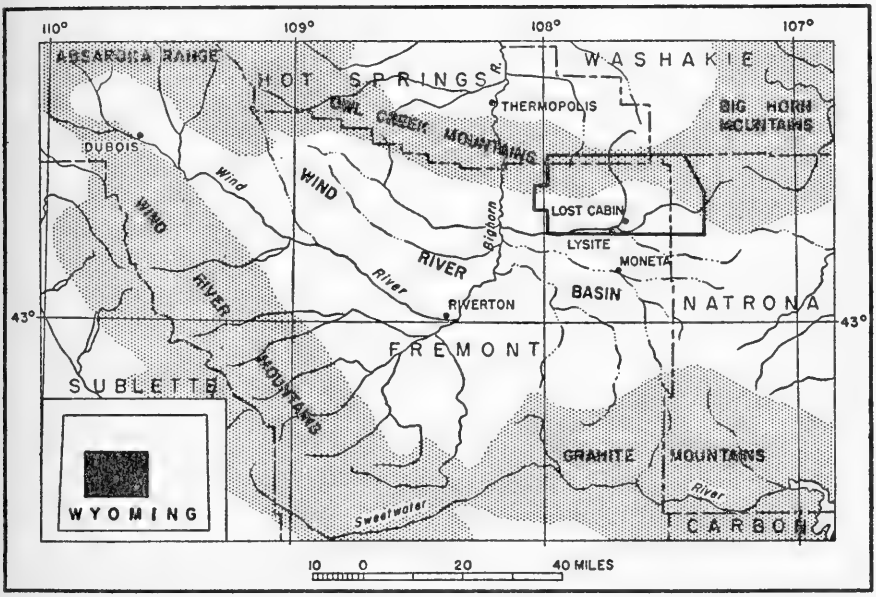

FIG. 1.—Sketch map showing location of area discussed in this report.

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[4] Data from these publications are included in this report without direct citation, for the most part.

ACKNOWLEDGMENTS

I am deeply grateful to J. D. Love for guidance and inspiration during the field investigations, which were carried out under his supervision. His knowledge of deposits of Tertiary age in Wyoming and the geology of that State, freely shared, enabled me to place concepts developed from observations in the northeastern part of the Wind River Basin within the framework of the regional geologic history. G. Edward Lewis aided greatly during the fieldwork by supplying prompt identifications of fossil vertebrates submitted to him for study and by participating in many helpful discussions of stratigraphic problems. The enthusiasm and constant encouragement of Dr. Gazin have aided much in the preparation of this report. E. B. Wasson assisted in the fieldwork in 1945 and R. A. Christman in 1947; both were able and pleasant field companions. I am indebted also to the residents of the area for many helpful courtesies. Particular mention should be made of Mr. and Mrs. R. W. Spratt, Mr. and Mrs. Frank Rate, and Mrs. William Twidale and the late Mr. Twidale.

STRATIGRAPHY

THE WIND RIVER FORMATION

The Wind River formation is divided into the Lysite and Lost Cabin members, each of which consists of two facies. The members are differentiated on the basis of the composition of roundstones in the conglomerate beds and the colors of the fine-grained beds. The two members have been distinguished only in the area east of the west line of R. 91 W. In other areas, such as the remainder of the Wind River Basin, the Big Horn Basin, and elsewhere, the two names are used only to identify faunal zones, the younger of which, the Lost Cabin, is characterized by *Lambdotherium* (Sinclair and Granger, 1911; Van Houten, 1945).

The Lysite member, the oldest part of the Wind River formation exposed in the northeastern part of the Wind River Basin, consists of orange-red and yellowish-gray variegated siltstone with beds of tan to brown fine-grained to conglomeratic sandstone and some boulder conglomerate. The boulder conglomerate is exposed near the center of T. 39 N., R. 89 W., in the northwest part of Cedar Ridge. Rock pieces as large as 2 feet in diameter are common, and exceptional pieces are as much as 10 feet in maximum diameter. Conglomeratic sandstone along Cottonwood Creek, near the fault that separates the Wind River formation from the strata of middle(?)

and late Eocene age, grades southward along the scarp into orange-red fine-grained rocks. These, in turn, grade southward into gray siltstone and claystone associated with thin carbonaceous beds and sandstone in channels. The boulder conglomerate and conglomeratic sandstone contain pieces of sandstone, limestone, and dolomite derived by erosion from Paleozoic rocks. Fragments of Mesozoic rocks are included in the Lysite member along Lysite Creek in T. 39 N., R. 90 W., and sec. 9, T. 39 N., R. 89 W.

The Lost Cabin member of the Wind River formation consists chiefly of violet-red, purple, and gray variegated siltstone and claystone with beds of gray to brown fine-grained to conglomeratic sandstone and boulder conglomerate. The boulder conglomerate makes up the main mass of Cedar Ridge in the southeastern part of T. 39 N., R. 89 W. The average size of the rock pieces in the conglomerate is about 1 foot, but pieces as large as 6 feet in diameter are locally present. The boulder conglomerate grades southward into finer grained rocks, and claystone and siltstone become prominent in the sequence as the conglomeratic beds disappear. Channels filled with sandstone are a conspicuous feature of the fine-grained facies of the member. The boulder conglomerate is made up almost entirely of granite, gneiss, and other igneous and metamorphic rocks eroded from the Big Horn Mountains.

The two members of the Wind River formation could not be separated west of R. 91 W., but boulder conglomerate similar to that in Cedar Ridge forms prominent hills just south of the Cedar Ridge fault in T. 39 N., R. 92 W., and also grades southward into finer grained rocks.

Together, the composition and other characteristics of the Lysite and Lost Cabin members of the Wind River formation indicate a tectonically active mountain front shedding debris into the adjacent basin. The coarseness of the boulder conglomerate suggests that depositional slopes may have been steep. The Paleozoic and Mesozoic materials in the Lysite member and the Pre-Cambrian material in the overlying Lost Cabin indicate the progressive nature of the deformation undergone by the mountains and their contemporaneous erosion.

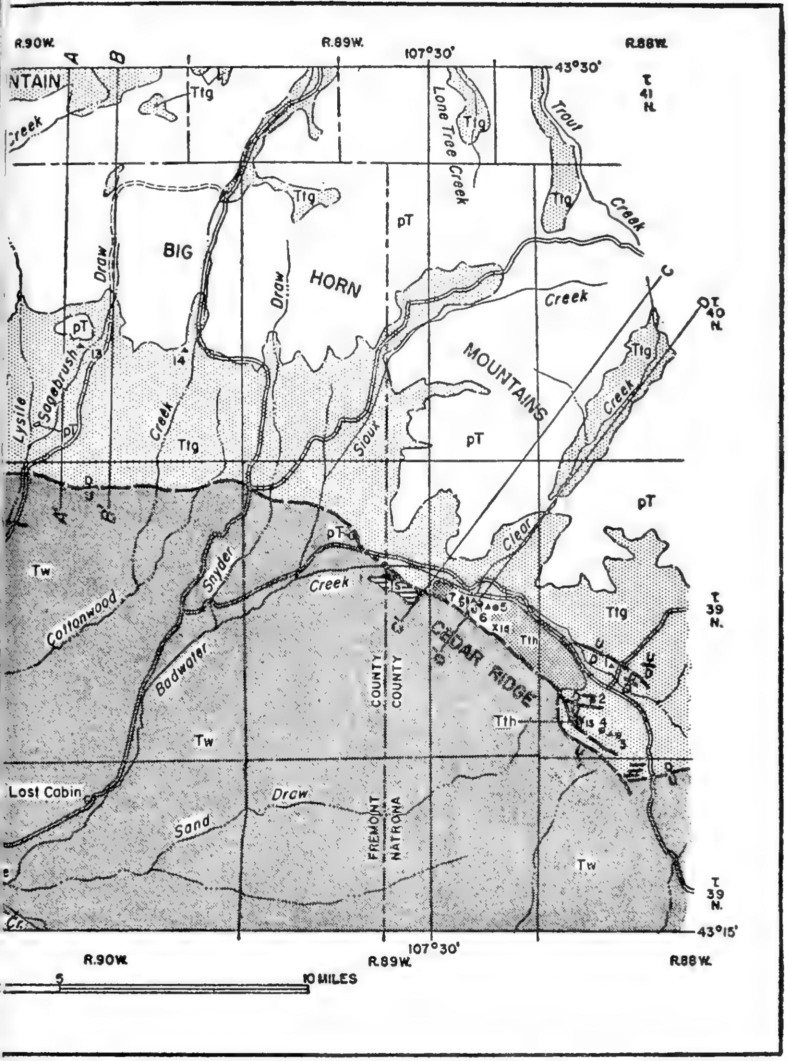
THE TEPEE TRAIL FORMATION

In the Absaroka Range, about 70 miles west-northwest of the northeastern part of the Wind River Basin, Love applied the formation name "Tepee Trail" to a thick sequence of volcanic sedimentary rocks that also include volcanic breccias, tuffs, and some flows. The formation was named for a local trail near the East Fork River about 18 miles northeast of Dubois (Love, 1939, pp. 73-79). The Tepee Trail formation was provisionally assigned a late Eocene age on the basis of a small number of vertebrate fossils and the position of the formation above strata of middle Eocene age and beneath strata assigned an Oligocene age. Love commented (1939, p. 78) on the similarity in composition and age between the Tepee Trail formation and the strata in the northeastern part of the Wind River Basin of middle(?) and late Eocene age.

Masursky (1952) traced the Tepee Trail formation of Love eastward along the north side of the Owl Creek Mountains to a point in T. 43 N., R. 100 W., Hot Springs County. Tourtelot and Thompson (1948) mapped the andesitic sequence of middle(?) and late Eocene age westward along the northern margin of the Wind River Basin to a point in T. 6 N., R. 4 E., which is about 30 miles southeast of the easternmost area of the Tepee Trail formation of Love mapped by Masursky. The andesitic sequence is correlated with the Tepee Trail formation of Love on the basis of lithologic and compositional similarity, and age; the name "Tepee Trail" is here applied to the andesitic sequence in the northeastern part of the Wind River Basin.

The Tepee Trail formation in the northeastern part of the Wind River Basin forms a belt of outcrop along the south side of the Owl Creek and Big Horn Mountains. The south boundary of the belt is relatively straight and is everywhere marked in the area shown in figure 2 by a normal fault along which the Tepee Trail formation has been dropped down against the Wind River formation. The north boundary of the belt of outcrop is highly sinuous, reflecting the overlap of the Tepee Trail on the rough topography of the pre-Tertiary rocks of the mountains. Isolated masses of strata rich in volcanic material and assigned to the Tepee Trail formation occupy the upper part of stream basins on both the south and north sides of the mountains. Examples are upper Clear Creek in T. 40 N., R. 88 W. (fig. 2), and the basins of Trout, Lone Tree, and Nowood Creeks on the north side of the Big Horn Mountains, and West Bridger and smaller creeks to the west on the north side of the Owl Creek Mountains. Lysite Mountain is a plateau-like remnant of the Tepee Trail formation in which the strata lap southward on and across both the Big Horn and Owl Creek Mountains and extend into the Wind River Basin. The Tepee Trail strata of Lysite Mountain form a sharp escarpment facing north into the Big Horn Basin about 8 miles north of the north edge of the area shown in figure 2.

The maximum thickness of the Tepee Trail formation is not readily


R.90W.
R.89W.
107°30'
R.88W.
43°30'
T. 41 N.
A
B
NTAIN
Creek
Ttg
Lone Tree Creek
Trout
Creek
pT
BIG
HORN
MOUNTAINS
Draw
Draw
Creek
C
T. 40 N.
Sagebrush
Lysite
13
14
Creek
Sioux
Clear
A'
B'
C'
Tw
Cottonwood
Snyder
Creek
Badwater
CEDAR RIDGE
Tth
T. 39 N.
FREMONT COUNTY
NATRONA COUNTY
Lost Cabin
Sand
Draw
T. 39 N.
43°15'
R.90W.
R.89W.
107°30'
R.88W.
5
10 MILES

on.

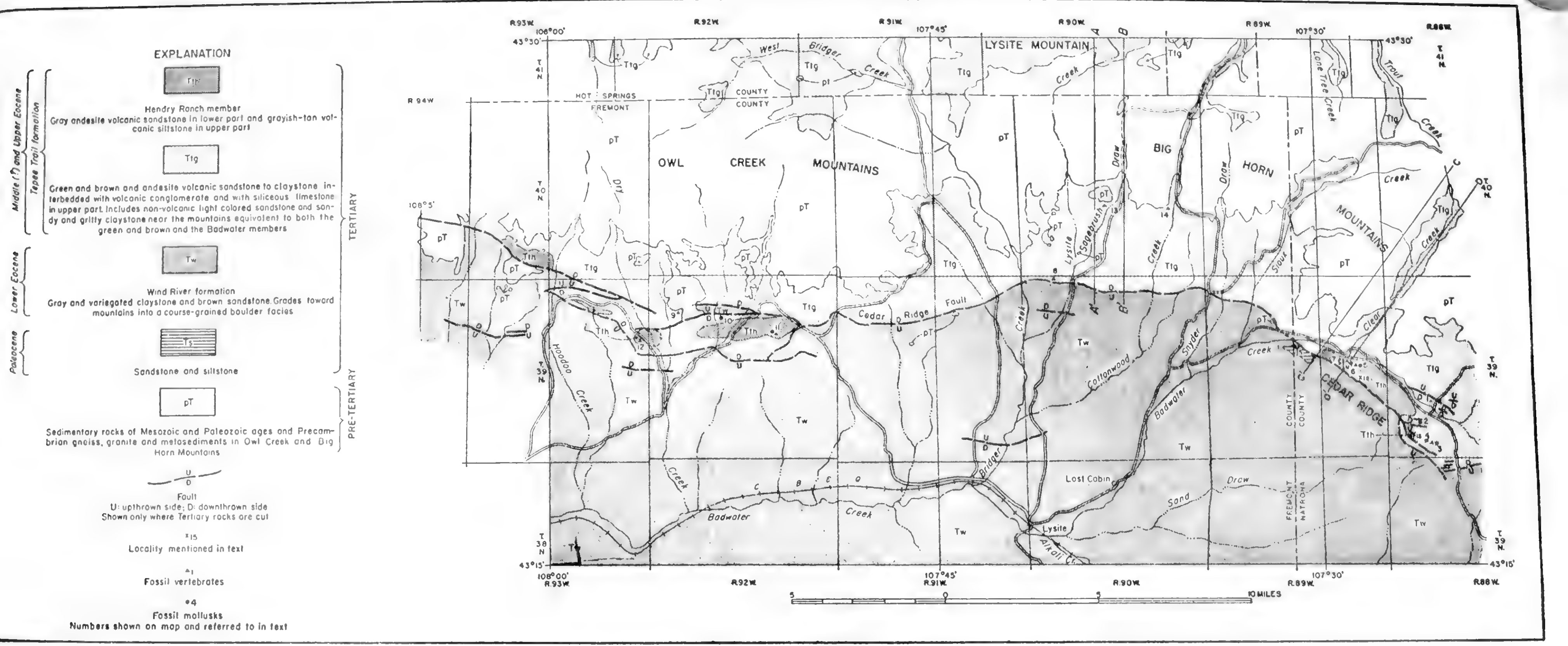


FIG. 2.—Geologic map of northeastern Wind River Basin showing distribution of Tepee Trail formation.

determinable because of its overlap on the topography of the mountains and because the base of the formation is not exposed within the area of figure 2. The top of the formation is everywhere an erosional surface. A composite section of the formation, pieced together from exposures between Cedar Ridge and Badwater Creek in T. 39 N., R. 89 W., indicates the presence of about 700 feet of strata assigned to the Tepee Trail formation (fig. 5). Correlations between the sections are made somewhat uncertain by discontinuous exposures and by minor faulting. On the north face of Lysite Mountain, about 520 feet of Tepee Trail strata are present. As much as 150 feet of the Tepee Trail is exposed in a continuous section at only a few places on the south side of the mountain ranges. The Tepee Trail formation consists of a sequence of green, brown, and gray strata rich in volcanic material of andesitic composition.[5] The sequence can be divided into lower and upper members in exposures south of the mountain front, and an essentially nonvolcanic facies equivalent to both members directly adjacent to the mountains or in some reentrants within them (fig. 3). The lower member consists chiefly of green and brown rocks ranging in texture from conglomerate to claystone with some limestone. The upper member consists chiefly of gray and greenish-gray fine-grained strata overlain by tan siltstone. The nonvolcanic facies is made up of white and light-gray pebbly claystone and mudstone and is referred to as the white clastic facies.

Green and brown member.—The most characteristic lithologic features of the green and brown member of the Tepee Trail formation are bedded sedimentary rocks rich in volcanic material and zones of conglomerate containing roundstones of hard andesite and hard tuff(?) embedded in a coarse-grained matrix of similar volcanic material. The colors are independent of the lithology, in large part, and at some places the green color seems to be a secondary feature, the nature and origin of which have not been studied. Along Badwater Creek (southwestern part of T. 39 N., R. 88 W.) and along Dry Creek (sec. 8, T. 39 N., R. 92 W.), light-colored siliceous freshwater limestone is prominent in the upper part of the member. Just east of Snyder Draw (sec. 29, T. 40 N., R. 89 W.) is a small out-

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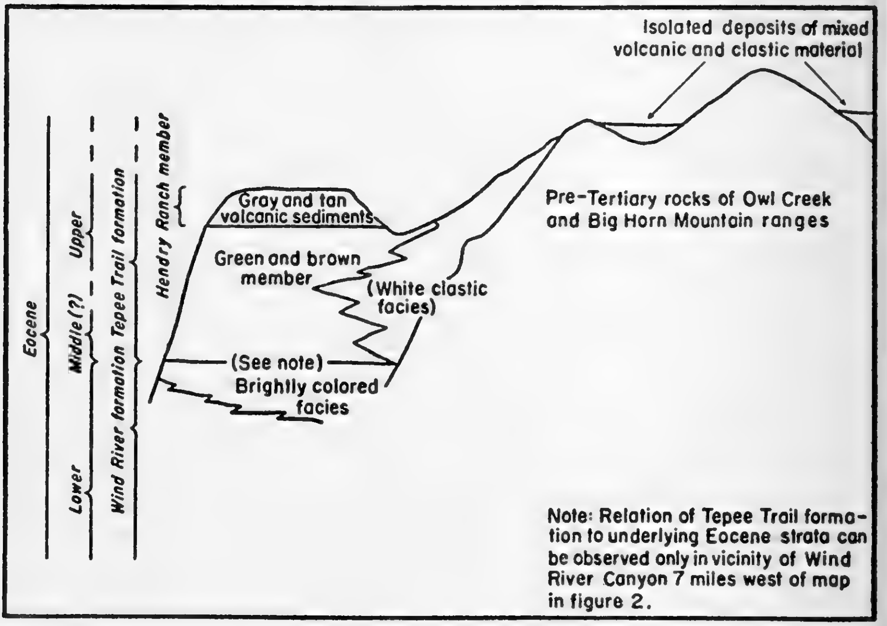
[5] In previous reports on this area, the Tepee Trail rocks have been called "tuffs." Actually, the final depositing agent of nearly all the rocks was running water and the aerial transport of the volcanic material to the area, necessary for the use of the pyroclastic rock name "tuff" (Wentworth and Williams, 1932; see also Hay, 1952), can only be inferred. Although many of the strata are clearly resedimented tuffs that have been transported only a short distance by water, use of the terms proposed by Wentworth and Williams for water-laid volcanic material is more accurate and is followed in this report.

crop of fresh-water limestone interbedded with coarse-grained volcanic sandstone. The beds of limestone contain some fine-grained volcanic material, and at most places are highly siliceous with large irregular masses of gray to green chalcedony and chert that has replaced the limestone. Small well-defined nodules of black chalcedony are common. The limestone is abundantly fossiliferous in localized areas; gastropods are commonest, pelecypods and vertebrate remains being less abundant. Prop roots of palms, replaced by bluish-black chalcedony, are abundant and conspicuous in the limestone. On Badwater Creek, the siliceous limestone apparently passes laterally to the northwest into bright emerald-green volcanic sandstone.



Note: Relation of Tepee Trail formation to underlying Eocene strata can be observed only in vicinity of Wind River Canyon 7 miles west of map in figure 2.

FIG. 3.—Diagrammatic cross section showing relations of facies of Tepee Trail formation.

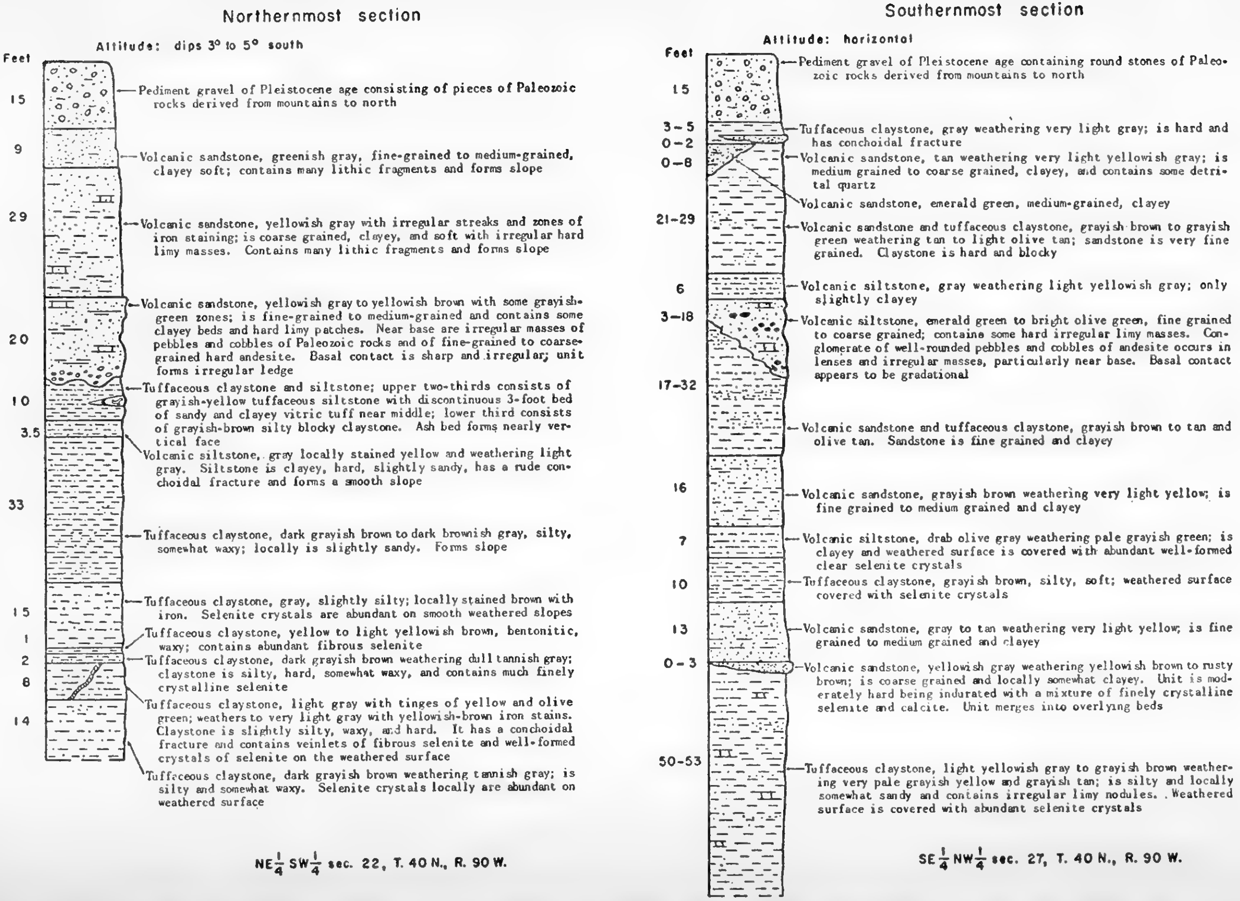
The volcanic rocks in the Absaroka centers are mostly andesitic, although basaltic breccias and tuffs are present (Love, 1939, p. 76). The detrital volcanic rocks in the northeastern part of the Wind River Basin are similar in composition to the Absaroka rocks. Labradorite, as determined by measurement of extinction angles, is the commonest plagioclase, although one thin section contained bytownite. Biotite and euhedral hornblende are abundant; hypersthene and pigeonite are common. Shards of somewhat altered glass are abundant in some of the finer grained rocks. The minerals occur mostly as anhedral to euhedral crystals and the rocks would be classified as crystal tuffs, for the most part, except for their deposition in running water. Lithic fragments are common in most rocks, however, and are the major constituent in some. The lithic fragments are subrounded and are most abundant in association with strata that contain roundstones of volcanic rock.

The green and brown member is fairly uniform in its gross lithologic characteristics, being readily recognizable by its colors alone at most places. On the north side of Badwater Creek (loc. 1 and vicinity, fig. 2), the rocks consist of light-gray to grayish-brown hard ledgy fine-grained limy andesitic volcanic sandstone and siltstone somewhat different in gross appearance from most beds in the Tepee Trail. A fragmentary tooth identified as *Amynodon?*, characteristic of the Tepee Trail of this area, suggests that this sequence is only a locally different facies of the Tepee Trail formation.

The abrupt lithologic changes, on a bed-by-bed basis, that characterize the green and brown member of the Tepee Trail are shown by two sections in adjacent parts of secs. 22 and 27, T. 40 N., R. 90 W. (fig. 4), near the mouth of Sagebrush Draw. Green colors are striking in the rocks at the exposures in sec. 27 but are entirely missing in the section only about half a mile to the north. Both sections have more yellow and gray colors than is common along the south end of the Big Horn Mountains. The only feature that appears to be common to the two sections is a conglomerate zone 40 to 50 feet below the base of the gravel that caps the pediment surface below which the two sections are exposed. The conglomerate zone, however, is not continuous between the two sections.

Gypsum and crystalline selenite are abundant on the weathered surface of these exposures. Selenite also forms on the weathered surface of Tepee Trail strata in other parts of the area but is particularly conspicuous here. The siltstone and claystone have no obvious pyrite content and the origin of the selenite is not known. It is possible that these outcrops are the "deeply disintegrated clays . . . and much gypsum" mentioned by Granger (Sinclair and Granger, 1911, p. 105).

At several places, rocks of the green and brown member contain abnormally large amounts of selenium, as much as 187 parts per million being found in one bed in sec. 3, T. 39 N., R. 91 W., Fremont County (Beath, Hagner, and Gilbert, 1946, p. 11). At this place, the rocks are red, white, ocher, green, and brown, and range from coarse grained to fine grained. The red colors are anomalous in the



Northernmost section

Attitude: dips 3° to 5° south

Feet	
15	Pediment gravel of Pleistocene age consisting of pieces of Paleozoic rocks derived from mountains to north
9	Volcanic sandstone, greenish gray, fine-grained to medium-grained, clayey soft; contains many lithic fragments and forms slope
29	Volcanic sandstone, yellowish gray with irregular streaks and zones of iron staining; is coarse grained, clayey, and soft with irregular hard limy masses. Contains many lithic fragments and forms slope
20	Volcanic sandstone, yellowish gray to yellowish brown with some grayish-green zones; is fine-grained to medium-grained and contains some clayey beds and hard limy patches. Near base are irregular masses of pebbles and cobbles of Paleozoic rocks and of fine-grained to coarse-grained hard andesite. Basal contact is sharp and irregular; unit forms irregular ledge
10	Tuffaceous claystone and siltstone; upper two-thirds consists of grayish-yellow tuffaceous siltstone with discontinuous 3-foot bed of sandy and clayey vitric tuff near middle; lower third consists of grayish-brown silty blocky claystone. Ash bed forms nearly vertical face
3.5	Volcanic siltstone, gray locally stained yellow and weathering light gray. Siltstone is clayey, hard, slightly sandy, has a rude conchoidal fracture and forms a smooth slope
33	Tuffaceous claystone, dark grayish brown to dark brownish gray, silty, somewhat waxy; locally is slightly sandy. Forms slope
15	Tuffaceous claystone, gray, slightly silty; locally stained brown with iron. Selenite crystals are abundant on smooth weathered slopes
1	Tuffaceous claystone, yellow to light yellowish brown, bentonitic, waxy; contains abundant fibrous selenite
2	Tuffaceous claystone, dark grayish brown weathering dull tannish gray; claystone is silty, hard, somewhat waxy, and contains much finely crystalline selenite
8	Tuffaceous claystone, light gray with tinges of yellow and olive green; weathers to very light gray with yellowish-brown iron stains. Claystone is slightly silty, waxy, and hard. It has a conchoidal fracture and contains veinlets of fibrous selenite and well-formed crystals of selenite on the weathered surface
14	Tuffaceous claystone, dark grayish brown weathering tannish gray; is silty and somewhat waxy. Selenite crystals locally are abundant on weathered surface

NE$\frac{1}{4}$ SW$\frac{1}{4}$ sec. 22, T. 40 N., R. 90 W.

Southernmost section

Attitude: horizontal

Feet	
15	Pediment gravel of Pleistocene age containing round stones of Paleozoic rocks derived from mountains to north
3–5	Tuffaceous claystone, gray weathering very light gray; is hard and has conchoidal fracture
0–2	Volcanic sandstone, tan weathering very light yellowish gray; is medium grained to coarse grained, clayey, and contains some detrital quartz
0–8	Volcanic sandstone, emerald green, medium-grained, clayey
21–29	Volcanic sandstone and tuffaceous claystone, grayish brown to grayish green weathering tan to light olive tan; sandstone is very fine grained. Claystone is hard and blocky
6	Volcanic siltstone, gray weathering light yellowish gray; only slightly clayey
3–18	Volcanic siltstone, emerald green to bright olive green, fine grained to coarse grained; contains some hard irregular limy masses. Conglomerate of well-rounded pebbles and cobbles of andesite occurs in lenses and irregular masses, particularly near base. Basal contact appears to be gradational
17–32	Volcanic sandstone and tuffaceous claystone, grayish brown to tan and olive tan. Sandstone is fine grained and clayey
16	Volcanic sandstone, grayish brown weathering very light yellow; is fine grained to medium grained and clayey
7	Volcanic siltstone, drab olive gray weathering pale grayish green; is clayey and weathered surface is covered with abundant well-formed clear selenite crystals
10	Tuffaceous claystone, grayish brown, silty, soft; weathered surface covered with selenite crystals
13	Volcanic sandstone, gray to tan weathering very light yellow; is fine grained to medium grained and clayey
0–3	Volcanic sandstone, yellowish gray weathering yellowish brown to rusty brown; is coarse grained and locally somewhat clayey. Unit is moderately hard being indurated with a mixture of finely crystalline selenite and calcite. Unit merges into overlying beds
50–53	Tuffaceous claystone, light yellowish gray to grayish brown weathering very pale grayish yellow and grayish tan; is silty and locally somewhat sandy and contains irregular limy nodules. Weathered surface is covered with abundant selenite crystals

SE$\frac{1}{4}$ NW$\frac{1}{4}$ sec. 27, T. 40 N., R. 90 W.

FIG. 4.—Sections of green and brown member of Tepee Trail formation near mouth of Sagebrush Draw.

member and are found in a fan-shaped area having its apex in a strike valley eroded in the Amsden formation of Pennsylvanian age on the north flank of the Owl Creek Mountains. The red color presumably is derived from the Amsden formation, which contains red fine-grained rocks. Selenium-bearing vegetation on the green and brown member is detectable by its odor, particularly in the spring or after a shower of rain, in sec. 24, T. 40 N., R. 90 W., and at several places along the south flank of the Owl Creek Mountains in the northwestern part of T. 39 N., R. 91 W., and the northeastern part of T. 39 N., R. 92 W. The selenium content of the rocks is thought to be related to their volcanic constituents (Beath, Hagner, and Gilbert, 1946). Uranium minerals have been found in the green and brown member at a few places (Love, 1954).

Hendry Ranch member.—The green and brown member is overlain by gray and greenish-gray claystone and siltstone and tan siltstone rich in volcanic material in five areas along the northern margin of the Wind River Basin. The easternmost, and largest, area lies between the Cedar Ridge fault and Badwater Creek in T. 39 N., Rs. 88 and 89 W., Natrona County. The other four are in Tps. 39 and 40 N., Rs. 92 and 93 W., Fremont County, in the western part of the map in figure 2. In each of these areas, the gray and greenish-gray unit and tan siltstone form the youngest part of the Eocene section. The new name "Hendry Ranch member" is applied to this sequence. The name is derived from Hendry Ranch in the NE¼SE¼ sec. 14, T. 39 N., R. 89 W., Natrona County, as shown on the topographic map of the Badwater quadrangle. Good but discontinuous exposures of the Hendry Ranch member are found south of the ranch and to the southeast along Badwater Creek; from them was collected the largest part of the late Eocene fauna described by Gazin (1956) in Part 2. The type section (fig. 5) of the Hendry Ranch member is a composite one including three localities, all in Natrona County: locality 15 (fig. 2), NE¼ sec. 31, T. 39 N., R. 88 W., which includes the contact of the Hendry Ranch member with the fresh-water limestone of the underlying green and brown member of the Tepee Trail formation; locality 7 (fig. 2), SW¼ sec. 14, T. 39 N., R. 89 W., which displays typical exposures of fossiliferous gray and greenish-gray rocks; and locality 16 (fig. 2), NE¼ sec. 23, T. 39 N., R. 89 W., which contains the tan siltstone that makes up the upper part of the Hendry Ranch member. The maximum preserved thickness of the Hendry Ranch member is about 550 feet, based on measurements in localities 7 and 16 above.

The lower part of the Hendry Ranch member of the Tepee Trail

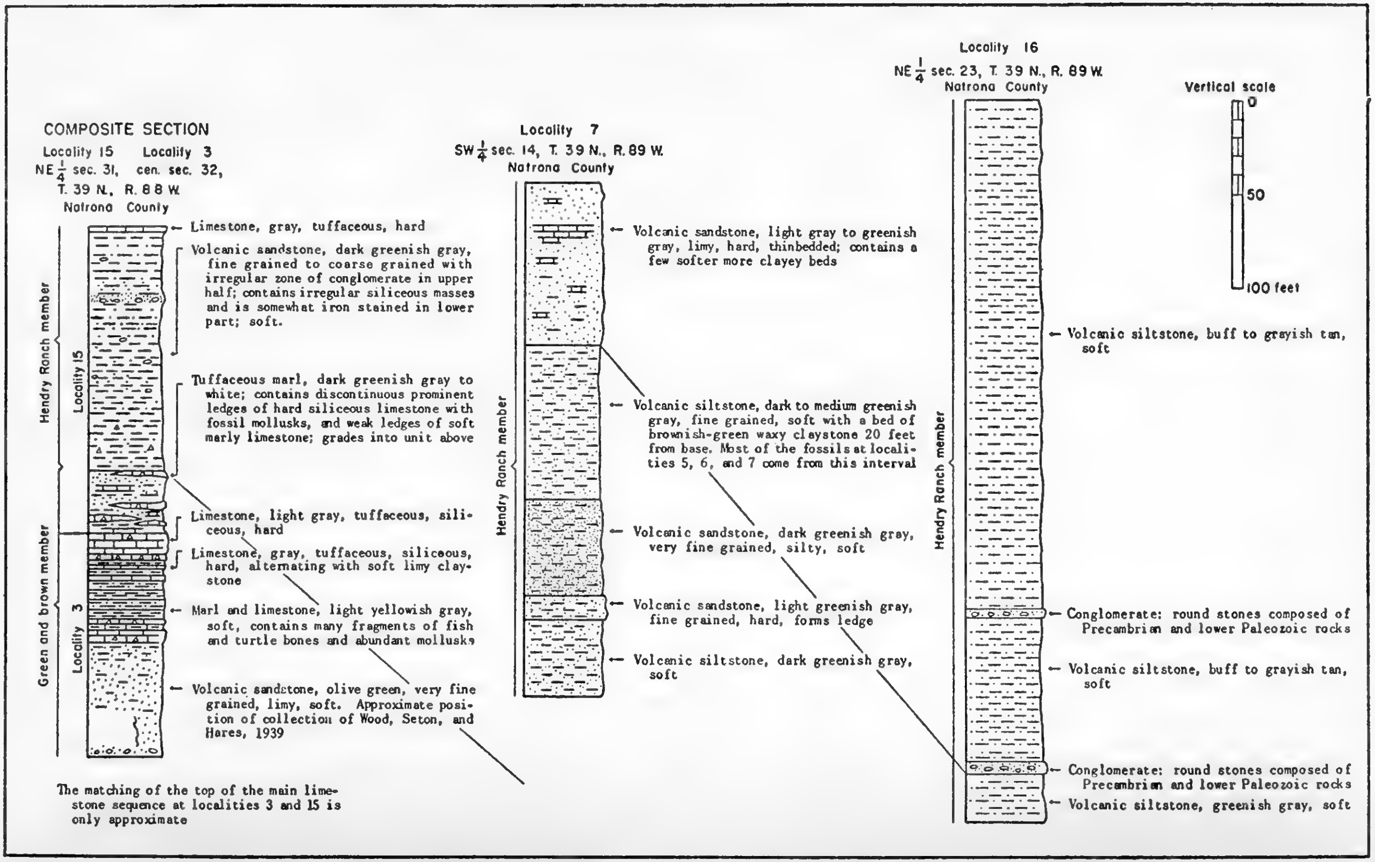


FIG. 5.—Stratigraphic sections of Hendry Ranch member of Tepee Trail formation.

Fossiliferous strata of Hendry Ranch member of Tepee Trail formation. Upper, locality 7 (see figs. 2 and 3), part of the type section of the Hendry Ranch member. Lower, locality 6, about half a mile east of locality 7. The ledge near the bottom of the sequence marks the same horizon at both localities. The first fossils from the Hendry Ranch member were found at these localities. (See table 1 for list of fossils.)

formation is made up of gray and greenish-gray andesitic volcanic sedimentary rocks and the upper part is tan volcanic siltstone. The greenish-gray unit has a maximum thickness of about 200 feet and the siltstone unit has a maximum thickness of about 350 feet. Single exposures of the lower unit do not reveal more than about 150 feet of strata. The siltstone unit is the youngest part of the sequence and its top is an erosional surface; the original thickness of the siltstone cannot be determined.

The Hendry Ranch member is consistent in its major lithologic characteristics and is easily recognizable wherever seen, even in areas of only partial exposure. The member is confined to isolated areas of outcrop, and no facies changes were detected.

The greenish-gray volcanic claystone and siltstone weathers to smooth badland slopes at most places. In general, the rocks in the greenish-gray unit are finer grained than the rocks in the underlying green and brown member. Irregular ledges of harder and more limy siltstone and sandstone are present in some exposures and one such ledge is particularly prominent at localities 6 and 7 (pl. 1). Thin beds of gray to black waxy claystone are present in the upper part of the same exposures. Crystals of selenite are abundant on the surface of most outcrops. Local lenses of fine-grained chert and quartz pebble conglomerate are interbedded with the tuffs.

The volcanic material in the rocks corresponds in composition to an andesite. The plagioclase feldspar is andesine, instead of labradorite as in the green and brown member of the Tepee Trail formation. Not enough petrographic work has been done on the Tepee Trail to evaluate the significance of the apparent difference in feldspars in the two members. Light-tan to greenish-brown biotite and hornblende are abundant and a few delicate shards of altered glass are present in most thin sections.

At many places the rocks weather to a nodular surface very similar to the "nodular zones" of the Oligocene sequences in Nebraska and South Dakota. Some of such nodular zones have been interpreted as parts of paleosol complexes by Schultz, Tanner, and Harvey (1955). The nodular zones in the lower part of the Hendry Ranch member contain *Glypterpes,* cf. *G. veternus,* a large land snail, and also clay- and calcite-filled borings similar to the fossil larval chambers of insects described by Brown (1934, 1935), apparently indicating subaerial conditions during deposition of the rocks. The nodules have yielded most of the fragmentary fossil vertebrates found in the Hendry Ranch member, a type of occurrence typical of the paleosol complexes reported by Schultz, Tanner, and Harvey (1955).

The tan volcanic siltstone unit of the Hendry Ranch member was found only along Badwater Creek north of Cedar Ridge and in a small area just north of locality 11 (sec. 10, T. 39 N., R. 92 W.). The siltstone is soft and forms poorly exposed slopes in contrast to the lower member, which forms badlands areas. The siltstone ranges in color from grayish tan to pale greenish gray, and gray; it is somewhat limy throughout, poorly bedded, and irregularly jointed. At most places, two beds of white limy vitric tuff as much as 3 feet thick are present in the lower part of the sequence. The vitric tuff beds are highly lenticular and are missing at locality 16 (figs. 2 and 5). The siltstone unit contains much admixed volcanic material, however, particularly in its lower part. Lenses of bright-green volcanic-rich sandstone are present at some places. At locality 7 (figs. 2 and 5), medium-grained to coarse-grained volcanic sandstone at the base of the siltstone unit lies on greenish-gray claystone and siltstone.

Lenses of conglomerate and coarse-grained sandstone made up of pieces of Pre-Cambrian and Cambrian rocks as much as 1 foot in diameter are common in the lower part of the siltstone unit and in the upper part of the greenish-gray unit. In some places, fragments of light-grayish-green siltstone from the lower unit are included in lenses of intraformational conglomerate in the lower part of the siltstone unit.

The change from greenish-gray rocks below to tan siltstone above takes place within a few feet, but no consistent criteria were found for separating the two units along their contact. The most usable contact for field mapping is where the material in which the conglomerate lenses are included changes from the gray claystone and siltstone of the lower unit to the tan siltstone of the upper unit. Where conglomerate or coarse-grained material is not present, this change occurs about at the base of a bed of white vitric tuff. However, in local areas, there is prominent channeling at the contact. This channeling may account in part for the thinning of the underlying lower greenish-gray unit from place to place.

The white clastic facies.—The white clastic facies (fig. 3) consists chiefly of material eroded from the Owl Creek and Big Horn Mountains and deposited directly adjacent to the mountains or in reentrants within them. Volcanic material is mixed in different amounts with the derived clastics but the essential characteristic of the rocks of the white clastic facies is the general absence of volcanic material compared to the rest of the Tepee Trail formation. The white clastic facies is particularly well developed along the south side of the Owl Creek Mountains and is conspicuous in the area embraced by the forks of Dry Creek (Tps. 39 and 40 N., Rs. 92 and 93 W.). The facies is prominent also between the westernmost fork of Dry Creek and Hoodoo Creek. In the Dry Creek drainage, the facies consists of very light-gray to white pebbly and sandy claystone and very clayey sandstone. The rather uniform admixture of sand and pebbles gives the claystone a somewhat cementlike appearance. Although some of the sandstone beds show sorting and bedding, in general, the facies shows an absence of sorting during its deposition. Pebbles of quartz and feldspar and abundant sand grains are scattered through the claystone like raisins in a pudding. The very poor sorting and general lack of bedding is suggestive of mudflows but no other evidence of this kind of deposition was recognized. Most of the clay beds in this sequence weather to a soft puffy surface and the clay in such beds probably is bentonitic. Some of the light-colored claystone is hard and only slightly plastic when wet. The forks of Dry Creek drain an area in the Owl Creek Mountains made up chiefly of pink to brown granite and the feldspars in these rocks could have yielded kaolinitic weathering products during Tepee Trail time. Such claystone may be kaolinitic but no mineralogical study was made.

East of Hoodoo Creek, the facies is yellow to brown and contains several distinctive dull-red beds. Cobbles of granite and dark-colored gneiss, phyllite, and schist are abundant. The generally more somber color of these exposures and lack of the white claystone characteristic of the Dry Creek area is believed to be related to the dark-colored gneiss, schist, and phyllite in the area drained by Hoodoo Creek. The lateral gradation of the clastic material eroded from the mountains into the green and brown volcanic sediments of the Tepee Trail is well displayed along the sides of pediment benches in the area between Hoodoo Creek and the west fork of Dry Creek.

The white clastic facies is typically developed along Lysite Creek (T. 40 N., R. 90 W.) and was derived chiefly from Paleozoic rocks. Red colors are common in the facies near where it overlaps Pennsylvanian and Permian rocks in the mountains. This is particularly noticeable in the reentrant in the Big Horn Mountain front in T. 39 N., R. 88 W., north of locality 1 (fig. 2).

The equivalence of outcrops of the white clastic facies and the Hendry Ranch member of the Tepee Trail formation can only be inferred. The Hendry Ranch member is found only in areas isolated from the Tepee Trail strata adjacent to the mountains. At the same time, the equivalence of material of the white clastic facies and the Hendry Ranch member is believed certain because material of the white clastic facies is found in the mountains at altitudes much above the outcrops of the Hendry Ranch member. Some part of the intermixed volcanic and clastic material in the Clear Creek Basin (fig. 6), for example, undoubtedly is equivalent to at least part of the Hendry Ranch member.

Age.—The age of the Tepee Trail formation in the northeastern part of the Wind River Basin is considered to be middle(?) and late Eocene. The Hendry Ranch member has yielded a fauna that is late Eocene in age and suggests equivalence with an upper Uintan stage according to Gazin (see Part 2). The green and brown member has not yielded many or very well preserved fossils but those that are known, according to Gazin, also are late Eocene in age. Locality lists of vertebrate and invertebrate fossils from the Tepee Trail formation in the northeastern part of the Wind River Basin are shown in table 1. Tentative assignment of a possible middle Eocene age to the lower part of the Tepee Trail formation is based upon the absence of recognizable rock sequences yielding middle Eocene fossils in the northeastern part of the Wind River Basin and upon the relation of the Tepee Trail formation to underlying rocks in adjacent areas.

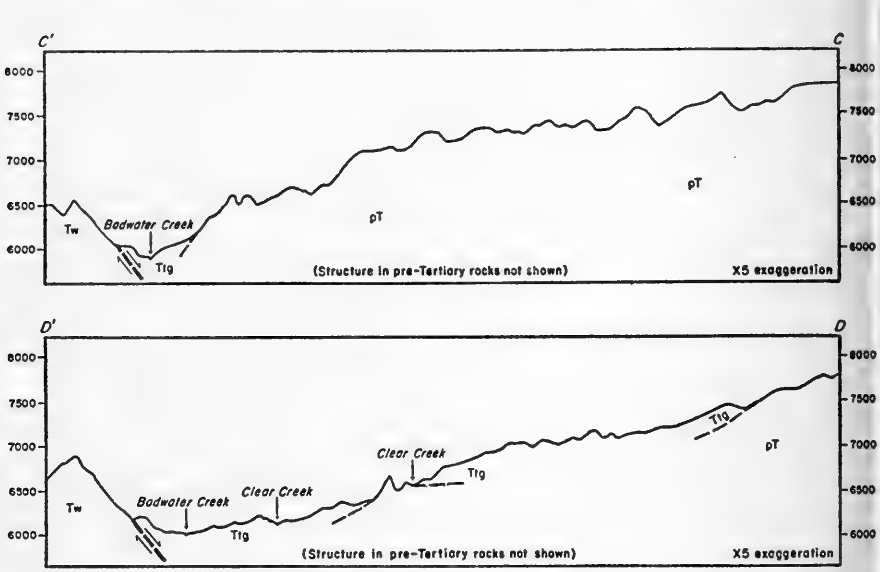


FIG. 6.—Cross sections along Clear Creek Valley (D′-D) and along ridge parallel to and 1 mile northwest of Clear Creek (C′-C) showing Tepee Trail formation filling valley.

The type Tepee Trail formation in the Absaroka Range lies unconformably upon the Aycross formation, the type area of which has yielded middle Eocene fossils (Love, 1939, p. 70). In exposures on

TABLE 1.—*Upper Eocene fossils from northeastern Wind River Basin, Wyoming*

Map number	Location	Formation or member	Fossils
1	29-39N-88W, SWNE	Tepee Trail	*Amynodon?* sp.
2	29-39N-88W, SWSW	Tepee Trail	*Lymnaea similis, L. vetusta, Lymnaea* sp., *Physa* cf. P. *bridgerensis, Physa* cf. *P. pleromatis, Australorbis spectabilis, Vertigo arenula* [1]
3	32-39N-88W, NWSE	Tepee Trail	*Amynodon advenus,* brontotheriid indet., crocodilian, *Australorbis spectabilis, Lymnaea* sp.[2]
4	32-39N-88W, SENW	Tepee Trail	*Goniobasis ternera, Lymnaea similis, Australorbis* cf. *A. spectabilis, Unio haydeni, Unio* sp.[1]
5	13-39N-89W, SWSW	Hendry Ranch	Carnivora indet., *Miacis* cf. *M. robustus, Limnocyon?* sp., *Epihippus* cf. *gracilis, Desmatotherium woodi, Dilophodon* cf. *D. leotanus, Epitriplopus?* sp., *Pentacemylus?* sp., *Protoreodon pearcei, P. petersoni, Leptotragulus* cf. *medius,* Leptoreodon? sp., *Peratherium* sp., *Glypterpes* cf. *G. veternus, Rapamys?* sp., large paramyid, smaller paramyid, *Sciuravus dubins, Protadjidaumo* sp., rodent indet., *Mytonolagus wyomingensis* [3]
6	14-39N-89W, SESE	Hendry Ranch	*Epitrilopus?* sp., *Hyopsodus* cf. *H. uintensis, Protoreodon petersoni, Diplobunops* cf. *D. matthewi, Dilophodon* cf. *D. leotanus, Leptotragulus* cf. *L. medius, Glypterpes* sp., *Physa* sp.
7	14-39N-89W, SWSE	Hendry Ranch	*Epihippus* cf. *parvus, Dilophodon* cf. *leotanus, Desmatotherium woodi, Apriculus praeteritus, Malaquiferus tourteloti, Protoreodon pearcei?,* leptomerycid.
8	6-39N-90W, NENE	Tepee Trail	*Palaeosyops?* sp.
9	7-39N-92W, NENE	Tepee Trail	*Hyrachyus*(?) sp.
10	9-39N-92W, NWSW	Tepee Trail	*Lymnaea similis, Lymnaea* sp., *Physa* sp., *Australorbis spectabilis, Vertigo arenula* [1]
11	10-39N-92W, SESE	Hendry Ranch	*Malaquiferus tourteloti, Eomoropus anarsius,*[4] *Glypterpes* cf. *G. veternus*
12	13-39N-93W, NWNE	Hendry Ranch	*Sciuravus?* sp.
13	21-40N-90W, SWSE	Tepee Trail	Titanothere
14	23-40N-90W, SWSE	Tepee Trail	Titanothere

[1] Yen, 1948, 1949.
[2] Wood, H. E., 2d, Seton, and Hares, 1936.
[3] Wood, A. E., 1949.
[4] Fieldwork by Gazin in 1956 has shown this specimen to be from SE¼SE¼ sec. 9, T.39N., R.92W.

the north face of Lysite Mountain, Tepee Trail strata lie with apparent conformity on lake beds of Green River type about 220 feet thick (Tourtelot, 1946). These lake beds are identical in type to those in the Tatman formation in the central part of the Big Horn Basin to the north. The relations between the Tatman formation and the lake beds and the overlying strata of the Tepee Trail formation of Lysite Mountain actually are indeterminable, but the available data suggest that middle Eocene time may well be represented in the lower part of the Tepee Trail.

The top of the lake beds at Lysite Mountain is at an altitude of about 6,400 feet. On Tatman Mountain, 70 miles northwest of Lysite Mountain, the Tatman formation is about 700 feet thick (Van Houten, 1944, p. 194) and the uppermost beds preserved are at an altitude of about 6,200 feet. At Squaw Buttes, 55 miles northwest of Lysite Mountain, the Tatman formation is about 800 feet thick (Van Houten, 1944, p. 192), and the uppermost beds preserved are at an altitude of about 5,900 feet. Although the present altitude of the Tatman formation is in part the result of post-Tatman structural movements (Van Houten, 1944), the essential uniformity of altitude of the youngest lake beds in the three areas mentioned makes it possible to interpret them as parts of a single episode of lake deposition. The Tatman formation is considered to be early Eocene in age in the central part of the Big Horn Basin (R. L. Hay, personal communication, 1956), but the lake beds on Lysite Mountain could be either early or middle Eocene in age, or both. Even if the lake beds on Lysite Mountain should be considered to be middle Eocene in age, there is no line of evidence to suggest that all of middle Eocene time is represented there. The continuation of lake deposition from early to middle Eocene time in southwestern Wyoming and Utah is well known. Dane (1954) has shown that parts of the ancient Green River Lake persisted even into late Eocene time.

Somewhat similar age relations of the lower part of the Tepee Trail formation can be deduced from the sequence in the Boysen area (Tourtelot and Thompson, 1948), just west of the area shown in figure 2. In the Boysen area, near Wind River Canyon, the Tepee Trail formation rests with apparent conformity on a brightly colored sequence continuous with the lower part of the Wind River formation. The brightly colored sequence was considered by Tourtelot and Thompson to be a part of the Wind River formation that might be of early middle Eocene age. This leaves most of the middle Eocene to be accounted for, and, provisionally, it is here considered to be represented in the lower part of the Tepee Trail formation of the northeastern part of the Wind River Basin. The Tepee Trail formation in the northeastern part of the Wind River Basin thus may include rocks of the same age as the upper part of the Aycross formation in the northwestern part of the Wind River Basin.

Van Houten (1950, 1954, 1955) has described a formation of both middle and late Eocene age, rich in volcanic material, along the southern margin of the Wind River Basin. This formation includes material from both the Absaroka volcanic center and the Rattlesnake Hills, a volcanic field of middle and late Eocene age in southern Natrona County. The middle Eocene part of this sequence is not separable from the late Eocene part of the sequence on a lithologic basis.

STRUCTURE

The Tepee Trail strata of the northeastern part of the Wind River Basin are moderately deformed. The most prominent structural feature involving the Tepee Trail formation is the Cedar Ridge fault, which everywhere within the area of figure 2 forms the southern boundary of the Tepee Trail outcrop area. Most of the structural features within the outcrop area of the Tepee Trail are related to this fault, the displacement of which is indeterminable. A minimum displacement of about 1,000 feet, however, is indicated for that part of the fault in T. 39 N., R. 89 W. Here, a total of about 500 feet of Tepee Trail strata is exposed near the fault, and the top of these beds is about 500 feet below the top of Cedar Ridge which is made up of Wind River boulder beds. This is the largest displacement that can be demonstrated but the actual displacement on the fault may be much larger.

In the Dry Creek drainage, the Cedar Ridge fault divides into several branches that enclose grabens in which Tepee Trail strata are found, and horsts made up of boulder beds assigned to the Wind River formation. Some parts of the faults in this area cut pre-Tertiary rocks.

The Tepee Trail strata exposed along the north side of Cedar Ridge probably are cut by many normal faults of small displacement and extent. Only a few of these could be mapped and shown on figure 2. Most of the minor faults join the trace of the Cedar Ridge fault at large angles. Similar minor faults, essentially normal to the Cedar Ridge fault, probably cut Tepee Trail strata at other places along the Cedar Ridge fault but they could not be recognized. All are believed to be the result of adjustments in the relatively downward-moving block as the major faulting took place.

Near the mountains, the Tepee Trail strata dip at low angles away from the mountains. Some part of this angle of dip may represent original depositional slope; the rest is the result of the southward tilting of the mountain block in response to the movement on the Cedar Ridge fault. Near the Cedar Ridge fault, the strata dip northward at many places, the strata having been dragged upward by movement along the major fault.

The age of the Cedar Ridge fault and associated structures cannot be placed more closely than post-late Eocene. It seems likely, however, that the Cedar Ridge fault is as young as Pliocene, to conform with the pattern of normal faulting that resulted from epeirogenic uplift of the Rocky Mountain region, as pointed out by Love (1939, p. 114).

SEDIMENTATIONAL HISTORY

The sedimentational interpretation of the Eocene strata in the northeastern part of the Wind River Basin can contribute to the reconstruction of the geologic history of the Wyoming basins, which has been reviewed by Van Houten (1952). This history, briefly stated, applies chiefly to the Wind River and Big Horn Basins and is one of mountain and basin formation in late Cretaceous and early Tertiary time, with the rising mountains shedding much debris into the basins by early Eocene time. Much of the present mountain topography had been shaped by the end of early Eocene time, which seems also to mark the end of differential movement between the mountain ranges and the basins until much later in Tertiary time. From middle Eocene time through at least some part of Miocene time, and perhaps into the Pliocene, the basins were progressively filled, chiefly with volcanic material from the Absaroka-Yellowstone volcanic region. As the basins were filled the mountain ranges were buried, and eventually a broad constructional plain resulted from which are inherited many of the features of the present drainage system.

The process of basin filling was essentially continuous but it was interrupted locally from time to time (Love, 1952). During Paleocene and early Eocene time, the surfaces of deposition in the basins were not far above sea level, the increasing amount of sediments in the basins being accommodated by differential movements between the mountains and the basins. From middle Eocene time on, the surfaces of deposition were gradually raised higher and higher, in part because the sediments accumulated without basin sinking and perhaps in part because of progressive epeirogenic uplift. Epeirogenic uplift had its major pulsation, or reached its culmination, probably in Pliocene time, as pointed out by Love (1939). It is believed that faulting, represented by the Cedar Ridge fault, and others mentioned by Love, by which the relations between mountain ranges and basins were again changed, took place at this time.

The sedimentational history of Eocene rocks in the northeastern part of the Wind River Basin can now be discussed against this background. The rocks of the Tepee Trail formation present two interesting sedimentational problems. One is the mode of transport of such large volumes of volcanic material. The other is the conditions that permitted the accumulation of volcanic material directly adjacent to a rugged topography in the pre-Tertiary rocks and prevented the erosion of them and the incorporation of the debris with the volcanic material.

Discussion of these problems necessarily is speculative in large part. Perhaps a somewhat imaginative reconstruction of events and conditions will stimulate the gathering of data bearing on such problems.

The Wind River formation in the northeastern part of the Wind River Basin represents a complex of depositional conditions. Extremely coarse debris was shed by the mountains into the basin, as evidenced by the boulder conglomerate in Cedar Ridge and in the western part of the area included in figure 2. These conglomerate masses did not extend far into the basin, however, and at the time they were accumulating near the mountains red-banded fine-grained sediments were being deposited no more than 4 or 5 miles to the south. Apparently these were derived from the uplands, large areas of which were covered with red residual soil according to Van Houten (1948). The manner of deposition of the conglomerate has not been studied. The great size of some of the boulders suggests that mudflows may have been important in moving the coarse material out of the mountains. Mudflow structures were not recognized in the conglomerate, though, perhaps because they had been obscured by reworking of the mudflow masses by streams.

In the Boysen area, west of that shown in figure 2, the mountain debris, none as coarse as that in the northeastern part of the Wind River Basin, was moved southeast from the mountain front by relatively short tributaries to a generally eastward-flowing master drainage system (Tourtelot and Thompson, 1948). The locus of successive levels of the master drainage system seems to lie about along the south margin of figure 2. The depositional pattern of the numerous channel sandstones that mark the locus of the drainageway does not change as the eastern border of the Wind River Basin is approached, and it is concluded that the basin was open to the east during at least the later part of early Eocene time.

Conditions of deposition of the Tepee Trail formation were quite different. First, the bulk of the sediment being deposited was derived from the volcanic centers in the Absaroka-Yellowstone region. Second, very little material was being eroded from the mountain ranges in contrast to the vast amount of debris that had been shed by them during early Eocene time. There is little or no evidence of any marked general climatic change, although the local climate probably was somewhat modified by the seemingly great volcanic activity no more than 70 miles or so to the west.

The well-developed bedding and rounded pebbles, cobbles, and grains of volcanic material indicate that the final agent acting on most of the material in the Tepee Trail formation was running water. Pond or quiet-water environments certainly existed, as is indicated by the fresh-water limestone and beds of claystone, but these seem to be minor in the environment as a whole. It is possible that the pebbles and cobbles of volcanic material were carried from their source to the northeastern part of the Wind River Basin entirely by streams. The presence of cobbles, however, seems to imply streams of great carrying power. Other evidence for such streams, such as channeling and relatively thick accumulations of conglomerate, are largely lacking. Also, it is difficult to imagine streams with such carrying power having courses essentially parallel to the mountain fronts and as close to them as the distribution of cobbles would indicate.

At present, the volcanic breccia, tuff, and minor intrusive rocks of the Tepee Trail formation in the Absaroka Range form steep escarpments above the Wind River Basin on the south and the Big Horn Basin on the east. These erosional escarpments clearly have little relation to the possible former extent of the materials into the Wind River and Big Horn Basins. Squaw Buttes, in the southwestern part of the Big Horn Basin, is an isolated remnant of the Early Basic Breccia (Van Houten, 1944). Although the pieces of the rock have been somewhat rounded, and the mass should be called a volcanic conglomerate (R. L. Hay, personal communication, 1956), the rock is similar in appearance and physical characteristics to the breccias of the Absaroka Range. Squaw Buttes thus appears to be a remnant of volcanic material in the deposition of which running water was not the dominant agent. Probably masses of volcanic material once extended much farther into the Wind River and Big Horn Basins than they do now. Anderson (1933) has described volcanic mudflows that traveled much farther than the present distance between Squaw Buttes and the Absaroka Range, and on slopes that were similar to those that must have existed in the Big Horn Basin. The interpretation that formerly much more extensive volcanic mudflow masses were present in both the Wind River and Big Horn Basins is believed to be reasonable and helps explain the presence of volcanic cobbles in the northeastern part of the Wind River Basin.

The volcanic cobbles have a somewhat peculiar distribution along the south side of the Big Horn Mountains. The northernmost section of figure 4 illustrates this distribution. The rocks shown in the section are exposed at the mouth of Sagebrush Draw where that stream leaves a canyon as much as 500 feet deep in the pre-Tertiary rocks and has its course on the Tepee Trail formation. A cross section through this canyon and a parallel section through the ridge a mile west of the canyon is shown in figure 7. At the north end of the section, strata of the Tepee Trail formation from the main mass of Lysite Mountain almost enter the upper part of the canyon. A remnant of Tepee Trail strata is preserved within the canyon, and Tepee Trail strata extend into the lower part of the canyon from its mouth. The strata in the northernmost section of figure 4 are very nearly within the mouth of the canyon, being less than half a mile distant from pre-Tertiary rocks both to the east and to the west. Volcanic conglomerate is moderately abundant in a unit about 50 feet below the top of the Tepee Trail strata exposed there but, curiously, is present in somewhat larger amounts than similar-sized material

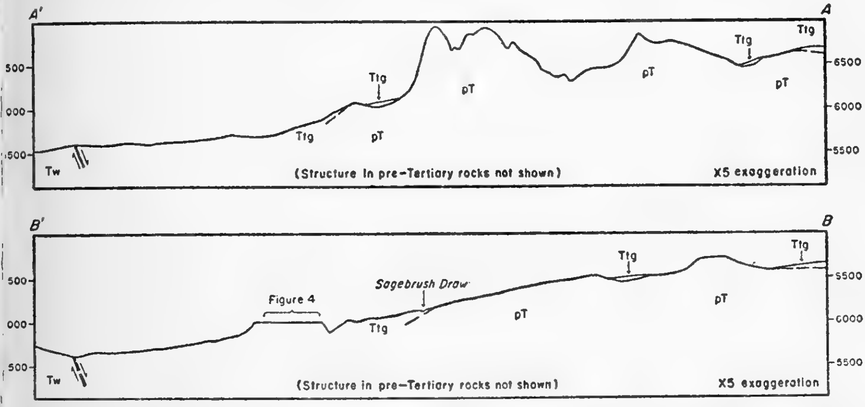


FIG. 7.—Cross sections along Sagebrush Draw (B′-B) and along ridge parallel to and 1 mile west of Sagebrush Draw (A′-A) showing position of Tepee Trail formation on north flank of Big Horn Mountains and in valley on south flank of mountains.

derived from the pre-Tertiary rocks. It is difficult to imagine how the volcanic material could have been placed almost within the canyon mouth by streams flowing eastward or northeastward in the Wind River Basin, even though a source for the volcanic material might have been a mudflow 50 or even 20 miles away. A similar topographic setting for Tepee Trail deposition is shown in figure 6, a cross section along Clear Creek, and a contrasting section along the ridge a mile west of the creek.

In considering this anomalous distribution of volcanic conglomerate, it should be recalled that both the Wind River Basin and the Big Horn Basin to the north were being filled at about the same time. Inasmuch as the Wind River Basin is believed to have been open to the east, and the Big Horn Basin was either closed or open to the north, there is no reason for the two basins to have filled at the same rate. Quite the contrary seems much more reasonable, in fact, when it is considered that volcanic material could enter the Wind River Basin chiefly through a relatively narrow passage at the northwest end of the basin. The middle and late Eocene volcanic material had access to the Big Horn Basin, obviously, all along the west side of the basin, 70 miles or so long. It seems logical to believe, therefore, that the Big Horn Basin was filled to the lowest topographic point between the Owl Creek and Big Horn Mountains at a time when the floor of the Wind River Basin on the south side of the mountains was still several hundred feet below this point. The lowest point between the ranges probably is concealed by the Tepee Trail strata along Bridger Creek (T. 41 N., R. 91 W.). As successively higher low points in the mountains were reached, such as the upper part of Sagebrush Draw, material would flood down the canyons to the south. Some downcutting of the canyons probably took place at this time and soon erosion into the Big Horn Basin fill permitted volcanic cobbles to move down the canyons and be deposited in their mouths.

The white clastic facies of the Tepee Trail formation clearly represents erosion of the mountains during Tepee Trail time. At very few places, however, do the rocks of the white clastic facies indicate as much vigorous sedimentational activity as suggested by the coarse volcanic sediments in the Tepee Trail. The general lack of sorting and possible mudflow deposition of some of the white clastic facies have been mentioned. The white kaolinitic appearance of some parts of the white clastic facies, particularly adjacent to areas underlain by granite, may be the result of leaching of iron from the early Eocene residual soils that were suggested by Van Houten (1948). Further investigation of this possibility would be interesting.

Although the white clastic facies and scattered fragments of pre-Tertiary rocks in the Tepee Trail formation, such as those at the mouth of Sagebrush Draw, indicate some erosion of the uplands of pre-Tertiary rocks, the amount of such materials seems anomalously small. This is particularly evident where the Tepee Trail formation was deposited at the foot of relatively steep canyons such as shown in figures 6 and 7. Whatever may have been the actual amount of material eroded from the pre-Tertiary rocks of the mountains in Tepee Trail time, it seems obvious that such locally derived material was considerably diluted and may have been masked by the larger amount of volcanic material.

A further possible explanation related to the mode of transport of the volcanic material also seems attractive. Hypothetical mudflows, of which possibly Squaw Buttes is the only remnant, have been suggested as an agent in the transport of cobbles of volcanic rock to the northeastern part of the Wind River Basin in addition to possible stream transport of such materials from the Absaroka source. Mudflows of such magnitude seemingly would be most likely to occur during long-continued volcanic activity in the Absaroka-Yellowstone region. It is easy to believe that large amounts of relatively fine-grained ejecta would have been carried aerially to the east. The presence of glass shards in most rocks and abundant euhedral crystals of feldspar in some of the resedimented crystal tuffs point to such a condition. If this truly pyroclastic material was transported aerially to the northeastern part of the Wind River Basin and deposited on the slopes in large enough amounts, the streams would have been choked with such debris and incapable of eroding the pre-Tertiary rocks. The pyroclastic material would have moved down the slopes either by rill wash or various kinds of mass movement. The streams at the bottoms of the slopes were short, draining only the south sides of the Big Horn and Owl Creek Moutains, and their capacities would be overloaded by relatively small amounts of pyroclastic debris. Hence, except for canyons that may have been delivering material from the Big Horn Basin into the Wind River Basin, little pre-Tertiary material could be expected to be incorporated in the Tepee Trail formation even though it was deposited at the foot of well-developed highlands.

The upper unit of the Hendry Ranch member reflects a rather large change in depositional conditions. Vitreous volcanic ash became really conspicuous for the first time in strata assigned to the Tepee Trail. In addition, erosion of the pre-Tertiary rocks seems to have become more effective, judging from the conglomerate made up of

Pre-Cambrian and Cambrian rocks in the lower part of the unit. Evidently, the rocks of later Paleozoic age now fringing the south side of the Big Horn Mountains for 3 or 4 miles both northwest and southeast of Clear Creek had been covered by older Tepee Trail strata, leaving only the Pre-Cambrian and Cambrian rocks of the highlands along the upper reaches of Clear Creek available for erosion.

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TROCHAMMINIDAE AND CERTAIN LITUOLIDAE (FORAMINIFERA) FROM THE RECENT BRACKISH-WATER SEDIMENTS OF TRINIDAD, BRITISH WEST INDIES

(With 4 Plates)

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INTRODUCTION

The study of foraminiferal material obtained during a comprehensive program of sampling in the brackish-water environment around the coasts of Trinidad, B.W.I., has brought to light a number of taxonomic problems. This paper describes all the Recent brackish-water Trochamminidae known from Trinidad, some Lituolidae requiring emendation, and others not previously recorded from Trinidad.

In 1948, Cushman and Bronnimann published two papers (1948a, 1948b) on the brackish-water Foraminifera of Trinidad. These papers were pioneers in this branch of the study of Recent faunas. Since then, many papers written in North America have added considerably to the knowledge of brackish-water faunas there.

In the inshore, brackish-water environment in Trinidad, salinities are always lower than in the open sea as precipitation is higher than evaporation and streams continue to bring down fresh water into the marsh areas throughout the year. The range of salinities is higher than in the open sea, especially in river estuaries. Temperatures are exceedingly variable, as mud banks may be under only a very shallow water cover at low tide. The percentage of dissolved oxygen is also variable, depending on whether fresh water is being introduced or whether semistagnant conditions exist.

The calcareous forms that can flourish in the coastal swamps and river estuaries belong mainly to the genera *Rotalia* and *Criboelphidium.* The arenaceous forms are described herein, except for

Ammoastuta inepta (Cushman and McCulloch) and species of *Ammobaculites.* The arenaceous tests are all thin walled and fragile, often with a "chitinous" inner layer which may be the only wall in the early chambers. Several of the lituolid genera develop multiple apertures, at least in the late stages (*Ammoastuta, Haplophragmium,* and *Trochamminita*). It is possible that this is an adaptation to the environment. This being the case, the danger of erecting new genera based on multiple apertures alone becomes apparent, as has been stressed previously (e.g., Glaessner, 1955).

Two new genera, *Siphotrochammina* and *Tiphotrocha,* are erected for Trochamminidae with stable apertural features that prevent their inclusion in the genus *Trochammina.* It is to be expected that this specialized environment should cause the development of new genera especially adapted to it. Their recognition is of value, as they may be of great help in the detection of similar biofacies in fossil deposits.

All figured types are deposited in the United States National Museum, Washington, D. C. An additional set of types will be deposited in the British Museum (Natural History), London.

Sincere thanks are due Dr. Helen Tappan Loeblich and Dr. Alfred R. Loeblich, Jr., who have been consulted at all stages and who have compared the author's material with that in the U. S. National Museum. The excellent illustrations were prepared by Patricia Isham, scientific illustrator at the U. S. National Museum. Dr. H. M. Bolli has read the manuscript and made many valuable suggestions for which the author is indebted to him. Acknowledgment is made to the Management of Trinidad Leaseholds, Ltd., for the use of laboratory facilities.

SYSTEMATIC DESCRIPTIONS

Family LITUOLIDAE Reuss, 1861

Genus HAPLOPHRAGMOIDES Cushman, 1910

HAPLOPHRAGMOIDES MANILAENSIS Andersen

PLATE 1, FIGURES 1, 2

Haplophragmoides manilaensis ANDERSEN, Contr. Cushman Found. Foram. Res., vol. 4, pt. 1, p. 22, pl. 4, fig. 8, 1953.

Diagnosis.—Shape of test: Planispiral, completely or almost completely involute, with a lobate equatorial periphery; area around the umbilicus depressed relative to the periphery. Axial periphery rounded. *Wall:* Fine sand grains with little cement; an inner, flexible, "chitinous" layer is exposed on abraded specimens where the agglutinated, outer layer has been removed. The surface exhibits a fine "sugary" texture. Color light brown to fawn. *Chambers:* Wedge shaped when viewed both equatorially and axially; 7 to 10 (usually 8) in the last whorl, increasing rapidly in size. Chamber shape tends to be irregular in the last whorl of some specimens. The last chamber may become wider and flattened across the axial periphery with a terminal face that is flattened or even slightly concave (pl. 1, fig. 1). *Sutures:* Radial, slightly depressed in the umbilical area becoming more depressed toward the periphery. *Aperture:* An equatorial, interiomarginal, symmetrical, low-arched slit surmounted by a narrow, projecting lip. *Size of hypotype* of figure 2: Maximum diameter 0.55 mm., maximum thickness 0.28 mm.

Locality.—Figured hypotypes (U.S.N.M. Nos. P5092a, b) from sample J.S. 273, Carenage Swamp, west coast of Trinidad, B.W.I.

Distribution.—Haplophragmoides manilaensis Andersen is more restricted in its distribution in Trinidad than is *Haplophragmoides wilberti* Andersen. It is uncommon in the river estuaries and in most of the swamps, though it occurs in great numbers in the Carenage Swamp on the west coast. Here it may be found in shallow drains cut through mangroves and water-logged coconut plantations. At low tide the mud is above water level.

Remarks.—Trinidad representatives of this species resemble closely Andersen's holotype described from Louisiana (Andersen, 1953).

HAPLOPHRAGMOIDES WILBERTI Andersen

PLATE 2, FIGURE 1

Haplophragmoides wilberti ANDERSEN, Contr. Cushman Found. Foram. Res., vol. 4, pt. 1, p. 21, pl. 4, fig. 7, 1953.

Diagnosis.—Shape of test: Planispiral, involute, with a smooth or very slightly lobate equatorial periphery; the small, deep umbilici may be closed by the chambers of the last whorl. Axial periphery symmetrically rounded. *Wall:* Fine sand grains set in abundant cement; surface smooth, polished. The sutural faces of the chambers are frequently of a somewhat coarser texture than the lateral walls. Color red-brown to light fawn. *Chambers:* Slightly inflated; wedge shaped in side view, with apices meeting around a small umbilicus or completely closing it; seven to nine chambers in the last whorl, increasing gradually in size. Terminal face of last chamber somewhat convex with a slight depression parallel to each lateral margin. *Sutures:* Distinct, very slightly depressed, straight or faintly sigmoid. *Aperture:* An equatorial, interiomarginal, symmetrical, low-arched slit surmounted by a narrow but prominent lip. *Size of figured hypotype:*

Diameter 0.32 mm., thickness 0.16 mm.

Locality.—Figured hypotype (U.S.N.M. No. P5114) from sample Bo. 262, Ortoire River, east coast of Trinidad, B.W.I.

Distribution.—Haplophragmoides wilberti lives in large numbers in all the swamps and in the brackish sections of the rivers in Trinidad.

Remarks.—Specimens from Trinidad resemble very closely those described by Andersen (1953) from the Louisiana coast, although Andersen's holotype is larger than the average size for Trinidad material.

Genus TROCHAMMINITA Cushman and Bronnimann emend. Saunders

Type species.—Trochamminita irregularis Cushman and Bronnimann emend. Saunders.

Emended diagnosis.—Test planispiral throughout or planispiral in the early stage with adult chambers added very irregularly. Wall arenaceous. Aperture in planispiral tests either a single areal opening or multiple areal openings on the terminal face of the final chamber; where adult chambers are irregularly added, multiple apertures are usual, their position being very variable. All apertures are surrounded by prominent lips.

Remarks.—Emendation of the type species necessitates these changes in the generic definition, including the removal of *Trochamminita* from the Trochamminidae to the Lituolidae.

The type species, *Trochamminita irregularis* Cushman and Bronnimann emend. Saunders, shows all transitions of test form from wholly planispiral to almost completely irregular. A second species, *Trochamminita salsa* (Cushman and Bronnimann) emend. Saunders, is included in the genus. In this species only planispiral forms are developed though some tests show a slight tendency toward irregular growth. The taxonomic position of *Trochamminita salsa* is discussed in the remarks on that species (p. 7).

TROCHAMMINITA IRREGULARIS Cushman and Bronnimann emend. Saunders

Plate 2, figures 2-8

Trochamminita irregularis Cushman and Bronnimann, Contr. Cushman Lab. Foram. Res., vol. 24, pt. 1, p. 17, pl. 4, figs. 1-3, 1948.

Emended diagnosis.—Shape of test: All intermediate stages found between forms that are planispiral throughout and those that have a planispiral or slightly irregularly planispiral early portion followed by an adult stage of very irregularly arranged chambers. *Wall:* Thin, of coarse sand grains with almost no cement; in the late chambers of very irregular forms, large quartz grains may be incorporated. An inner "chitinous" layer is present. Surface rough. Color brown. *Chambers:* In planispiral tests, normally six to seven inflated chambers in the last whorl increasing fairly rapidly in size; where an additional irregular stage is present, the later chambers are inflated, of variable size, and added at random. *Sutures:* Radial, depressed in the planispiral portion of the test. *Apertures:* Single or multiple areal apertures in chambers of the last whorl of planispiral tests. In tests with irregular adult chambers the aperture is single or multiple and areal in the planispiral early part, normally multiple (usually from two to six openings) in irregular later development. *Size:* Planispiral form of figure 2, maximum diameter 0.45 mm., approximate thickness 0.23 mm. Irregular form of figure 5, length approximately 0.7 mm. Irregular form of figure 6, length 0.64 mm., maximum thickness approximately 0.37 mm.

Locality.—Figured hypotypes (U.S.N.M. Nos. P5093 to P5099) from sample J.S. 65, Maracas Bay River, north coast of Trinidad.

Distribution.—*Trochamminita irregularis* Cushman and Bronnimann emend. Saunders occurs in great numbers in the Maracas Bay River on the north coast of Trinidad; elsewhere on the island its distribution seems to be sporadic. The rich locality in Maracas Bay (sample J.S. 65) is in a shallow tributary drain of the Maracas Bay River. The drain runs parallel to the sea a short distance behind the beach, from which it is separated by a screen of mangroves and coconut palms.

Remarks.—The very well preserved material used in the present study has shown that the original description is incorrect. The main difference lies in the discovery of all types of test form, from regular planispiral tests with one or more areal apertures in the last chamber (pl. 2, fig. 2) to forms with only a small planispiral or very slightly trochospiral early stage followed by irregular chambers in which areal apertures are usually multiple (pl. 2, figs. 6-8). Commonly found are intermediate types which are largely planispiral but have one or two final chambers added out of the original plane of coiling, and normally have multiple apertures in the last chamber (pl. 2, figs. 3, 4). All stages may be found in the same sample. The final, highly irregular forms are close to the figures of the holotype and paratypes of *Trochamminita irregularis* given by Cushman and Bronnimann (1948a, pl. 4, figs. 1-3). However, Cushman and Bronnimann did not record the presence of multiple apertures.

The present author has dissected a number of specimens to study the apertures in what Cushman and Bronnimann (1948a, p. 17) called "the early trochoid stage." Results show a planispiral or slightly irregularly planispiral early stage with single or multiple (usually two), areal apertures between the chambers. All apertures are definitely areal and are completely surrounded by very prominent lips. No sign of the interiomarginal apertures mentioned by Cushman and Bronnimann has been seen; if present at all they can only be in the very early chambers of the planispiral portion of the test.

TROCHAMMINITA SALSA (Cushman and Bronnimann) emend. Saunders

PLATE 1, FIGURES 3-8

Labrospira salsa CUSHMAN and BRONNIMANN, Contr. Cushman Lab. Foram. Res., vol. 24, pt. 1, p. 16, pl. 3, figs. 5, 6, 1948.

Emended diagnosis.—Shape of test: Planispiral, semi-involute or involute, with a lobate equatorial periphery. Axial periphery rounded. Although normally symmetrically planispiral, some individuals show slight irregularity of coiling. *Wall:* Sand grains set in fine cement; surface smooth, may be somewhat polished. Coarseness of wall varies considerably in specimens from different localities. Color fawn to light brown. *Chambers:* Slightly inflated; seven to eight in the last whorl, increasing fairly rapidly in size. Earlier chambers may be partially visible. *Sutures:* Slightly curved, depressed. *Aperture:* In the adult stage may be represented by a single areal slit near the base of the terminal face of the chamber, or multiple pores of rounded, though somewhat irregular, shape. If the aperture is multiple, the pores are usually in a linear series where the single areal aperture would otherwise be situated (pl. 1, fig. 6), though some specimens show multiple apertures distributed widely across the terminal face. If a single aperture is present, it may show one or more constrictions, suggesting a tendency toward the formation of a number of separate openings. All apertural openings are completely surrounded by prominent lips. Dissection shows that multiple apertures are not restricted to the last chamber but may be present in several of the chambers of the last whorl. *Size:* Hypotype of figure 3—maximum diameter 0.32 mm., maximum thickness 0.16 mm. Hypotype of figure 7, maximum diameter 0.43 mm., maximum thickness, 0.2 mm. Hypotype of figure 8, maximum diameter 0.65 mm., maximum thickness 0.29 mm.

Locality.—All figured hypotypes (U.S.N.M. Nos. P5100 to P5105) are from sample Bo. 262, Ortoire River, east coast of Trinidad.

Distribution.—*Trochamminita salsa* (Cushman and Bronnimann) emend. Saunders occurs commonly in all inshore, brackish-water areas of Trinidad.

Remarks.—The specific description has been emended to cover the presence of multiple apertures in some individuals. Presumably this feature was not seen by Cushman and Bronnimann in their material, but examination of a large number of specimens from all coasts of Trinidad has shown that the development of more than one aperture in the adult stage of the test is quite a common feature. A number of specimens, when dissected, show multiple apertures in up to four chambers of the last whorl before which a single areal aperture is seen.

Cushman and Bronnimann placed this species in the genus *Labrospira* Höglund. *Labrospira* is considered to be a junior synonym of *Cribrostomoides* Cushman by Frizzell and Schwartz (1950). Loeblich and Tappan (1953, p. 28) maintain that *Labrospira* is a junior synonym of *Alveolophragmium* Stschendrina whereas *Cribrostomoides* is a distinct genus. The present author's examination of the species under discussion shows that it cannot be placed in the genus *Alveolophragmium* owing to the presence of multiple apertures. In addition, he considers that it should not be placed in the genus *Cribrostomoides* Cushman emend. Frizzell and Schwartz, the holotype of which is a deep-water form in which multiple apertures, if present, are produced by the fusion of toothlike projections across the normal single areal aperture. The multiple apertures of *Cribrostomoides bradyi* Cushman are situated in a single line near the base of the terminal face of the chamber.

Reexamination of *Trochamminita irregularis* Cushman and Bronnimann has led to an emendation of the species (see p. 4) and therefore of the genus (see p. 4). The new information shows that *Trochamminita salsa* (Cushman and Bronnimann) emend. Saunders and planispiral forms of *Trochamminita irregularis* Cushman and Bronnimann emend. Saunders only differ in chamber shape and coarseness of wall texture. These features are constant, even when the two species are found in the same sample, but they are only of specific value. Therefore, the inclusion of the two species under the same genus appears to be the only logical course.

Family TROCHAMMINIDAE Schwager, 1877

Genus TROCHAMMINA Parker and Jones, 1859

TROCHAMMINA LAEVIGATA Cushman and Bronnimann

PLATE 3, FIGURE 3

Trochammina laevigata CUSHMAN and BRONNIMANN, Contr. Cushman Lab. Foram. Res., vol. 24, pt. 2, p. 41, pl. 7, figs. 21, 22, 1948.

Diagnosis.—Shape of test: Trochospiral, with a round, slightly lobate equatorial periphery; dorsal side slightly convex or almost flat, ventral side concave owing to the presence of a small, deep umbilicus; axial periphery rounded. In large specimens, with highly inflated last chambers, the dorsal side may be very slightly concave. *Wall:* Minute sand grains set in a fine cement; surface smooth, somewhat polished. Color reddish brown to fawn. The protoconch and first whorl are dark brown; the wall of this early portion of the test is apparently composed of a chitinous layer with no adherent agglutinated material. Being extremely fragile, the early chambers have often been excavated. *Chambers:* Inflated ventrally, less strongly dorsally. Seventeen to twenty chambers arranged in about three whorls with five to six chambers in the last whorl. The rate of increase in size of the chambers in the last whorl varies, some specimens having relatively larger, more inflated, final chambers than others. *Sutures:* Distinct, almost flush with surface dorsally, depressed ventrally. Straight or slightly curved. *Aperture:* An interiomarginal slit on the ventral side of the last chamber extending from the umbilicus one-third to one-half the distance to the periphery; a narrow, prominent lip is seen in well-preserved specimens. *Size:* Maximum diameter of figured hypotype 0.48 mm., thickness of hypotype 0.21 mm.

Range for species.—Diameter approximately 0.3 mm. to approximately 0.8 mm. Thickness approximately 0.15 mm. to approximately 0.37 mm.

Locality.—Figured hypotype (U.S.N.M. No. P5106) from sample J.S. 273, Carenage Swamp, west coast of Trinidad, B.W.I.

Distribution.—Trochammina laevigata Cushman and Bronnimann is widespread in all inshore, brackish-water areas of Trinidad.

Remarks.—This species is very close to *Trochammina inflata* (Montagu). Montagu's original figure and description of *Nautilus inflatus* (Montagu, 1808, p. 81, pl. 18, fig. 3) are too poor to be used for comparison. Brady's description and figures of *Trochammina inflata* (Montagu) (Brady, 1884, p. 338, pl. 41, figs. 4a-c), shows extremely slight differences between this species and *Trochammina* *laevigata* Cushman and Bronnimann. *Trochammina inflata* has a slightly more convex dorsal surface with more deeply incised sutures and its last chambers are more inflated. Papers on brackish faunas of the coasts of North America (Phleger and Walton, 1950; Parker, Phleger, and Peirson, 1953; Ronai, 1955) describe as *Trochammina inflata* (Montagu) specimens that are almost certainly identical to *Trochammina laevigata* Cushman and Bronnimann.

SIPHOTROCHAMMINA Saunders, new genus

Type species.—Siphotrochammina lobata Saunders, new species,

Diagnosis.—Test trochospiral, involute ventrally. Dorsal side flat or convex, ventral side concave. Wall arenaceous; some specimens have very little agglutinated material on the basic "chitinous" wall. The last chamber has a ventral, siphonlike lobe extending partially across the umbilicus. The aperture is situated at the umbilical end of this lobe and is directed forward. The aperture of the penultimate chamber opens into the ventral lobe of the last chamber. A plate may extend across the umbilicus concealing the primary aperture; in this case, irregular secondary apertures are present on one or both sides of the plate.

Remarks.—Siphotrochammina is closely related to *Trochammina* Parker and Jones, 1859, from which it differs in the nature of its aperture. In *Trochammina* the aperture is an arched slit at the inner margin of the ventral side of the chamber whereas in *Siphotrochammina* the aperture is a forward-directed, circular opening at the inner end of a siphonlike lobe that extends from the last chamber into the umbilicus. The aperture of the penultimate chamber opens into the "siphon" of the last chamber. *Siphotrochammina* is somewhat similar to the free stage of *Tritaxis* Schubert, 1920, emend. Loeblich and Tappan, 1955. In the emended description of this latter genus the aperture in the free stage is "an ovate opening at the base of the last-formed chamber near the umbilicus, and surrounded by a distinct lip . . ." (Loeblich and Tappan, 1955).

SIPHOTROCHAMMINA LOBATA Saunders, new species

PLATE 3, FIGURES 1, 2

Diagnosis.—Shape of test: Trochospiral, with a lobate equatorial periphery; dorsal side convex, ventral side slightly concave. Axial periphery rounded. *Wall:* Thin, consisting of fine sand grains with little cement. Surface smooth and somewhat polished. An inner "chitinous" layer is present and, in very fragile specimens, agglutinated material may be almost entirely lacking. This is the case in the first whorl of nearly all specimens, the chambers of which have often been excavated. Color light brown to fawn with dark brown early chambers. *Chambers:* Test of three to three and a half whorls with five or six chambers in the last whorl. Chambers increasing regularly in size; slightly inflated dorsally, more so ventrally. The last chamber possesses a narrow, siphonlike lobe which may partially obscure the umbilicus. From this ventral lobe of the last chamber, a "plate" of sand grains may extend over the whole umbilicus. *Sutures:* Depressed; straight dorsally and straight or slightly sinuous ventrally. *Aperture:* Typically situated at the umbilical end of the ventral lobe of the last chamber and directed forward. In some specimens it is possible to look into the last aperture and see the penultimate aperture opening into the back of the siphonlike lobe of the last chamber. If a plate extends across the umbilicus, there may be irregularly shaped secondary apertures present on one or both sides of it. *Size:* Maximum diameter of holotype 0.43 mm. Maximum thickness of holotype 0.20 mm.

Locality.—Holotype (U.S.N.M. No. P5107) and figured paratype (U.S.N.M. No. P5108) from sample J.S. 273, Carenage Swamp, west coast of Trinidad.

Distribution.—This species is fairly common in some of the Trinidad swamps as, for example, in the Carenage Swamp where it is found in considerable numbers associated with *Haplophragmoides manilaensis* Andersen (see p. 3 for note on conditions in this area). In the rivers its distribution is sporadic.

Remarks.—*Siphotrochammina lobata* Saunders differs from *Trochammina laevigata* Cushman and Bronnimann in the nature of its aperture. *Siphotrochammina lobata* has a circular aperture at the umbilical end of a ventral lobe of the last chamber whereas *Trochammina laevigata* has an interiomarginal slit surmounted by a lip and situated on the ventral side of the last chamber. In *Siphotrochammina lobata* the umbilicus, and the primary aperture as well, may be obscured by a "plate" of sand grains, but such a phenomenon has not been observed in Trinidad material of *Trochammina laevigata.* The two species are found associated in the same localities.

Siphotrochammina lobata differs from *Tiphotrocha comprimata* (Cushman and Bronnimann) emend. Saunders in that the apertures do not open separately into the umbilicus. In both species, the umbilicus may be covered by a platelike outgrowth from the chambers.

TIPHOTROCHA Saunders, new genus

Type species.—Trochammina comprimata Cushman and Bronnimann, 1948, emend. Saunders.

Diagnosis.—Test trochospiral, involute ventrally. Dorsal side flat or convex, ventral side concave. In well-developed specimens the chambers of the last whorl have inflated projections into the umbilicus. Wall arenaceous. The apertures of the chambers of the last whorl open separately into the umbilicus at the ends of the inflated chamber projections, if these are present. The last chamber may have a lip extending partially or wholly across the umbilicus and concealing all but the last aperture. The umbilical area may be covered by a "plate" formed by the coalescence of the lips of the ventral, inflated lobes of the chambers in the last whorl; in this case, most if not all of the primary apertures may be concealed.

Remarks.—The new genus differs from *Trochammina* Parker and Jones, 1859, in that the aperture of each chamber in the last whorl opens separately into the umbilicus and not into the next succeeding chamber as in the latter. Also, the umbilicus of the new genus may be concealed beneath a platelike outgrowth from the chambers. A similar umbilical cover may be present in *Siphotrochammina,* which differs from *Tiphotrocha* in lacking separate apertures from the chambers into the umbilicus.

TIPHOTROCHA COMPRIMATA (Cushman and Bronnimann) emend. Saunders

PLATE 4, FIGURES 1-4

Trochammina comprimata CUSHMAN and BRONNIMANN, Contr. Cushman Lab. Foram. Res., vol. 24, pt. 2, p. 41, pl. 8, figs. 1-3, 1948.

Emended diagnosis.—Shape of test: Trochospiral, compressed, with an irregularly lobate equatorial periphery; dorsal side slightly convex, ventral side concave. Axial periphery rounded; subangular in very compressed forms. *Wall:* Thin, consisting of fine sand grains with little cement. Surface smooth but not polished. Color brown to fawn, the first whorl may be darker in color than the rest of the test. *Chambers:* Test of two to three whorls with four to six (usually five) chambers in the last whorl. The chambers of the early whorls increase regularly in size but those in the last whorl may be rather irregular in shape and are considerably elongated in the direction of coiling. The chambers of the last whorl have inflated lobes projecting into the umbilicus. In large specimens, the last chambers are inflated and roughly T-shaped in ventral aspect. *Sutures:* Slightly depressed and markedly curved on the dorsal surface in the last whorls; less depressed and less curved in earlier whorls. Ventrally, depressed, especially toward the umbilicus. *Apertures:* In the last whorl situated at the umbilical ends of the ventral lobes of the chambers. They point into the umbilicus under shelflike lips and may be directed toward the center of the umbilicus or backward toward the earlier chambers of the whorl. Where the last chamber is highly developed, the lip on its umbilical projection may obscure the earlier apertures. Many specimens show a fusion of the umbilical projections of the chambers, obscuring most if not all of the apertures. *Size:* Hypotype of figure 1, maximum diameter 0.53 mm., approximate thickness 0.16 mm. Hypotype of figure 2, maximum diameter 0.35 mm., approximate thickness 0.13 mm.

Locality.—Hypotypes (U.S.N.M. Nos. P5109a, b) from sample Bo. 262. Ortoire River, east coast, Trinidad. Hypotype (U.S.N.M. No. P5110) from sample Bo. 261, Ortoire River, east coast, Trinidad. Hypotype (U.S.N.M. No. P5112) from sample J.S. 135, Ortoire River, east coast, Trinidad.

Distribution.—This species is especially characteristic of the brackish-water sections of the Trinidad rivers; it is found less commonly in the swamps.

Remarks.—The true character of the apertures in this species was not described by Cushman and Bronnimann. The apertural features noted in this emended diagnosis make is necessary to remove this species from the genus *Trochammina* Parker and Jones, 1859. In *Trochammina,* only the last aperture opens to the exterior; each earlier aperture is concealed by the addition of the next chamber.

Genus ARENOPARRELLA Andersen, 1951, emend. Andersen, 1951

ARENOPARRELLA MEXICANA (Kornfeld) emend. Andersen

PLATE 4, FIGURE 5

Trochammina inflata (Montagu) var. *mexicana* KORNFELD, Contr. Stanford Univ. Geol. Dept., vol. 1, p. 86, pl. 13, figs. 5a-c, 1931.

Arenoparrella mexicana (Kornfeld) ANDERSEN, Journ. Paleontol., vol. 25, No. 1, p. 31, figs. 1a-c, 1951. ANDERSEN, Contr. Cushman Found. Foram. Res., vol. 2, pt. 3, p. 96, pl. 11, figs. 4a-c, 1951.

Diagnosis.—*Shape of test:* Trochospiral, involute ventrally with a smooth or very slightly lobate equatorial periphery; dorsal side slightly convex; ventral side with a small, depressed, closed umbilicus. Axial periphery rounded. *Wall:* Fine sand grains set in abundant cement;

surface smooth, may be polished. Color brown to fawn. *Chambers:* Slightly inflated dorsally, more strongly so ventrally, especially toward the umbilicus; five to six, or more rarely seven, in the last whorl; increasing in size regularly and gradually. *Sutures:* Distinct, almost flush with the surface dorsally, depressed ventrally; straight or slightly curved. *Apertures:* Primary aperture: a narrow slit in the terminal face of the chamber commencing in an interiomarginal position and with its long axis roughly parallel to the dorsal surface. In shape it may be a straight slit though it is more usually arcuate and may even be slightly sigmoid; though normally parallel sided, it is sometimes enlarged toward the ends. Supplementary apertures: at the apex of the last chamber is an area, commonly triangular in shape, where the wall is perforated by up to 11 or 12 circular, cribrate openings. Really well-preserved specimens invariably show these cribrate apertures; when not seen, they are presumed to have been filled and obscured by foreign matter. The sievelike area of the wall forms a weak point in the test which, in many specimens, has been broken out leaving one or more irregular holes. In one test the cribrate apertures were observed in an earlier chamber of the last whorl though normally they are obscured, as was stated by Andersen (1951b). *Size:* Maximum diameter of figured hypotype 0.47 mm., thickness 0.18 mm.

Locality.—Figured hypotype (U.S.N.M. No. P5113) from sample Bo. 261, Ortoire River, east coast of Trinidad, B.W.I.

Distribution.—This species is exceedingly common and widespread in all inshore, brackish-water areas of Trinidad.

Remarks.—The Trinidad representatives of the species are identical to those described by Andersen from Louisiana.

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EXPLANATION OF PLATES

Plate 1

LITUOLIDAE

Page

Figs. 1, 2. *Haplophragmoides manilaensis* Andersen...................... 2

1a, Side view of hypotype (U.S.N.M. No. P5092a). 1b, Edge view. This large specimen shows a wide, flattened last chamber, a condition commonly seen in Trinidad specimens of this species. 2a, Side view of another hypotype (U.S.N.M. No. P5092b). 2b, Edge view. This specimen is typical for the species in Trinidad. Both from Carenage Swamp, Trinidad. × 87.

Figs. 3-8. *Trochamminita salsa* (Cushman and Bronnimann) emend. Saunders 6

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3, Edge view of hypotype (U.S.N.M. No. P5100) showing a single oval areal aperture surrounded by a prominent lip. This type of aperture is shown by Cushman and Bronnimann (1948a) in their illustration of *Labrospira salsa*. 4, Edge view of hypotype (U.S.N.M. No. P5101) showing a slitlike areal aperture surrounded by a prominent lip. 5, Edge view of hypotype (U.S.N.M. No. P5102) showing two circular areal apertures. 6, Edge view of hypotype (U.S.N.M. No. P5103) showing three circular areal apertures in a transverse line across the chamber. 7a, Side view of hypotype (U.S.N.M. No. P5104). 7b, Edge view showing three circular areal apertures. 8, Edge view of hypotype (U.S.N.M. No. P5105) showing a partly constricted slitlike areal aperture and two irregular-shaped areal apertures. The specimens in figures 3-8 show the range of apertural pattern to be found in the adult stage of this species. All from Ortoire River, Trinidad. × 100.

PLATE 2

LITUOLIDAE

Fig. 1. *Haplophragmoides wilberti* Andersen.......................... 3

1a, Side view of hypotype (U.S.N.M. No. P5114). 1b. Edge view. This specimen is typical for the species, which shows only very slight variation in Trinidad. From Ortoire River, Trinidad. × 75.

Figs. 2-8. *Trochamminita irregularis* Cushman and Bronnimann emend. Saunders 4

2a, Side view of hypotype (U.S.N.M. No. P5093); a regular planispiral form. 2b, Edge view showing two circular areal apertures in the last chamber surrounded by prominent lips. 3, Edge view of hypotype (U.S.N.M. No. P5095) showing specimen that is planispirally coiled except for the last chamber. 4, Side view of hypotype (U.S.N.M. No. P5094) showing planispiral early portion with irregularly coiled later chamber. 5, View of hypotype (U.S.N.M. No. P5096) showing a much more irregular test with four areal apertures present in the final chamber. 6, View of hypotype (U.S.N.M. No. P5097) showing small planispiral early portion followed by irregularly arranged chambers. 7, View of hypotype (U.S.N.M. No. P5098) showing a very irregular arrangement of chambers with four areal apertures in the last chamber. 8a-c, Three views of hypotype (U.S.N.M. No. P5099) showing a very irregular arrangement of visible chambers with six areal apertures in the last chamber. All specimens from Maracas Bay River, Trinidad. Figs. 2-4, × 112; figs. 5-8, × 83.

PLATE 3

TROCHAMMINIDAE

Figs. 1, 2. *Siphotrochammina lobata* Saunders, new genus, new species.. 9

1a, Dorsal view of paratype (U.S.N.M. No. P5108). 1b, Ventral view. 1c, Edge view showing aperture of penultimate chamber visible within

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the "siphon" of the final chamber. × 165. 2a, Dorsal view of holotype (U.S.N.M. No. P5107). 2b, Ventral view. 2c, Edge view. From Carenage Swamp, Trinidad. × 165.

Fig. 3. *Trochammina laevigata* Cushman and Bronnimann.............. 8

3a, Dorsal view of hypotype (U.S.N.M. No. P5106). 3b, Ventral view, and 3c, edge view, both showing the well-developed lip over the aperture. From Carenage Swamp, Trinidad. × 120.

Plate 4

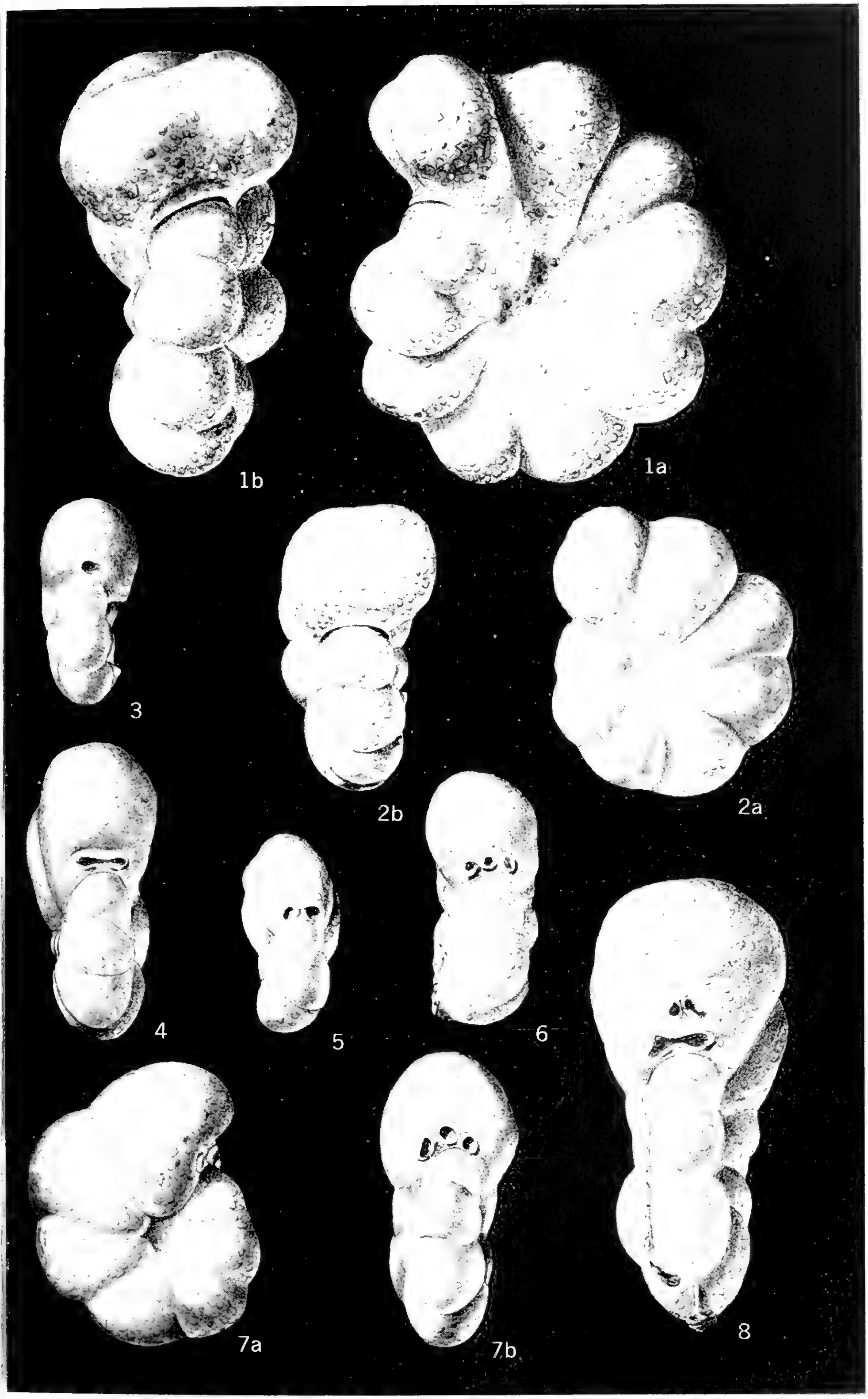
TROCHAMMINIDAE

Figs. 1-4. *Tiphotrocha comprimata* (Cushman and Bronnimann) emend. Saunders 11

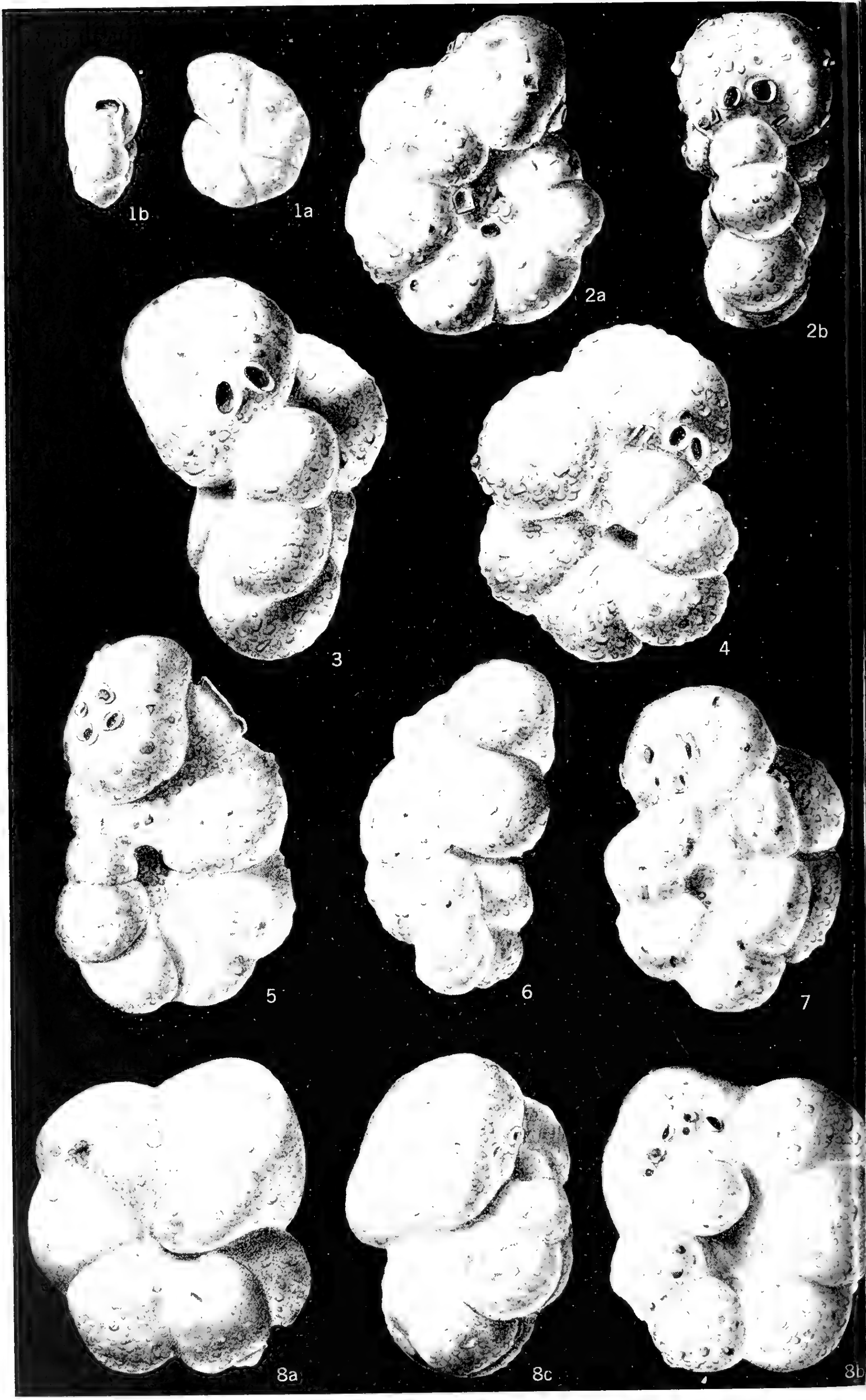
1a, Dorsal view of hypotype (U.S.N.M. No. P5109a) showing the chambers of the last whorl elongated in the axis of coiling. 1b, Ventral view showing the apertures of the chambers of the last whorl opening separately into the umbilicus. 1c, Edge view. 2a, Dorsal view of small hypotype (U.S.N.M. No. P5110). 2b, Ventral view showing less well developed ventral lobes on the chambers of the last whorl and apertures opening separately into the umbilicus. 2c, Edge view. 3, Ventral view of hypotype (U.S.N.M. No. P5112) showing a plate-like cover over the umbilicus fusing with the ventral lobes of the chambers and obscuring the apertures. 4, Ventral view of hypotype (U.S.N.M. No. P5109b) showing the large ventral lobe of the final chamber partially obscuring the umbilicus. All from Ortoire River, Trinidad. × 106.

Fig. 5. *Arenoparrella mexicana* (Kornfeld) emend. Andersen........... 12

5a, Dorsal view of hypotype (U.S.N.M. No. P5113) showing eight of the areal apertures of the last chamber. 5b, Ventral view showing the interiomarginal aperture and three of the areal apertures in the last chamber. 5c, Edge view showing the interiomarginal aperture and 12 areal apertures in the last chamber. From Ortoire River, Trinidad. × 122.

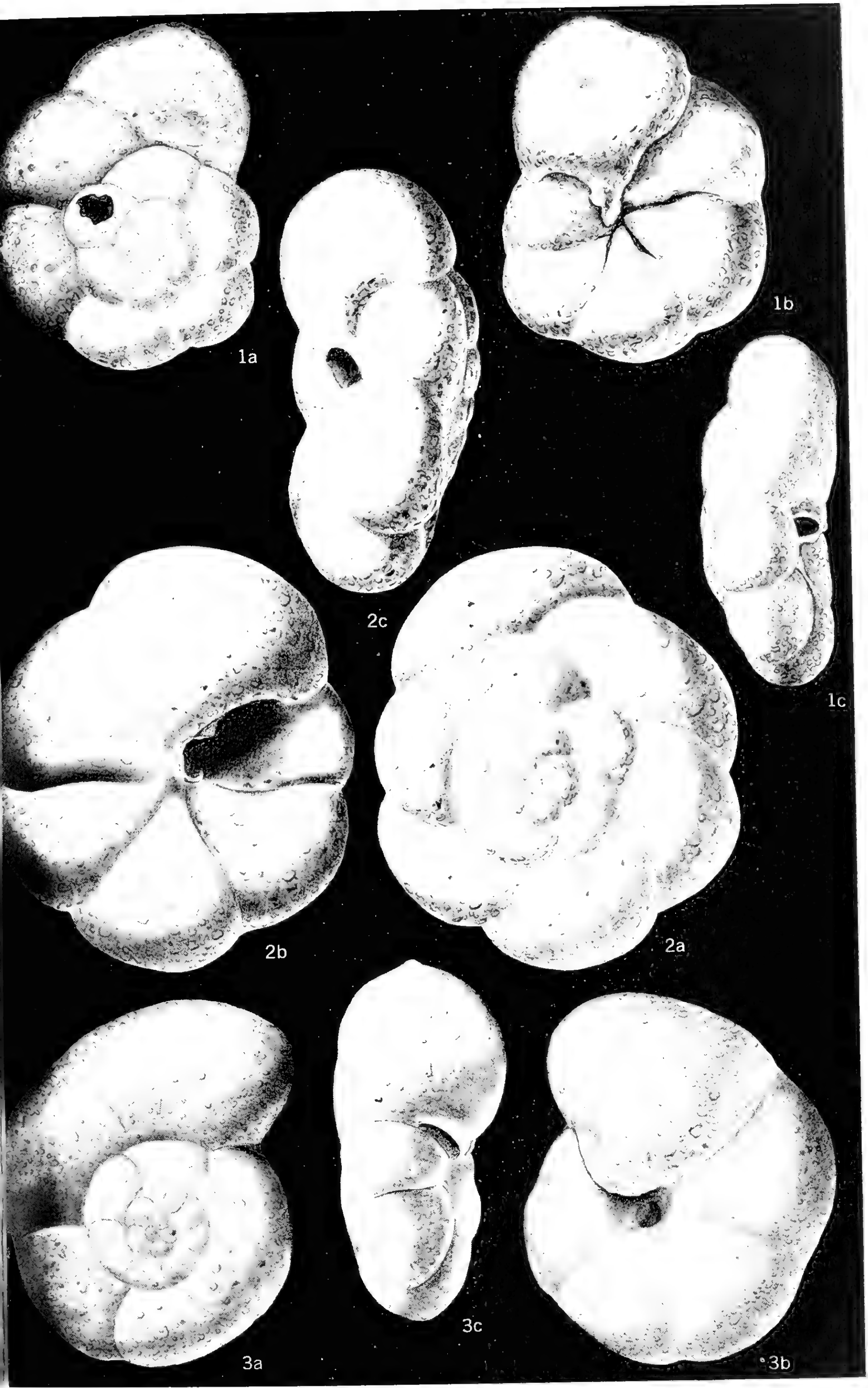


LITUOLIDAE
HAPLOPHRAGMOIDES AND TROCHAMMINITA
(See explanation at end of text.)

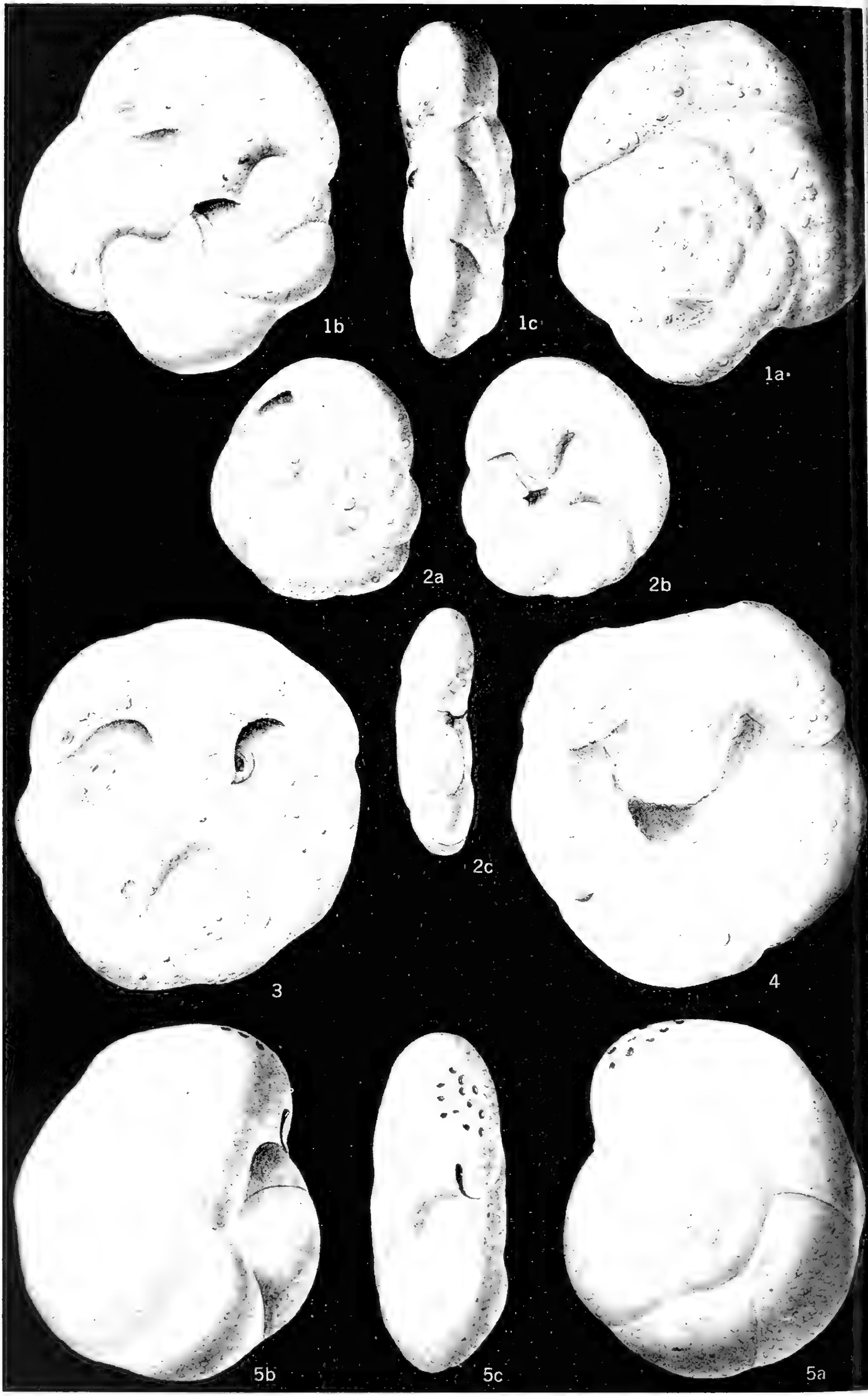


Lituolidae

Haplophragmoides and Trochamminita



TROCHAMMINIDAE
SIPHOTROCHAMMINA AND TROCHAMMINA



TROCHAMMINIDAE
TIPHOTROCHA AND ARENOPARRELLA
(See explanation at end of text.)

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STUDIES BY PHASE-CONTRAST MICROSCOPY ON DISTRIBUTION OF PATTERNS OF HEMOLYMPH COAGULATION IN INSECTS

(With One Plate)

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STUDIES BY PHASE-CONTRAST MICROSCOPY ON DISTRIBUTION OF PATTERNS OF HEMOLYMPH COAGULATION IN INSECTS[1]

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(WITH ONE PLATE)

A category of hyaline hemocytes (coagulocytes) is playing an important part in the inception of the plasma coagulation in insect hemolymph (Grégoire and Florkin, 1950). Differences in the reactions of these corpuscles to contact with foreign surfaces and in those of the surrounding plasma were recorded previously for various insects (Grégoire, 1951). On the basis of these differences, a classification of the process of hemolymph coagulation in insects into four patterns of microscopic pictures has been suggested (Grégoire, 1951).

In former observations on the distribution of the patterns in 420 species of insects, predominance of one of these patterns has been recorded in several groups of various extension in the classification (Grégoire, 1955a). The material used in these studies consisted exclusively of representatives of insects from the Old World fauna (mostly European, and a few Mediterranean and African species).

The aim of the present investigations is to compare the previous results with data obtained from Neotropical species. In July and August 1954, during a stay at the Canal Zone Biological Area, the Smithsonian Institution's tropical preserve on Barro Colorado Island, the writer collected and examined samples of hemolymph from 630 insects, belonging to about 230 species.

METHODS

The samples of hemolymph were prepared by the procedure used in former studies (Grégoire, 1951, 1955). In most specimens the hemolymph issuing from severed or punctured appendages (antennae, legs, wings, joints of the wing cases) was dropped as rapidly as possible onto the edge of a cover glass lying on a slide and was allowed to spread out into films. Under optimal conditions, streaming of the

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[1] This is No. 7 in the series of papers entitled "Blood Coagulation in Arthropods" published in various journals.

FIGS. 1-4.—The four tentative microscopical patterns of coagulation (schematic). The drawings have been combined from observations, by means of the phase-contrast microscope, of about 5,300 samples of hemolymph, in standard conditions of preparation of the films between slide and coverglass.

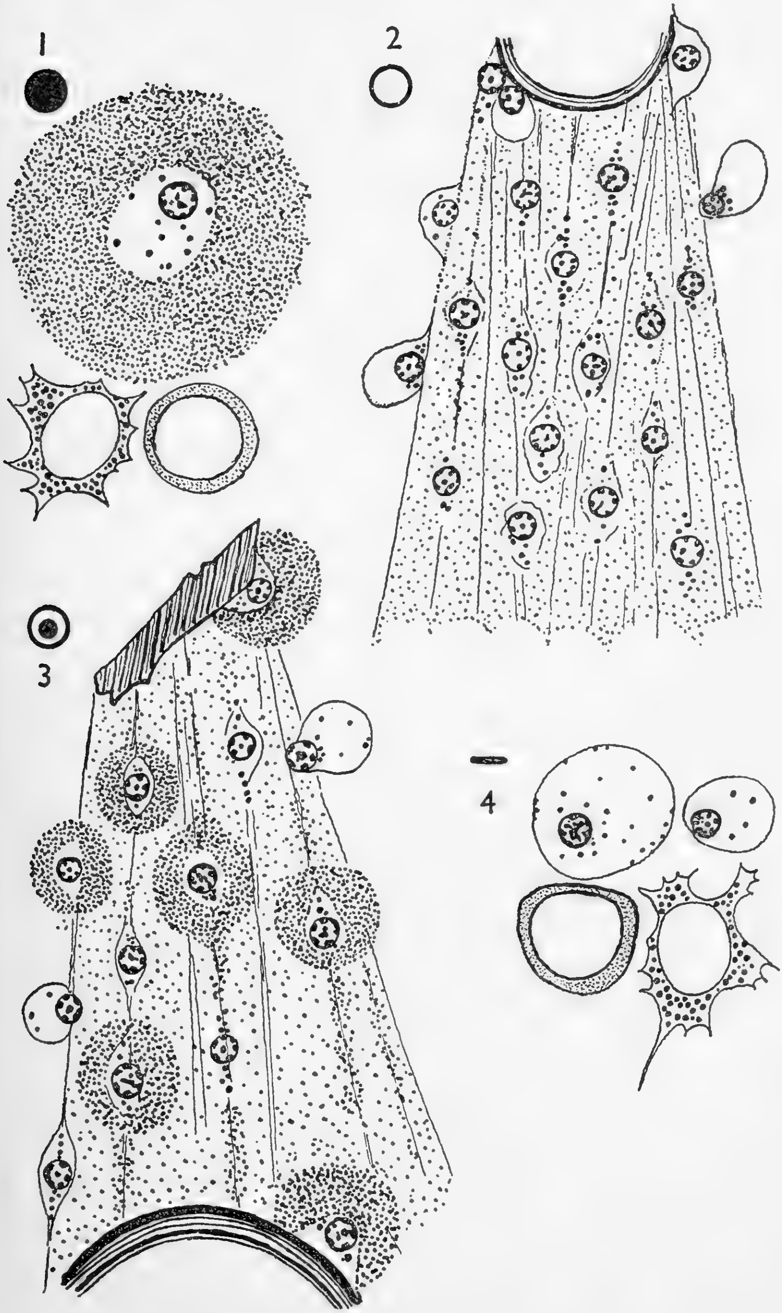
Fig. 1: *Pattern I.* Island of coagulation around a hyaline hemocyte (coagulocyte). A granular hemocyte and a macronucleocyte of small size are not involved in the process of coagulation. Extension of the coagulum around the island and reorganization of the granular clot into meshworks of granular fibrils have not been represented in the drawing. (Compare with photomicrographs in Grégoire and Florkin, 1950, pls. 1 to 10; Grégoire, 1951, figs. 1-3, 10-12, 14, 27, 28; 1953b, figs. 1, 2, 20, and 22; 1955a, figs. 1-6, 10, 15, 21, 23; 27; and in the present paper, pl. 1, figs. 1, 2, 3, 4, 5, and 7.)

Fig. 2: *Pattern II.* Extrusion of cytoplasmic expansions by hyaline hemocytes, which appear in the drawing elongated and reduced in size, except three corpuscles, bulging out at the periphery. The fan-shaped direction of the cytoplasmic filaments from an incidental bubble is induced in part by currents in the spreading film of hemolymph. However, this picture has also been observed to develop slowly, when the hemolymph was at a standstill. Reaction in the plasma in the shape of glassy elastic veils (no cell fibrin) inside of the cytoplasmic systems built up by the unstable hemocytes. The veils are frequently detected only by their stretched folds. By pressure exerted on the coverglass, the structures embedded in the veils move backward and forward, and preserve their relative positions and distances to each other. The other categories of hemocytes, agglutinated at random in strands along the highly adhesive cytoplasmic expansions of the fragile hemocytes, are not represented on the drawing. (Compare with photomicrographs in Grégoire, 1951, figs. 24-26; 1955a, figs. 17-19, 22, 26, 38, 39, 41; and in this paper, pl. 1, fig. 6.)

Fig. 3: *Pattern III.* Association of patterns I and II in the same film of hemolymph: extrusion of cytoplasmic expansions by the hyaline hemocytes, as in pattern II. Reaction of the plasma consisting of granular veils and of islands of coagulation. The islands appear within the veils as circular areas of greater density around the hyaline hemocytes. In this drawing, the reaction was initiated by alterations in hyaline hemocytes to contact with a foreign body (hatched). For the fan-shaped disposition of the structures, see above, pattern II. The other categories of hemocytes are not represented on the drawing. (Compare with photomicrographs in Grégoire, 1955a, figs. 11 and 20; and in this paper, pl. 1, fig. 9.)

Significance of pattern III might be questioned as representing merely a subsidiary variation of pattern II. However (see legend, plate 1, fig. 9, *Zophobas latticollis* Kraatz, Tenebrionidae), pattern III depicts actual differences appearing consistently in the microscopical picture of coagulation of the hemolymph, between groups of insects such as Cetoninae (typical pattern II) and Tenebrionidae (typical pattern III). On the other hand, as already pointed out (Grégoire, 1951), strong mechanical agencies are apt to give deceptive pictures of pattern III, by inducing extrusion of cytoplasmic expansions from hyaline hemocytes in insects in which these reactions do not develop spontaneously in the standard conditions of preparation of the films used for these studies (for instance, Orthopteroid complex).

FIG. 4: *Pattern IV.* No visible modification detected by means of the phase-contrast microscope in the plasma surrounding inert or altered hyaline hemocytes, similar in their appearance to the hyaline hemocytes playing a selective part in the coagulation of the plasma in the other patterns. (Compare with photomicrographs in Grégoire, 1951, figs. 29 and 30; 1955a, figs. 12, 13, 14, and 16.)



FIGS. 1-4.—(See legend on opposite page.)

fluid hemolymph reached a standstill before alterations started in the fragile hyaline hemocytes. The successive steps of the coagulation were observed by phase-contrast microscopy (Wild M/10). Whenever possible, several samples were collected from each specimen. In view of the rapid completion of the process (within a few seconds in many insects), desiccation did not interfere with the observations, and the edges of the preparations were not sealed. When the reactions failed to appear (see pattern IV, below), the preparations were stored in petri dishes under high moisture and examined subsequently at different times. Some degree of evaporation and moderate condensation of the plasma along the edges of the films were incidentally detected in those preparations kept for several hours in moistened petri dishes.

RESULTS

DESCRIPTION OF THE PATTERNS OF COAGULATION

The classification of coagulation of insect hemolymph into four tentative patterns, used in the present study, is essentially based on differences in the following processes:

1. The irreversible alterations affecting a category of hyaline hemocytes, highly sensitive to contact with solid surfaces, and playing a selective part in the inception of the coagulation, in contrast with the other blood corpuscles. In the conditions of phase-contrast microscopy, the unstable hyaline hemocytes appear, especially after their alterations, as pale, round vesicular elements. Their nucleus is sharply outlined, relatively small. A few dark granules are scattered in the hyaline cytoplasm. In the other categories of hemocytes (small stem cells, transitional forms, and various kinds of granular hemocytes) the nucleus is distinctly larger and the cytoplasm darker. The cytological differences between the fragile hemocytes and the other kinds of blood cells have been illustrated in previous papers (Grégoire and Florkin, 1950; Grégoire, 1951, 1953, 1955a), and appear in figures 1, 2, 8, and 9 of plate 1.

2. The modifications of the plasma, following or accompanying the alterations in the fragile hyaline hemocytes.

Text figures 1-4 illustrate schematically the microscopical characters of the four patterns.

Pattern I. Inception of the plasma coagulation in the shape of islands of coagulation around the hyaline hemocytes (text fig. 1; pl. 1, figs. 1, 2, 3, 4, 5, and 7).—Selective alterations in the unstable hyaline hemocytes result in exudation or in explosive discharge of cell material into the surrounding fluid. Coagulation of the plasma starts in the shape of circular islands of granular consistency around the altered hyaline hemocytes. The islands of coagulation develop to a certain size, with individual and specific variations, then their increase stops. At the beginning of the process, the islands are scattered and separated by fluid channels. When the coagulation proceeds farther, the plasma in these channels clots into a granular substance in which the islands preserve generally their original size and shape. General solidification of the film may occur. The coagulum, of granular appearance, is progressively modified into delicate meshworks of granular fibrils.

Pattern II. Extrusion of cytoplasmic expansions by hyaline hemocytes, with development of cytoplasmic meshworks. Reaction in the plasma in the shape of veils (text fig. 2; pl. 1, fig. 6).—On contacting the glass, a category of fragile hyaline hemocytes undergo alterations that differ from those observed in pattern I. These elements extrude threadlike cytoplasmic expansions, which may reach a great length. These expansions exhibit intense thigmotropism toward solid particles, other hemocytes, and physical interfaces (bubbles). These alterations result in constitution of cytoplasmic meshworks of various complexity, on which the other kinds of hemocytes are passively agglutinated.

The reaction in the plasma after these cellular changes occurs in the shape of transparent, elastic, and contractile veils, developed within the cytoplasmic systems built up by the hyaline hemocytes, or in their vicinity. The other categories of hemocytes do not take part in the formation of these cytoplasmic meshworks. They are passively agglutinated along the highly adhesive cytoplasmic filaments sent out by the hyaline hemocytes and are subsequently embedded with them in the plasma veils.

In several insects the alterations in the unstable hemocytes are not followed by changes in the plasma and the modifications of the hemolymph in vitro consist only of a cellular reaction.

Pattern III. Patterns I and II combined (text fig. 3; pl. 1, fig. 9).—The microscopical picture of pattern III consists of an association of the reactions described above in patterns I and II. In the same film of hemolymph, hyaline hemocytes produce cytoplasmic expansions (pattern II) while islands of coagulation (pattern I) develop around the body of these corpuscles. The islands are either isolated or appear as denser areas within the veils characterizing the reaction in the plasma in pattern II.

Pattern IV. No modification in the hyaline hemocytes, or alterations not followed by visible reaction in the plasma (text fig. 4).—In the hemolymph of various insects, hemocytes resembling in their cytological characters the fragile corpuscles involved in the other patterns do not visibly alter. They appear as large, pale vesicles in which a few dark particles are scattered. In several insects these elements are the remnants of darker refractile hyaline hemocytes, which undergo clarification after explosive discharge of a part of their cytoplasm. In the vicinity of these inert or altered hyaline hemocytes no change can be detected under the phase-contrast microscope in the consistency of the plasma, which remains permanently fluid.

DISTRIBUTION OF THE PATTERNS OF COAGULATION IN THE DIFFERENT GROUPS OF INSECTS INVESTIGATED

In the table below, the names of the species are followed by the numbers of specimens studied (adults, unless otherwise stated) and by the patterns of coagulation provisionally found predominant or representative on the basis of the microscopical study of several samples of hemolymph obtained from these specimens. Incidental findings of other patterns are also reported under "Comments."

In several taxonomic groups, the average pattern recorded on corresponding material from the Old World previously studied (Grégoire, 1955a; Grégoire and Jolivet, unpublished) follows the list of the Neotropical material in the table.

The patterns of coagulation described above have been represented in the table by the following symbols:

●: pattern I: inception of the plasma coagulation in the shape of islands of coagulation around hyaline hemocytes.
○: pattern II: development of cytoplasmic meshworks by hyaline hemocytes. Reaction in the plasma in the shape of veils.
⊖: pattern II: incomplete. Emission of cytoplasmic expansions, characterizing the reactions of the hyaline hemocytes in pattern II, but unaccompanied by formation of veils in plasma.
◉: pattern III: patterns I and II combined.
—: pattern IV: no visible coagulation.
( ): pattern incidentally or exceptionally recorded in limited fields of preparations exhibiting predominantly another pattern.
(?): microscopical characters of a pattern not clear-cut or equivocal.

Other abbreviations used: sp., species; spm., specimen.

Gradations in the intensity of the reactions, especially with regard to pattern I, are indicated by the following symbols: I poor (scarce fringes of clotted plasma around the altered hyaline hemocytes, without extension of the coagulation; I (scattered islands of coagulation of various sizes, with moderate coagulation of the fluid in the channels); I*, I**, I*** (islands around all the hyaline hemocytes, substantial and general coagulation. In I***, the films appear to the naked eye with a bluish opalescent color).

MICROSCOPY (PARTICULAR REACTIONS)

Orthopteroid Complex.—Pattern I has been uniformly recorded in all the insects of the orthopteroid complex listed above. However, intensity in the reaction differed in the various groups: in this respect, Blattodea and Gryllidae exhibited the most substantial coagulation. These groups were followed, in order of decreasing intensity, by Mantodea, Phasmoptera, Tettigoniidae, and Acrididae.

In the present material, alterations in plasma appearing around hemocytes other than the fragile hyaline hemocytes were detected around a few macronucleocytes of small size (stem cells) in samples from *Paroecanthus podagrosus* and from *Phasma* sp. As already pointed out (Grégoire, 1951, 1955a) such reactions are exceptional.

Heteroptera.—As shown in the list, absence of visible change in the plasma was the predominant picture in all the specimens of the present material. The few modifications that might suggest subsidiary participation of a pattern other than pattern IV were equivocal.

In *Ghilianella* sp., *Triatoma dimidiata, Rhiginia* sp., *Apiomerus ochropterus* (Reduviidae), *Mecisthorhinus marmoratus* (Pentatomidae), dark oval hyaline hemocytes, surrounded by a refractile halo, underwent sudden clarification after explosive ejection of cytoplasmic substance into the surrounding fluid. These discharges did not bring about changes in the consistency of the plasma. Similar alterations have been described previously (Grégoire, 1955a) in various insects, especially in lepidopteran and dipteran larvae and in dipteran adults.

In several samples from different families, granular precipitates, unrelated to the presence of hemocytes in the vicinity, were found in films of hemolymph around air bubbles and along the edge of the coverglass. Though the preparations were maintained between the observations in petri dishes under high moisture, these modifications resulted probably from a slight degree of evaporation and condensation at the periphery of the films. Pressure exerted on these precipitates dispersed granular particles; this reaction is different from that taking place under similar mechanical agencies, in an actual coagulum, in which extension of the granular and fibrillar structures is followed by elastic contraction without dissociation.

TABLE 1.—*Patterns of Coagulation*

Orders, Families, Genera, and Species	Number of Specimens	Pattern of Coagulation Provisionally Representative or Predominant	Comments	Tentative Generalization
Orthopteroid Complex				
DICTYOPTERA				
BLATTODEA [1]				
Eublaberus posticus (Erichson)....	3	●	** and ***	
Blaberus colosseus (Illiger)........	2	●	** and ***	
" " (hatched larvae)..	10	●	**	
Epilampra azteca Saussure.........	2	●		
Nyctibora noctivaga Rehn.........	1	●	**	●
" " (larva).......	1	●	***	
Periplaneta brunnea Burmeister....	1	●		
Phortioeca phoraspoides (Walker)..	1	●	**	
Undet. sp. (larva)...............	1	●		
MANTODEA [2]				
Stagmomantis dimidiata (Burmeister) ♂	9	●	* in 3 spm.	
Angela guianensis Rehn ♂.........	2	●		
Pseudomiopteryx infuscata Saussure & Zehntner ♀.................	1	●	**	
Macromusonia (*Catamusonia*) *conspersa* (Saussure) ♂...........	1	●	Poor	●
Vates festae Giglio Tos ♂..........	1	●	**	
Phyllovates brevicornis (Stål) ♂...	3	●	Poor to **	
Parastagmaptoptera serricornis Kirby ♂	1	●		
Choeradodis rhombicollis (Latreille) ♂	2	●	Poor	

KALOTERMITIDAE				
Cryptotermes sp. (winged nymphs) .	10	●		●
PHASMOPTERA [4]				
Stratocles forcipatus Bol. ♂ ♀......	3	●		
Phasma sp. ♂....................	1	●		
Paradiapheromera strumosa Brunner von Wattenwyl ♂..............	3	●		
Pterinoxylus difformipes Serville ♂..	1	●		●
Bacteria ploiaria (Westwood) ♂....	1	●	**	
Bacteria sp. ♂....................	1	●		
Undet. sp.	1	●	Poor	
Undet. sp. (larva, 1.5 cm.)........	1	●		
ORTHOPTERA				
TETTIGONIIDAE [5]				
Hyperphrona sp. ♂................	2	●		
Insara bolivari (Griffini) ♂ ♀......	4	●		
Orophus sp. ♂....................	2	●		
Lamprophyllum micans Hebard ♂..	1	●		
Phaneroptera paronae (Griffini) ♀..	1	●		
Philophyllia guttulata Stål ♂.......	3	●		
Phylloptera dimidiata Brunner von Wattenwyl ♂ ♀................	2	●		●
Acanthodes curvidens (Stål) ♂.....	1	●		
Balboa tibialis Brunner von Wattenwyl ♂	1	●	*	
Bliastes punctifrons Stål ♀.........	1	●		
Bliastes banksi Hebard ♂..........	1	●	Poor	

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[1] Det. by Dr. C. Willemse. [2] Det. by Prof. L. Chopard. [3] Det. by Dr. Thos. E. Snyder. [4] Det. by Prof. L. Chopard. [5] Det. by Dr. C. Willemse and Dr. M. Beier.

TABLE 1.—*Patterns of Coagulation*—continued

Orders, Families, Genera, and Species	Number of Specimens	Pattern of Coagulation Provisionally Representative or Predominant	Comments	Tentative Generalization
ORTHOPTERA (continued)				
TETTIGONIIDAE (continued)				
Cocconotus wheeleri Hebard ♂.....	1	●		
Ischnomela gracilis Stål (larva) ♀..	1	●		
Schedocentrus sp.	1	●		
Euceraia insignis Hebard ♂ ♀......	3	●		
Gongrocnemis sp. (larva) ♀........	1	●	**	
Drepanoxyphus minutus Brunner ♂.	1	●		
Idiathron majus Hebard ♂........	1	●		
Microcentrum colosseum Brunner ♂.	1	●		
Microcentrum sp. ♂..............	1	●		
Peucestes championi Saussure & Pictet ♂	1	●		
Parabliastes punctifrons (Stål) ♀...	1	●		
Undet. sp. (Pseudophyllidae), larva, first stage ♂..................	1	●	Poor	●
Neoconocephalus maxillosus (Fabricius ♂ ♀....................	2	●		
Neoconocephalus triops (Linnaeus) ♂	1	●	*	
Neoconocephalus affinis (Beauvois) ♀	1	●		
Bucrates capitatus (De Geer) ♂.....	1	●		
Caulopsis microprora Hebard ♂....	1	●	Poor	
Copiphora brevirostris Stål ♀......	2	●	*	
" " (larva) ♂...	1	●	Poor	
Eleven unidentified sp. (adults and larvae)	11	●		

GRYLLIDAE[6]				
Anurogryllus muticus (De Geer) ♀	3	●	**	
Aphonomorphus sp. ♀	1	●		
" " (not adult) ♀	1	●	**	
Ponca venosa Hebard ♀ ♂	2	●	**(♂)	
Diatrypa sp. ♀	1	●	*	●
Paroecanthus podagrosus Saussure ♀	2	●		
Undet. sp.	5	●	In 2 spms. **	
ACRIDIDAE[7]				
Amblytropidia insignis Hebard ♂	1	●		
" " (larva)	1	●	Poor	
Orphulella punctata (De Geer) 4♀, 1♂	5	●		
Orphulella punctata (larva)	1	●		
Agriacris bilunata (Gerstaecker)) ♀.	1	●	**	
Agriacris (*bilunata*) (Gerstaecker?) (larva) ♀	1	●		
Agriacris tricristata (Serville) ♂	2	●		
" " (larva)	1	●		
Agriacris sp. (larva)	1	●		●
Aidemona azteca (Saussure) ♀	1	●	Poor	
" " (larvae) ♀ ♂	6	●	Poor	
Copiocera harroweri Hebard or *specularis* Gerstaecker ♂	1	●		
Osmilia flavo-lineata (De Geer) ♀ ♂.	8	●		
Phaeoparia rotundata Stål	1	●	*	
Schistocerca paranensis (Burmeister) ♂ ♀	2	●		
Schistocerca sp. (larva)	1	●	Poor	
Xyleus rosulentus (Stål) ♂ ♀	2	●	*(♀)	

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[6] Det. by Prof. L. Chopard. [7] Det. by Dr. C. Willemse.

TABLE I.—*Patterns of Coagulation*—continued

Orders, Families, Genera, and Species	Number of Specimens	Pattern of Coagulation Provisionally Representative or Predominant	Comments	Tentative Generalization
ORTHOPTERA (continued)				
ACRIDIDAE (continued)				
Xyleus rosulentus (Stål) (larvae) . .	3	●		
Undet. sp.	2	●		
DERMAPTERA[8]				
Carcinophora americana (Palisot de Beauvois) ♀	2	●		
Carcinophora sp. (probably *americana*) nymph	I	●	**	●
Doru lineare (Eschscholtz) ♂	I	●	Poor	
Spongiphora croceipennis (Serville) ♂	I	●	*	
Former data and unpublished observations on material from the Old World: Blattodea (10 sp.), Mantodea (6 sp.). ISOPTERA (3 sp.), PHASMOPTERA (4 sp.), Tettigoniidae (9 sp.), Gryllotalpidae (1 sp.), Gryllidae (4 sp.), Tetrigidae (1 sp.), Acrididae (19 sp.), and DERMAPTERA (5 sp.)	525	●		*Orthopteroid Complex* Consistently pattern I. ● Coagulation, substantial in Blattodea, *Gryllotalpa,* and in Gryllidae, moderate to scarce in PHASMOPTERA, in Tettigoniidae and in Acrididae. (For diverging results in workers of a termite sp., see Grégoire, 1953, 1954.)
Hemipteroid Complex				
HEMIPTERA[9]				
REDUVIIDAE				
Ghilianella sp.	I	—		

Saica apicalis Osborn & Drake	3	—		Reduviidae Pattern IV :— representative. In a few spm. (*Rhinocoris, Apiomerus, Ectrichodia, Ploegaster*) questionable pictures of pattern I recorded exceptionally in limited fields of preparations otherwise exhibiting pattern IV.
Triatoma dimidiata (Latreille)	6	—		
Rhodnius pallescens Barber	2	—		
Sirthenea stria (Fabricius)	2	—		
Rhiginia cruciata (Say)	1	—		
Rhiginia sp., possibly *cruciata* (Say) (nymph)	1	—		
Rhiginia sp.	1	—		
Apiomerus ochropterus Stål	1	—		
Apiomerus emarginatus Stål	1	—		
Apiomerus pilipes (Fabricius)	2	—	(●?)	
Zelurus spinidorsalis (Gray)	3	—		
Heza similis Stål	1	—		
Montina nigripes Stål	1	—		
Ploegaster gensana Kirkaldy	2	—	(●?)	
Brontostoma discus (Burmeister)	1	—	(⊖)	
Mestor rufotuberculatus (Champion)	1	—		
Panstrongylus geniculatus (Latreille)	3	—		
Zirta sp.	1	—		
Former data and unpublished observations on specimens from the Old World (8 sp.)	12	—		
COREIDAE				
Acanthocephala sp.	1	—		Coreidae Pattern IV: —
Undet. sp., prob. n.gen., n.sp. near *Staluptus*	1	—		
Hyalmenus pulcher Stål	1	—		
Grammopoecilus flavicornis (Fabricius)	1	—		
Former data and unpublished observations (5 sp.)	45	—		

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[8] Det. by Prof. Dr. W. D. Hincks.

[9] Det. by Dr. R. I. Sailer.

TABLE 1.—*Patterns of Coagulation*—continued

Orders, Families, Genera, and Species	Number of Specimens	Pattern of Coagulation Provisionally Representative or Predominant	Comments	Tentative Generalization
HEMIPTERA (continued)				
PENTATOMIDAE				
Mecistorhinus marmoratus (Erichson)	1	—		
Mecistorhinus piceus (Palisot de Beauvois)	1	—		
Berecynthus delirator (Fabricius)	1	—	(?)	
Proxys punctulatus (Palisot de Beauvois)	1	—		Pentatomidae Pattern IV: —
Loxa viridis (Palisot de Beauvois)	1	—		
Loxa flavicollis (Drury)	3	—		
Edessa rufomarginata (De Geer)	1	—	(?)	
Edessa celsa Distant	3	—		
Edessa sp.	1	—		
Neodine macraspis (Perty)	1	—		
Gen. near *Pharnus*, n.gen., n.sp.	1	—		
Acrosternum scutellatum (Distant)	4	—		
Former data and unpublished observations (22 sp.)	117	—		
CYDNINAE				
Prolobodes gigas Signoret	1	—		
Former data and unpublished observations on Nabidae (1 sp.), Gerridae (1 sp.), Pyrrhocoridae (1 sp.), Lygaeidae (2 sp.), Miridae (1 sp.), Naucoridae (1 sp.), Notonectidae (1 sp.), Corixidae (1 sp.)	83	—		Pattern IV: —

On Belostomatidae (4 sp.)	12	●	*** (— in 1 spm.)	Pattern I: ● very substantial coagulation
On Nepidae (4 sp.)	55	●	**	Pattern I: ● subtantial coagulation
HOMOPTERA[10]				
CICADIDAE[11]				
Fidicina mannifera (Fabricius)	2	●		
Fidicina sp.	1	●	Poor	Cicadidae
Fidicina sp.	1	●	**	Pattern I ●: substantial coagulation
Zammara calochroma Walker	2	●,●⊙	***	
Zammara sp. near *calochroma* Walker	3	●		
Proarna championi Distant	1	●		
FULGORIDAE				
Calyptoproctus elegans (Olivier)	4	●	* to ***	Fulgoridae
Copidocephala guttata (White)	1	●	***	Pattern I ●: One of the most substantial processes of coagulation recorded among all the insects investigated
Cathedra serrata (Fabricius)	1	●	**	
Laternaria servillei (Spinola)	2	●	***	
Phrictus quinquepartitus Distant	3	●	***	
Odontoptera carreñoi Signoret	1	●	***	
DICTYOPHARIDAE				
Hyalodicyton obtusifrons (Walker)	1	?	(● ?)*	
CICADELLIDAE (Tettigellinae)				
Diestostemma sp.	2	●	*	Cicadellidae
Gypona notanda ? Fowler	1	○		Pattern I: ●
Oncometopia sp.	1	●		
Undet. spm. (Tettigellinae)	1	●	*(⊙*?)	
NOGODINIDAE				
Biolleyana costalis (Fowler)	1	—		

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[10] Det. by Dr. D. A. Young.

[11] Det. by Miss Louise Russell.

TABLE I.—*Patterns of Coagulation*—continued

Orders, Families, Genera, and Species	Number of Specimens	Pattern of Coagulation Provisionally Representative or Predominant	Comments	Tentative Generalization
HOMOPTERA (continued)				
FLATIDAE				
Carthaeomorpha rufipes Melichar...	1	—		
Neocerus sp., or rel. gen.	1	—		
Former data on Cercopidae and Cicadellidae (4 sp.)	33	● ⊙		Substantial coagulation
COLEOPTERA				
ADEPHAGA				
CICINDELIDAE [12]				
Ctenostoma sp.	1	●	Possibly ⊙	
Megacephala (*Tetracha*) ***sobrina*** Dejean	1	—		
Odontochila exilis Bates..........	1	●	Poor (⊙?)	
Former data: *Cicindela campestris* Linnaeus	3	⊖̲	?	
CARABIDAE [13]				
Undet. sp. (Ozaeninae)..........	1	—	(○)	
Undet. sp. (Ozaeninae)..........	1	○	*(⊙?)	
Undet. sp. (Ozaeninae)..........	1	○	*(⊙?)	
Undet. sp. (Ozaeninae)..........	1	⊖		
Agra sp.	1	● ⊙	Poor	
Agra sp.	1	●	(⊙)	
Agra sp.	2	● ⊙	**	
5 undet. sp......................	5	—	(⊖)	
Former data and unpublished observations (26 sp.)	45	Varied reactions	Predominance of a pattern recorded at the genus level: f.i. *Carabus* (4 sp.): Pattern III ⊙ substantial	

DYTISCIDAE				
No specimen captured				
Former data and unpublished observations (13 sp.)	67	Varied reactions	Predominance of a pattern recorded at the genus level: f.i. *Hydaticus* (6 sp.: Pattern IV) — *Dytiscus* (2 sp.: Pattern III) ⦿ *Cybister* (2 sp.: Pattern I substantial) ●*	
POLYPHAGA				
HYDROPHILIDAE, HISTERIDAE, SILPHIDAE, CANTHARIDAE				
No specimen captured				
Former data and unpublished observations:				
Hydrophilidae (5 sp.)	50	—	Consistently recorded	Hydrophilidae Pattern IV: —
Histeridae (6 sp.)	13	○	(⦿)	
Silphidae (8 sp.)	27	Varied reactions	Possibly predominance of a pattern at the genus level (*Necrophorus*: Pattern I)	
Cantharidae (7 sp.)	29	—	(○?)	
STAPHYLINIDAE [14]				
Eulissus chalybaeus Mannerheim	2	—		Staphylinidae Pattern IV: — consistently recorded
Former data and unpublished observations (10 sp.)	14	—		

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[12] Det. by O. L. Cartwright.

[13] Det. by G. Fagel.

[14] Det. by Dr. R. E. Blackwelder.

TABLE I.—*Patterns of Coagulation*—continued

Orders, Families, Genera, and Species	Number of Specimens	Pattern of Coagulation Provisionally Representative or Predominant	Comments	Tentative Generalization
POLYPHAGA (continued)				
PASSALIDAE [15]				Passalidae
Passalus punctiger Serville........	3	Varied reactions	Mostly ⊖ or —; (●)	Probably pattern III: ⊙ Large intraspecific variations. Coagulation scarce in many samples. Pattern I: ● unmixed or associated with pattern II ○ (=III ⊙) detected in 6 out of 9 sp.
Verres cavicollis Bates............	2	○		
Veturius platyrhinus Westwood....	2	○	— also recorded	
Veturius sp.	1	○		
Unpublished observations (5 African sp.)	25	●⊙	Large intraspecific variations	
SCARABAEIDAE [15]				
Coprinae (Scarabaeinae)				
Canthon 7-maculatus Latreille......	2	○	Poor or ⊖	Coprinae
Canthon sp. (?)	3	⊖ or —		●⊙
Former data and unpublished observations (18 sp.)..................	39	●	(⊙) in 13 out of 18 sp.	
Rutelinae				
Anomala granulipyga Bates........	1	○		
Lagochile sparsa, subsp. *subandina* Ohaus	1	○	Probable	Rutelinae
Macraspis lucida Olivier...........	1	○		○
Pelidnota notata Blanchard.........	7	○		
Phalangogonia sperata Sharp......	1	○		
Trizogeniates foveicollis Ohaus.....	2	○		
Melolonthinae [16]				
Phyllophaga prolixa Bates [16] ♀......	1	○		

Dynastinae				
Aspidolea singularis Bates	7	○	Poor or inc. in 2 spm.	
Cyclocephala carbonaria Arrow	1	○		
Cyclocephala signata Drury	1	○		Dynastinae
Dyscinetus frater Bates	20	○	Some*	○
Bothynus quadridens Taschenberg	2	○	*	
Former data and unpublished observations: Aphodiinae (2 sp.); Geotrupinae (4 sp.); Rutelinae (3 sp.); Melolonthinae (5 sp.); Dynastinae (7 sp.); Trichiinae (4 sp.); Valginae (2 sp.), and Cetoninae (16 sp.)	131	○		Pattern II ○ highly predominant, especially in Rutelinae, Dynastinae, Trichiinae, and Cetoninae. Pattern III ◉ incidental or questionable in scattered specimens
SANDALIDAE[17]				
Gen. and sp. unknown	2	—(?)	(● ?)	
ELATERIDAE[18]				
Chalcolepidius near rugatus Candèze	1	◉		
Chalcolepidius porcatus (Linnaeus)	1	○	**, possibly ◉	
Dicrepidius ramicornis (or near sp.) (Palisot de Beauvois)	3	—		
Semiotus distinctus (Herbst) (or near sp.) (Chalcolepidinae)	2	○	**, possibly ◉	
Former data and unpublished observations (11 sp.)	21	Varied reactions		
LAMPYRIDAE				
Undet. sp.	1	— ?		
Undet. sp.	1	— ?		
Former data: *Lampyris noctiluca* Linnaeus	23	—		

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[15] Det. by O. L. Cartwright.

[16] Det. by Dr. M. W. Sanderson.

[17] Det. by Geo. B. Vogt.

[18] Det. by Ch. Jeuniaux.

TABLE I.—*Patterns of Coagulation*—continued

Orders, Families, Genera, and Species	Number of Specimens	Pattern of Coagulation Provisionally Representative or Predominant	Comments	Tentative Generalization
HETEROMERA				HETEROMERA
TENEBRIONIDAE [19]				Pattern I ●, unmixed or associated with pattern II ○ (=pattern III ⊙), recorded in all the sp. investigated Generally substantial coagulation, especially in Meloidae
Nyctobates gigas (Linnaeus)	1	●	Poor (⊙)	
Zophobas latticollis Kraatz	2	⊙		
Zophobas, probably *atratus* (Fabricius), *morio* of authors	2	⊙		
MELOIDAE [19]				
Epicauta grammica (Fischer von Waldheim)	7	●	***, (⊙) in 1 spm.	
Former data and unpublished observations on Heteromera:				
Tenebrionidae (28 sp.)	163	⊙	● unmixed recorded in 2 sp.	Pattern III ⊙
Lagriidae (3 sp.)	6	●		
Monommidae (2 sp.)	3	⊙		
Oedemeridae (4 sp.)	16	●		
Meloidae (6 sp.)	23	●	Substantial coagulation. Pattern III ⊙ recorded in several samples	
CERAMBYCIDAE [20]				
Prioninae				Prioninae
Stenodontes (Mallodon) molarius (Bates) ♀ ♂	5	●	***	Typical pattern I ●
Stenodontes (Mallodon) spinibarbis (Linnaeus) ♂ ♀	2	●	***	One of the most substantial processes of coagulation recorded among all the in-

				sects
Callipogon (*Orthomegas*) *cinnamomeum* (Linnaeus)	1	●	***	
Former data and unpublished observations (3 sp.)	9	●	***	
Cerambycinae				
Chlorida festiva (Linnaeus)	1	● ⊙	***	
Coleoxestia vittata (Thomson)	1	●	*	Cerambycinae Pattern I ● (⊙)
Malacopterus tenellus (Fabricius) ♂ ♀	4	● ⊙	*	
Nyssicus sp.	1	●	Poor	
Former data and unpublished observations (9 sp.)	15	●	Pattern III ⊙ recorded also in several samples. Moderate coagulation in various specimens	
Lamiinae				
Taeniotes scalaris (Fabricius)	1	●		
Lochmaeodes sp.	1	●	*(⊙)	
Acrocinus longimanus (Linnaeus)	1	●	***	
Steirastoma sp., probably *meridionale* Aurivillius	1	●		Lamiinae Pattern I ●
Lagochirus araneiformis (Linnaeus)	1	●	**	
Lagochirus sp., near *binumeratus* Bates	2	●	***(⊙)	
Acanthoderes circumflexus Jacquelin du Val	1	⊙		
Former data and unpublished observations (4 sp.)	9	●	Substantial coagulation. Pattern III ⊙ recorded in a few samples	

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[19] Det. by T. J. Spilman.

[20] Det. by George B. Vogt.

TABLE 1.—*Patterns of Coagulation*—continued

Orders, Families, Genera, and Species	Number of Specimens	Pattern of Coagulation Provisionally Representative or Predominant	Comments	Tentative Generalization
BRUCHIDAE [21]				
Caryedes faldermanni (Mannerheim)	1	—		
CHRYSOMELIDAE [22] (br. sense)				
EUMOLPIDAE				
Typophorus sp.	1	—		
Eumolpus sp., probably *surinamensis* Fabricius	1	○		
ALTICIDAE				
Oedionychus sp.	1	—		
Former data and unpublished observations (41 sp.)	187			
Crioceridae (5 sp.)		— ?	Coagulation scarce, not detected in several spm.	
Eumolpidae (2 sp.)		—		
Chrysomelidae s.s. (18 sp.)		●⊙		
CURCULIONIDAE [23]				
Exophtalmus jekelianus White.....	2	—		
Heilipus sp.	1	—		Curculionidae Pattern IV —
Rhinostomus barbirostris (Fabricius)	5	—		
Cosmopolites sordidus (Germar)....	1	—		
Former data and unpublished observations (21 sp.)	89	—	(⊖?) recorded in 6 sp. ○ recorded in 1 sp.	
COLEOPTERA: General				Pattern II ○ (especially emission of cytoplasmic ex-

				pansions by the unstable hyaline hemocytes) unmixed or associated with pattern I ● (=pattern III ◉), recorded in 240 out of 354 sp. investigated
Panorpoid Complex				
NEUROPTERA[24]				
MYRMELEONTIDAE				
Undet. sp. (larva)	1	●	Poor	
MANTISPIDAE				
Mantispa phtisica Gerstaecker	3	—		
ASCALAPHIDAE				
Probably *Episperches* sp., near *vacuus* Gerstaecker	1	○	(◉?)	
Former data (NEUROPTERA): *Chrysopa vulgaris* Linnaeus	2	●	Poor or (?)	
LEPIDOPTERA (late larval stages)				
Megalopyge lanata Stål[25]	1	⊖	Or ○ poor	LEPIDOPTERA ○
Undet. sp.	1	⊖		
Former data (20 families, 92 sp.)	331	○	Recorded in 83 out of 92 sp. Pattern III recorded in 10 out of 16 sp. of Saturniidae, in *Cossus*, and possibly in 1 sp. of Lasiocampidae and in 1 sp. of Sphingidae. Group differences recorded in the amount of coagulated material	

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[21] Det. by George B. Vogt.

[22] Det. by George B. Vogt.

[23] Det. by Miss Rose Ella Warner.

[24] Det. by Miss Sophy Parfin.

[25] Det. by James Zetek.

TABLE I.—*Patterns of Coagulation*—continued

Orders, Families, Genera, and Species	Number of Specimens	Pattern of Coagulation Provisionally Representative or Predominant	Comments	Tentative Generalization
DIPTERA [26]				DIPTERA
Pantophtalmus conspicabilis Austen.	1	—		Adults: —
Former data:				
Tipulidae (larvae) (6 sp.).......	23	○	Instantaneous and substantial coagulation	
Fourteen sp. (adults and larvae) from 12 other families........	112	—		
HYMENOPTERA [27]				
TENTHREDINIDAE				
No specimen collected.				Tenthredinidae
Former data (14 sp.).............	100	●⊙	Instantaneous and substantial coagulation	●⊙
BRACONIDAE				
Trigonophasmus, n.sp.	1	—	(?)	
FORMICIDAE				
Paraponera clavata (Fabricius) ♀...	2	●	* to ***	
" " " ♂...	5	●	* to ***	
" " " w....	9	●	***, (⊙) in 1 spm.	
Eciton burchelli (Westwood) (br. sense) w.	20	○	*, (⊙?)	
Eciton hamatum (Fabricius) w.....	8	○	(⊙?)	
Eciton (*Eciton*) sp. w............	8	○	(⊙?)	
Atta cephalotes (Linnaeus) (?) w...	10	⊙		
Atta sp. ♀.....................	1	●		
Camponotus abdominalis (Fabricius) (br. sense) w..................	40	●⊙		Formicidae Pattern I ● and/or III ⊙

Camponotus abdominalis (Fabricius) (larvae)	5	—	(○)	
Camponotus sericeiventris (Guérin) (br. sense) ♀	1	● ⊙		
Camponotus sericeiventris (Guérin) w.	43	○	** in several spm. (⊙)	
Camponotus sericeiventris (Guérin) (larvae)	20	—		
Former data (3 sp.)	43	● ⊙		
MUTILLIDAE				
Dasymutilla sp. ♂	1	⊙	*	
Hoplomutilla xanthocerata (Smith) ♀	1	⊙	Probable	Mutillidae Pattern III ⊙
Pseudomethoca sp. ♀	1	⊙		
VESPIDAE				
Apoica pallida var. *pallens* (Fabricius) ♂ ♀	4	⊙	Probable. *** in 1 spm. Large individual variations	
Mischocyttarus melanarius (Cameron) ♂ ♀	5	—	● poor in 1 spm.	Vespidae Possibly patterns I ● and III ⊙ Large intraspecific variations
Mischocyttarus melanarius (Cameron) (larvae)	5	—		
Mischocyttarus tolensis Richards, 1941	1	—	(⊖)	
Polistes canadensis var. *panamensis* Holmgren ♀	6	⊙	Probable. Large variations; —recorded in several samples	
Polistes fuscatus Fabricius (Cape Cod) ♀	2	—		
Former data (4 sp.)	22	⊙	● recorded in several spm.	

[26] Det. by Dr. W. W. Wirth. [27] Det. by K. V. Krombein, C. F. W. Muesebeck, and Dr. M. R. Smith.

TABLE I.—*Patterns of Coagulation*—continued

Orders, Families, Genera, and Species	Number of Specimens	Pattern of Coagulation Provisionally Representative or Predominant	Comments	Tentative Generalization
HYMENOPTERA (continued)				
POMPILIDAE				
Anoplius a.amethystinus (Fabricius) ♂	I	⊙		
Former data. *Anoplius viaticus* (Linnaeus)	I	●		
SPHECIDAE				
Chlorion mirandum (Kohl) ♀	2	●		Sphecidae Pattern I ●
Chlorion singulare (Smith) I♀	2	●	Poor	
Stictia signata (Linnaeus) ♂	3	●		
Trypoxylon busckii Richards ♂	I	—	(?)	
COLLETIDAE				
Ptiloglossa fulvo-pilosa (Cameron) ♀	I	○	Poor or —	
APIDAE				Apidae Coagulation scarce, not detected in many specimens
Centris vittata LePeletier ♀	I	—		
Euplusia mexicana (Mocsary) ♀	I	⊖	Or —	
Former data (9 sp.)	36	○ poor, ⊖ and —	● recorded only in *Nomada flava* Panzer	
ODONATA[28]				
Probably *Pantala* sp. near *hymenaea* (Say) (Libellulidae, Libellulinae) adult ♂	I	—		
Former data (*Anisoptera*) (6 sp.)	55	Varied reactions recorded in adults; ●⊙ in several larvae		

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[28] Det. by Miss Sophy Parfin.

Homoptera.—Pattern I, with general solidification of the plasma, was consistently observed in Cicadidae, Cicadellidae and Fulgoridae. In the last family (*Laternaria, Phrictus*), coagulation of the hemolymph was especially substantial; the films of hemolymph were instantaneously transformed into opalescent bluish clots, embedding all the hemocytes (altered fragile hemocytes, numerous small macronucleocytes, and transitional forms to various types of granular hemocytes).

Coleoptera.—The various groups of Coleoptera listed in the table exhibited a great diversity in the reactions of their hemolymph in vitro. However, predominance of one of the patterns characterized several groups.

Dark hyaline hemocytes, undergoing clarification after discharge of substance (see Heteroptera above, and Grégoire, 1955a, discussion, p. 129), were observed in *Agra* sp. (Carabidae) and in *Veturius platyrrhinus* (Passalidae).

The reactions detected in Scarabaeidae (especially Melolonthinae, Rutelinae, Dynastinae) were essentially identical to those reported previously as representative of this family. Upon withdrawal, the hemolymph became immediately viscous and ropy. The hyaline hemocytes, relatively numerous (64 percent of the total hemogram in *Lagochile sparsa* Ohaus) and of small size, extruded spontaneously cytoplasmic expansions, soon embedded, like the other hemocytes, in the veil-like reaction developing in the plasma (pl. 1, fig. 6).

In *Zophobas latticollis* Kraatz, pattern III, characterizing several species of Tenebrionidae, developed with a special clarity: cytoplasmic expansions of the hyaline hemocytes and transparent glassy veils (pattern II) appeared immediately upon withdrawal of the hemolymph. The consistency of the veils became granular, while circular areas of greater density (islands of coagulation: pattern I) grew out around several hyaline hemocytes already involved in the constitution of cytoplasmic systems (pl. 1, fig. 9).

In the specimens of Sandalidae, the film of hemolymph consisted of a substantial syrupy granulum embedding tiny nuclei of altered unidentifiable hemocytes. The pattern of coagulation could not be safely established in these specimens.

In Lampyridae, dense suspensions of particles normally present in the hemolymph of these insects, as in other groups (Coccinellidae, various Chrysomelidae), interfered with the detection of the pattern of coagulation.

Among Cerambycidae, subfamily Prioninae (*Stenodontes, Calli-*

pogon) exhibited one of the most substantial coagulations recorded among all the insects examined in this and in the previous studies.

Hymenoptera.—Rapid collection of the hemolymph without contamination with foreign tissues was difficult in small specimens and in dry ones. In ants, large numbers of specimens were used, and the only samples not discarded were those in which a limpid drop of hemolymph could be collected and a rapid spreading out of the films performed.

In view of the scarcity of the species available and the large interspecific and intraspecific variations in the reactions observed in this order of insects, the predominant patterns could not be established safely for several species and groups. Some patterns actually recorded in a part of the samples correspond possibly to incomplete reactions.

Pattern I was observed in all the samples collected from all the females, males, and workers of *Paraponera clavata* (Formicidae) and *Chlorion* (Sphecidae), and pattern III in the three specimens of Mutillidae captured.

In larvae of *Camponotus sericeiventris,* numerous hemocytes were loaded with refractile inclusions, and no modification of the plasma appeared in that material.

The Hymenoptera listed in the table were characterized by the small size of their hemocytes and of the islands of coagulation around the hyaline hemocytes, even in the samples in which a substantial coagulation was recorded. In the latter preparations, a considerable extension of the coagulation took place from around the islands of coagulation, which appeared in the granular clots as small circular areas of greater density, centered by the fragile hyaline hemocytes and remaining distinct in the general coagulation of the plasma (pl. 1, figs. 3, 4, 5).

Lepidoptera (larvae).—In the two specimens of lepidopteran larvae, the reactions of the hemolymph in vitro were identical to those described and illustrated elsewhere in a large number of caterpillars (Grégoire, 1955, pp. 118-120 and pls. IX and X: pattern II, with large individual variations in the completion of the process, frequently incomplete, as in the two specimens listed in the table). In the films of hemolymph, refractile hyaline hemocytes underwent clarification after rupture of the cell boundaries and discharge of substance, as illustrated in figures 42-50 of the above-cited paper.

DISCUSSION

1. The four patterns used in the present study are an attempt to classify the disparities recorded in insects with regard to the micro-

scopical picture of films of clotting hemolymph, observed by phase-contrast microscopy in standard conditions of preparation.

Objection that these patterns might result from random artifacts has been examined elsewhere (Grégoire, 1955a).

In control observations, the clotting process was compared in films of hemolymph spread out under glass by the standard procedure and in clot plugs spontaneously formed at the wound site and gently squeezed under glass after completion of the process. In both instances, the microscopical alterations characterizing the same pattern were recorded. The standard conditions of preparation of the samples of hemolymph seem therefore to be a faithful reproduction of the alterations occurring during the undisturbed natural process.

2. Whatever each pattern might signify at the cytological [2] or biochemical level,[3] most results of the present and other studies [4] suggest

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[2] Among the factors implied in the process of coagulation, the patterns reflect actual inequalities between species and higher taxonomic groups in the degree of sensitiveness to contact with solid surfaces of the fragile hyaline hemocytes selectively involved in the inception of the coagulation, in the nature of the alterations undergone by these unstable cells, and in the rapidity with which these alterations develop. These differences affect the subsequent reaction of the plasma. As shown in the present and in previous studies, a similar degree in sensitiveness of the fragile hemocytes is frequently shared by insects belonging to a same group.

A tentative identification of the fragile hyaline hemocytes has been reported elsewhere (Grégoire, 1953a; 1955a, p. 129). A part of these corpuscles exhibits cytological features in common with the oenocytoids. In several groups (Odonata, Hemiptera-Heteroptera, various species of Coleoptera, lepidopteran and dipteran larvae, Trichoptera, and some Hymenoptera) these corpuscles appeared in the films of hemolymph in the shape of highly refractive or dark hyaline hemocytes, which undergo clarification after explosive discharge of substance. The same corpuscles differ, however, in other characters from the classical description of the oenocytoids (1955a, discussion, p. 131). On the other hand, the fragile hemocytes selectively involved in coagulation are referred to by Jones (1954) as cystocytes, in *Tenebrio molitor.*

[3] The scarcity of the data available at the present time does not enable one to establish whether actual biochemical differences characterize each of the four patterns, and especially the two aspects presented by the reactions in the plasma, the granular substance (in the islands of coagulation and in the areas of extension: pattern I), and transparent glassy veils (pattern II). As suggested by observations of films of varying thickness, it is unlikely, as reported elsewhere (Grégoire, 1955a, discussion, p. 128) that the twofold aspect of the plasma changes is related merely to differences in concentration or in thickness of the clotted films. The veils are not to be identified with the products of general disintegration of the hemocytes (cell fibrin).

An adequate test of the validity of the patterns would be to determine whether biochemical differences correspond to microscopical pictures as different as those consistently recorded, for instance, in insects belonging to the that the patterns are not individual particularities, except in a few equivocal cases.[5] The patterns rather characterize species, more frequently taxonomic groups (genera, families, suborders, or orders).

Repeated samplings of hemolymph collected from several specimens of the same species, or from different species belonging to the same higher taxonomic category, made it possible to record consistently the same pattern in groups of various taxonomic importance such as the Orthopteroid complex (pattern I),[6] several families of Heteroptera (especially Reduviidae, Coreidae, Pentatomidae) (pattern IV), Belostomatidae and Nepidae (pattern I), three families of Homoptera (Cicadidae, Fulgoridae, Cicadellidae) (pattern I), among Coleoptera, Hydrophilidae (pattern IV), Staphylinidae (pattern IV), several subfamilies of Scarabaeidae (Rutelinae, Melolonthinae, Dynastinae, Geotrupinae, Trichiinae and Cetoninae) (pattern II), Heteromera (Tenebrionidae, Lagriidae, Monommidae, Oedemeridae and Meloidae; patterns I and III), Cerambycidae (pattern I), Curculionidae (pattern IV), several families of Lepidoptera (larvae; pattern II), Tenthredinidae (patterns I and III).

3. Other groups (Cicindelidae, Carabidae, Dytiscidae, Silphidae, Passalidae, Coprinae, Elateridae) exhibited large intraspecific and interspecific variations in the patterns of coagulation recorded. In view of the diversity of the reactions in these groups, the pattern representative or predominant could not be established with certainty. However, at the genus level predominance of a pattern appeared in genera such as *Carabus* (pattern III), *Agra* (pattern I), *Hydaticus* (pattern IV), *Dytiscus* (pattern III) *Cybister* (pattern I), *Necrophorus* (pattern I).

4. In the homogeneous groups listed above, the Neotropical material and the insects from the Old World supplied identical results

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orthopteroid complex (pattern I), in insects from several families of Scarabaeidae (Rutelinae, Melolonthinae, Dynastinae, Cetoninae) (pattern II), Heteromera (pattern III), and other groups of insects in which no visible modification could be detected in the plasma (e.g., Staphylinidae, Hydrophilidae, and many Heteroptera) (pattern IV) under the phase-contrast microscope.

[4] Grégoire (1951, 1955); Grégoire and Jolivet (unpublished). The total material investigated consists of approximately 5,300 samples of hemolymph, collected from 3,400 specimens belonging to about 850 species.

[5] In most of these cases, the scarcity of the material available suggests that individual variations, incomplete reactions, or accidental artifacts (mechanical agencies; see Grégoire 1955a, p. 124ff.) might confuse the actual pattern.

[6] In the highly homogeneous orthopteroid complex, differences in the intensity of the clotting reaction could be detected between several groups (see table).

with regard to the pattern of coagulation predominant or representative of the taxonomic category.

Such consistency suggests that the patterns of hemolymph coagulation are a character of taxonomic significance (in a broad sense). Whether that type of character is of more or less applicability in phylogenetical controversies, is a question left to competent phylogeneticists. It might, however, be stressed that the process of hemolymph coagulation is in no way related directly to any type of structural or ethological criteria commonly used for defining and grouping taxonomic categories. It is therefore of interest to check tentatively some taxonomic relationships on the basis of the presented data.

5. As pointed out elsewhere (Grégoire, 1955a, pp. 136-137), random coincidence does not seem to be entirely responsible for explaining some correlations between phylogenetic position of certain groups of insects and microscopical aspect of the coagulation of their hemolymph. In this respect, the Neotropical material examined here supports former tentative suggestions concerning most of these correlations.[7]

Pattern I has been heretofore uniformly recorded in Blattodea and in the other groups ranged within the orthopteroid complex. The mechanism involved in this pattern is identical to one of the types of coagulation described by Hardy (1892), Tait (1910, 1911), Tait and Gunn (1918), Numanoi (1938), and Grégoire (1955b) in crustacean blood, in which a special category of cells, the Hardy's explosive corpuscles, corresponding to the insect hyaline hemocytes or coagulocytes (Grégoire and Florkin, 1950), play a selective part in the inception of the coagulation of the plasma.

Pattern I has also been recorded among various unrelated groups of insects, especially in groups characterized by the retention of various primitive characters, such as the Homoptera. In this respect, the present study has brought information on groups not represented in the material previously investigated.

From these data, pattern I might be considered as a generalized primitive mechanism of coagulation of insect hemolymph.

The mechanism of coagulation illustrated in pattern II has been observed, unmixed or predominant, in relatively recent groups of

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[7] After the completion of this paper, the patterns of coagulation were recorded in 400 insects collected in September 1956 at Tingo María (Peru) and in October 1956 on Barro Colorado Island. The results are in agreement with those reported here, with regard to the predominance of one of the patterns in the following groups: Orthopteroid complex, Hemiptera, Homoptera, Scarabaeidae, Tenebrionidae, Cerambycidae, Curculionidae, Vespidae, and Diptera.

insects, such as Scarabaeidae (except Coprinae—see next paragraph) and lepidopteran larvae. As shown in the table, the present investigations have confirmed the predominance of the patterns previously reported for these groups.

6. In the samples of Neotropical species of Passalidae and of Coprinae, the islands of coagulation characterizing pattern I were absent or exceptionally recorded in the samples, while in the African specimens studied until now (Grégoire and Jolivet, unpublished), these islands of coagulation appeared frequently or consistently in many samples. In view of the scarcity of the material and the diversity in the reactions characterizing these two groups, random variations might be responsible for these divergences between the results.

SUMMARY

Coagulation of the hemolymph in vitro has been investigated by phase-contrast microscopy in 630 specimens from 230 Neotropical species of insects. The present material includes samples of hemolymph from insects belonging to 17 families not represented in previous related studies.

A tentative classification of the process of coagulation into four patterns, suggested previously, has been used, and the patterns characterizing provisionally each species have been determined and reported in tabular form.

The Neotropical material and the data collected formerly on species from the Old World (altogether approximately 850 species), supplied consistent results with regard to the predominance of some of the patterns in several taxonomic groups of various extension in the classification.

In a condensed form, the investigations on the distribution of the patterns of hemolymph coagulation in the different orders have shown: (1) In the Orthopteroid Complex, a great uniformity of reaction, in the shape of pattern I, possibly a generalized primitive mechanism of coagulation of the hemolymph; (2) in several families of Heteroptera, absence of a visible reaction in plasma (pattern IV), in striking contrast to two families of the same order, Belostomatidae and Nepidae, which exhibited a substantial coagulation (pattern I); (3) in Homoptera, a substantial reaction in the shape of pattern I, representative or predominant, in Cicadidae, Fulgoridae, and Cicadellidae; (4) in Coleoptera, as a taxonomic group, a large heterogeneity in the reactions. However, in this order, uniformity of reaction or predominance of a pattern was detected at the infraorder level, especially in Hydrophili-

dae (pattern IV), Staphylinidae (pattern IV), Scarabaeidae (pattern II, with the exception of Coprinae: patterns I and III), Heteromera (patterns I and/or III), Cerambycidae (pattern I), Curculionidae (pattern IV), and in a few genera reported in the table; (5) in Lepidoptera (larvae), predominance of pattern II, with the possible exception of Saturniidae (pattern III); (6) in Hymenoptera, occurrence of patterns I and III in several taxonomic groups, in Apidae, scarce coagulation or absence of plasma reaction.

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EXPLANATION OF PLATE 1

Films of hemolymph spread out between slide and coverglass, immediately upon shedding from severed appendages. Phase-contrast microscope (Wild M/10). Scale: 20 microns.

Figs. 1 and 2. *Stenodontes* (*Mallodon*) *molarius* Bates (Cerambycidae, Prioninae). (Pattern I***: very substantial coagulation.) All the hyaline hemocytes are surrounded by islands of coagulation. Considerable extension of the granular coagulum. In figure 1, three elements belonging to other categories of hemocytes are passively embedded in the clot.

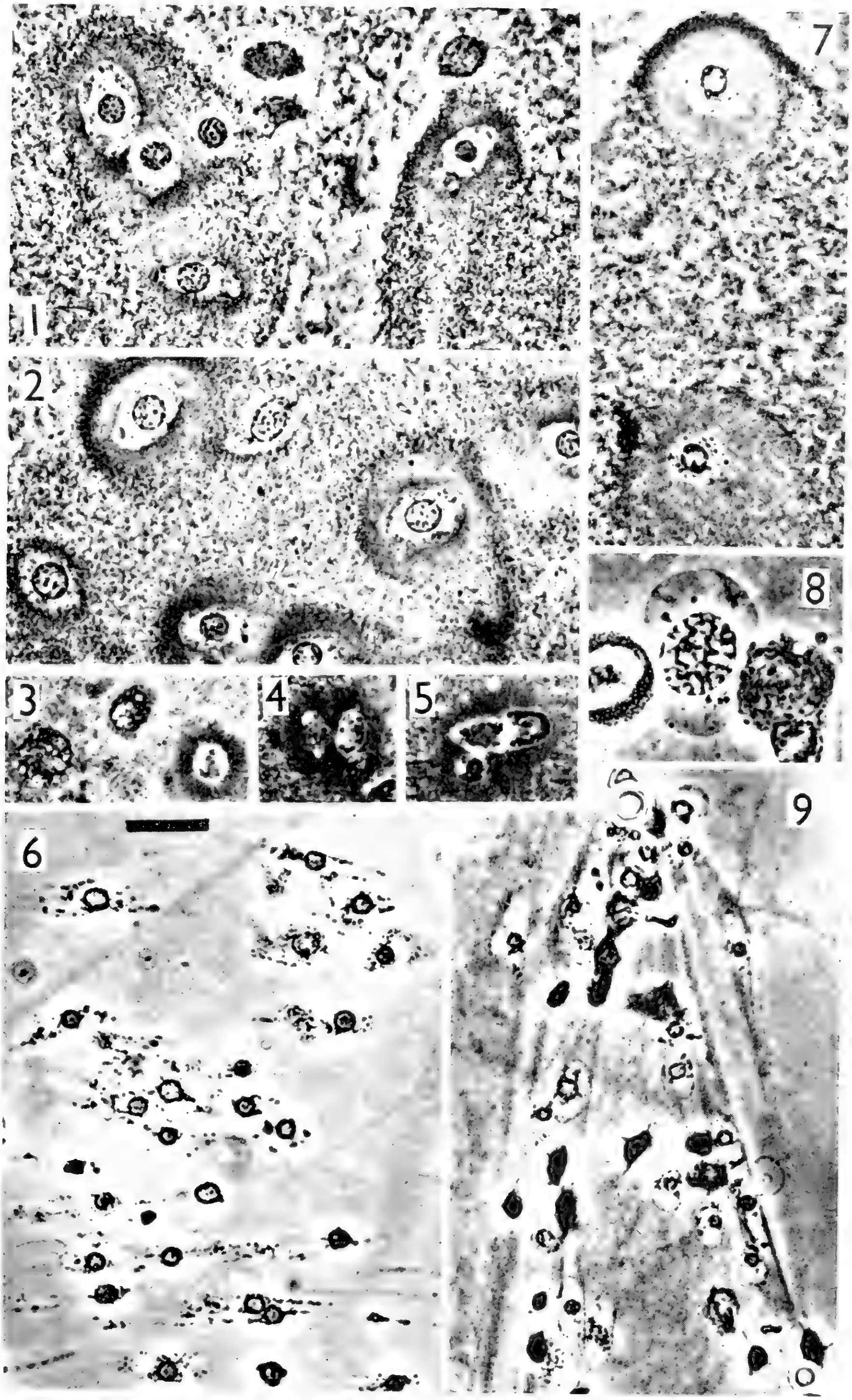
Figs. 3, 4, 5. *Paraponera clavata* (Fabricius) (Formicidae). (Pattern I ***). Islands of coagulation of small size. Extension of the coagulum. In figure 3, a small hyaline hemocyte (on the right) in the center of a small island of coagulation. On the left, two granular corpuscles embedded in the clot.

Fig. 6. Cetoninae sp. (Scarabaeidae). (Pattern II). Typical reaction of the hemolymph in vitro, as it appears in several subfamilies of this group (see table). Many hyaline hemocytes of small size with their cytoplasmic expansions are embedded in a substantial veil. Identical pictures were observed in several species listed in the table, especially in *Lagochile, Pelidnota, Phalangogonia, Trizogeniates, Aspidolea, Cyclocephala,* and *Dyscinetus.*

Fig. 7. *Phrictus quinquepartitus* Distant (Homoptera, Fulgoridae). (Pattern I***). Two hyaline hemocytes, each surrounded by an island of coagulation. Considerable extension of the coagulum between the islands, which preserve their size and shape.

Fig. 8. Pseudophyllidae (Tettigoniidae). Larva, first stage, male (Pattern I). The process of coagulation was slow and developed poorly in this specimen. When the picture was recorded, no reaction had yet developed in the plasma around the hyaline hemocyte shown in the center, between two other blood elements, including a granular hemocyte.

Fig. 9. Tenebrionidae sp. Picture representative of pattern III, predominant in this family (see description of the coagulation in *Zophobas latticollis* Kraatz, in the text, p. 27). Fan-shaped disposition of the threadlike cytoplasmic expansions of hyaline hemocytes, diverging from an air bubble on which these highly adhesive structures are anchored. Plasma reaction in the shape of a veil, with denser areas around hyaline hemocytes, corresponding to islands of coagulation. (Compare with Grégoire, 1955a, figs. 11 and 20. See legend of text figs. 2 and 3.)



(See explanation at end of text.)

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EARLY WHITE INFLUENCE UPON PLAINS INDIAN PAINTING

GEORGE CATLIN AND CARL BODMER AMONG THE MANDAN, 1832-34

(WITH 12 PLATES)

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During their visits to the Upper Missouri in the years 1832-34 the artists George Catlin and Carl Bodmer created some of the most authentic and best-known pictures of American Indians drawn or painted in the days before the development of photography. Their widely circulated originals and the published reproductions of their pictures have provided millions of viewers in this country and abroad, who never saw a Plains Indian, with a clear, accurate conception of the physical appearance and customs of those Indians as they appeared a century and a quarter ago.

Anthropologists, historians, and art critics have been accustomed to regard these artists as interpreters of Indian culture. Yet there is another point of view from which their contribution may be considered. While among the Indians they demonstrated their skill in handling an alien art style. They were in effect missionaries of the western European artistic tradition. To what extent was their example an influence upon native art? Might they not have been active as innovators in as well as observers of Indian culture?

I believe that data are now available to demonstrate precisely that Catlin's and Bodmer's artistic example *did* influence the development of the painting styles of at least two prominent Mandan Indian artists who had rare opportunities to observe their artistic activity closely while these white artists were recording the native culture of their tribe.

ABORIGINAL MANDAN INDIAN PAINTING

From the time of the first known visit of white men to the Mandan villages in 1738 until the appearance of George Catlin among them nearly a century later, the Mandan were repeatedly visited by white traders, explorers, and some Government officials. Several traders are known to have lived among these Indians for a number of years during that period. But no one skilled in drawing or painting in the traditional, realistic nineteenth-century style of western European culture is known to have practiced his art in the Mandan villages prior to the visit of George Catlin in the summer of 1832. Mandan Indian painting remained in the aboriginal tradition until that time.

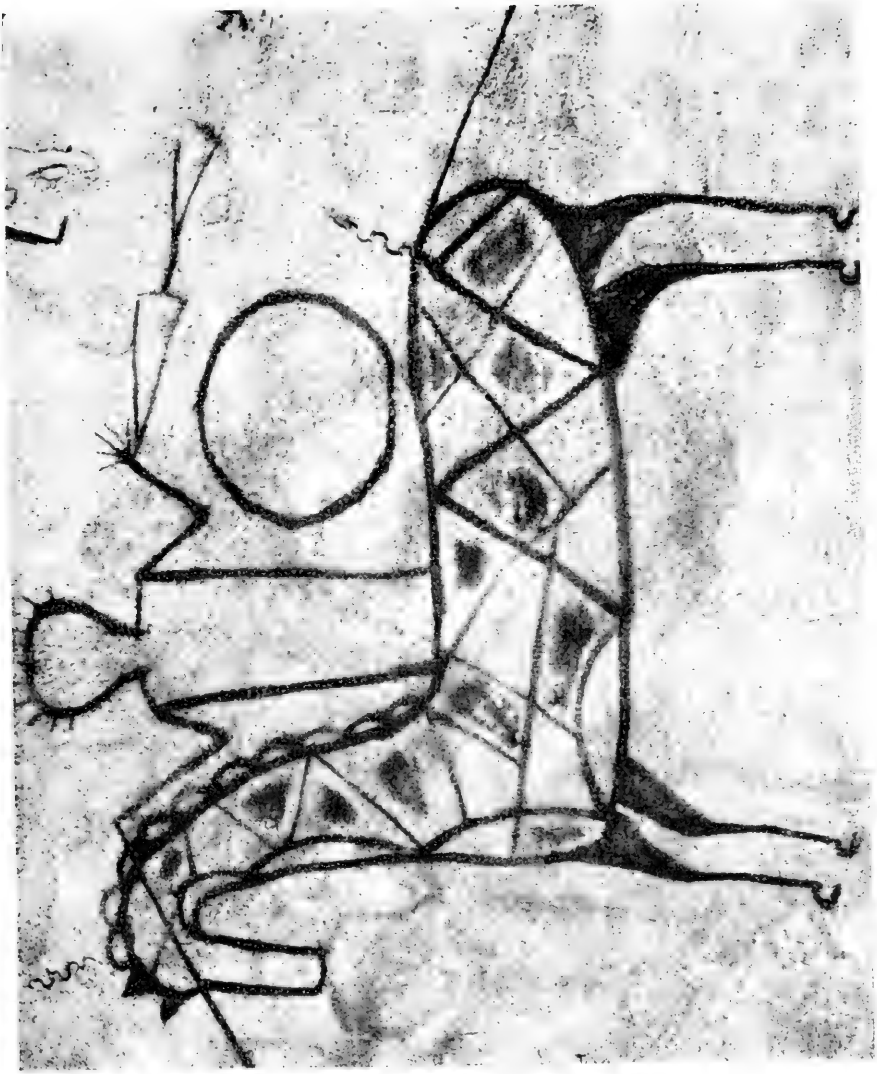
The origin of the Mandan painting tradition is lost in antiquity. La Verendrye, the French explorer-trader, observed, when he was in the Mandan villages on the Missouri in 1738, that these Indians traded painted buffalo robes to neighboring Assiniboin. (La Verendrye, 1890, p. 19.) However, the oldest example of Mandan painting that has been preserved (which is also the earliest dated specimen of the figure painting of any Plains Indian tribe) is a painted buffalo robe collected by the American explorers Lewis and Clark in 1805. This robe is preserved in the collections of the Peabody Museum of Archaeology and Ethnology of Harvard University, Cambridge, Mass. (See pl. 1.) Lewis and Clark included it among the collection of ethnological materials which they sent to President Jefferson from the Mandan villages on April 5, 1805, before they embarked on their overland trek westward to the Pacific. They reported that the paintings on this robe portrayed a battle fought between Mandan warriors and enemy tribesmen about the year 1797. (Lewis and Clark, 1906, vol. 1, pp. 281-288.) So this robe must have been painted within the period 1797-1805.

This is a most interesting example of the aboriginal style of painting employed by men who were the delineators of heroic deeds of the tribe or of individual warriors on the inner surfaces of buffalo robes. The painting comprises a composition of 44 foot warriors and 20 mounted men in combat. Their weapons include 15 trade guns and a pistol in addition to a larger number of native-made offensive and defensive weapons—bows and arrows, lances and shields. All the figures, human and animal, are heavily outlined in a very dark brown, almost a black. Some of the outlined forms are filled in with dark brown, blue green, reddish brown, or yellow.

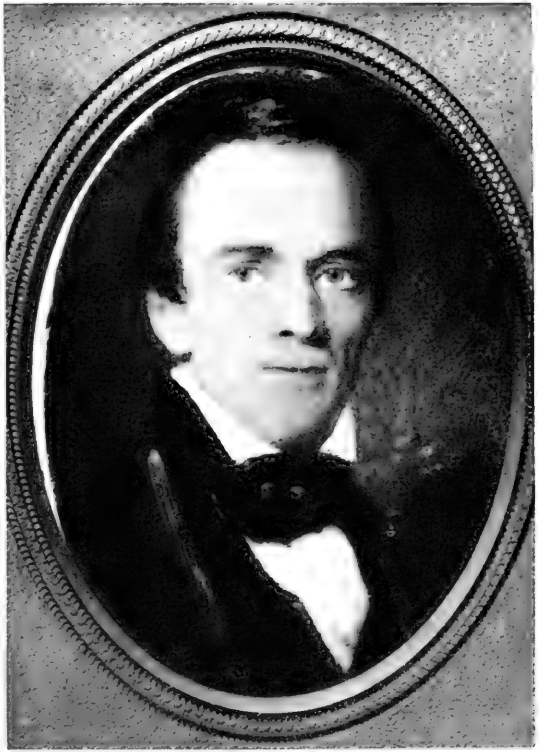
Careful examination of individual figures delineated on this specimen reveals some of the characteristics of the traditional native art style. An enlargement of one of the human figures on this robe (pl. 2), clearly illustrates the characteristic style of human figure in this composition. The head is a featureless, almost circular knob with pendent, conventionalized hair. The neck sits upon a separately

Battle between Mandan Indians and an enemy tribe. Painted buffalo robe collected by Lewis and Clark, 1805. (Peabody Museum, Harvard University.)

Detail of Mandan robe showing style of painting a foot warrior.
(Peabody Museum, Harvard University.)



Detail of Mandan robe showing style of painting a mounted warrior.
(Peabody Museum, Harvard University.)



1. George Catlin.

2. Carl Bodmer (self-portrait, right) accompanying Prince Maximilian zu Wied.

White artists among the Mandan, 1832-34.

rendered, elongated body which is geometric in character and drawn in outline only. The arms are lines extending outward from the shoulders and bent about midway of their length (i.e., at the elbows). At the ends of these arms are solid ball hands with the five fingers extended as lines. The legs are relatively short, bent at the knees. The grossly shaped upper legs are connected to linear lower legs. The foot is merely a continuation of the line of the lower leg at an angle from it. There is no attempt to portray body clothing. Yet the conventionalized representation of the phallus and scrotum may be an indication that the Mandan and their neighbors wore no breechcloths at that period. Some contemporary descriptions of those Indians also suggest the absence of the breechcloth in the men's costume of the time.

The enlargement of one of the mounted figures painted on this robe (pl. 3) shows the same style of rendering the head, arms, and body of the human figure. Notice that the man does not straddle the horse but merely sits atop it. There is no attempt to render the figure below the waist. The head and body of the horse are drawn in outline. The animal has neither eye nor mouth, but the ears are indicated one above the other and the mane is drawn in a conventionalized manner. The horse's neck and body are decorated in geometric fashion with lines forming angular patterns some of which are partially filled with spots of color. As in the human figures, the upper legs of the horse are thick and the lower ones are mere lines. The hoofs are hook-shaped extensions of the legs.

This primitive Mandan painting accented the general characteristics of the human form—the roundness of the head, the straightness of the limbs, the bilateral symmetry of the body, qualities Rudolf Arnheim has referred to as characteristics of the drawings of both primitives and children. (Arnheim, 1954, p. 131.)

Details of the human figure were unimportant to the primitive Mandan artist. His head remained featureless. Bodies were crudely proportioned and appendages grossly generalized. Although his medium was paint, he used color sparingly. His heavy outlines gave to his work more the character of drawing than painting. He had no knowledge of color modeling or such other sophisticated concepts as foreshortening and perspective. When one object overlapped another he did not try to eliminate the outlines of the more distant one. Note the handling of the quiver carried by the warrior illustrated in plate 2. But generally there was no overlapping of human or animal figures which were scattered over the surface of the robe, each being rendered individually beside, above, or below the others.

Anthropologists customarily refer to this primitive work as picture writing, a term which aptly expresses the major motive for its creation. The painter was more concerned with recording a memorable event by this pictorial shorthand than with the aesthetic appeal of his creation. He was more historian or biographer than artist.

GEORGE CATLIN AMONG THE MANDAN, 1832

George Catlin (pl. 4, fig. 1), spent the summer of 1832 on the Upper Missouri. He traveled upriver on the first steamboat to ascend the Missouri to Fort Union, stopping briefly at Fort Clark, the American Fur Company's post at the Mandan villages. He returned downstream by skiff, stopping over at Fort Clark for a period of two or more weeks. During that period the amazingly energetic Catlin created more than 40 pictures. Half this number were portraits of Mandan, Hidatsa, and Arikara Indians in the neighborhood of Fort Clark. The remainder were landscapes.

Catlin was a self-taught artist whose forte was portraiture. He possessed a remarkable ability to catch a likeness of his sitter with a few swift, bold strokes of his pencil or brush. Catlin's own account of his journey repeatedly referred to the Indians' delight and amazement at his ability to transfer their faces to canvas. They had seen nothing like this realistic portraiture before. (Catlin, 1841, vol. 1.)

Catlin was less skilled in rendering the human body. His interest in the details of Indian costume and ornament usually was secondary to his keen desire to record faithfully the heads and faces of his subjects. Not infrequently, he exaggerated or omitted important details of dress. (Ewers, 1956, pp. 495-498). Nevertheless, Catlin's very practice of painting from a model may have been a novelty in method of rendering the human figure that impressed some of his Indian sitters who had been familiar only with the generalized representations of humans created by native picture writers.

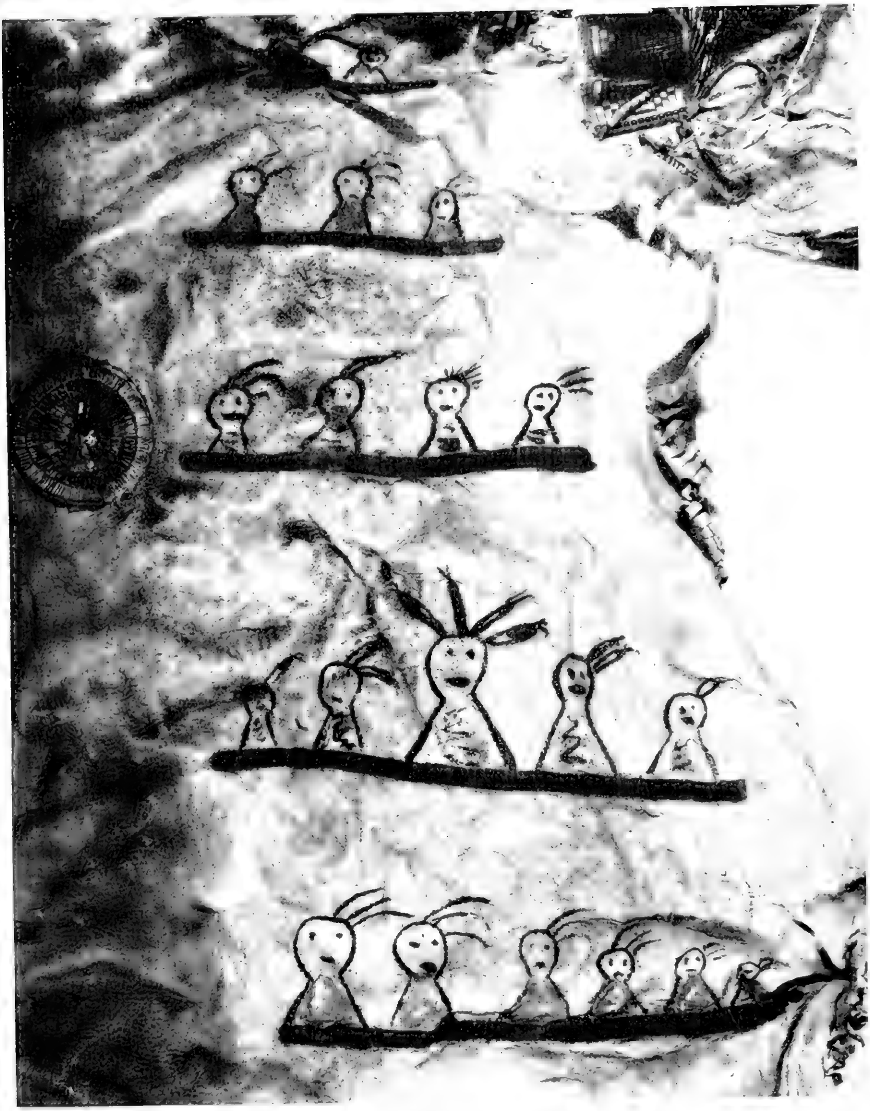
CARL BODMER AMONG THE MANDAN, 1833-34

Carl Bodmer, on the other hand, was a meticulous draughtsman thoroughly trained in the best European traditions of drawing from the model. The German scientist Prince Maximilian zu Wied carefully picked young, Swiss-born Bodmer (he was only in his early twenties) to accompany him on his travels in America for the purpose of making drawings that would illustrate his own scientific observations. The exacting scientist expected his artist's record to be no less accurate in every detail than would be his own writings.

1. Portrait by Catlin, 1832.

2. Portrait by Bodmer, 1834.

Four Bears, Mandan second chief and artist.



Detail of paintings on front of Four Bears' shirt, collected by George Catlin in 1832.

The Prince and the artist ascended the Missouri on an American Fur Company steamer in 1833. (See Bodmer's own field portraits of himself and the Prince, pl. 4, fig. 2.) They met some of the Mandan briefly on their way upriver in June. In the fall of that year, after more than a month of observation and picturemaking among the Blackfoot near Fort McKenzie, they returned to Fort Clark. There they spent the winter from November 8, 1833, to April 18, 1834, a period of more than five months. James Kipp, the fur company's manager of Fort Clark, provided the German nobleman and his artist associate with a whitewashed room in a newly built wooden building within the fort which served them as living quarters, studio, and workroom. Throughout their stay, Bodmer worked assiduously drawing and painting the likenesses of Mandan and other neighboring Indians in his studio, and scenes in the nearby Indian villages. He worked slowly and methodically, sometimes taking a full day or longer to complete a single portrait or view. During this period he created some of the most exact, realistic pictures of American Indians ever executed. These pictures possess a remarkable sharpness and depth of focus. Not only are the faces of the Indians truthful likenesses, but the minute details of costume and ornament are precisely delineated.

Although Catlin introduced realistic portraiture to the Mandan, the superior draughtsman, Carl Bodmer, showed them how every detail of a picture could be rendered with absolute truthfulness. Bodmer was the missionary par excellence of the white man's tradition of realism in art.

Nor was Bodmer content merely to exhibit his own work among the Indians. He furnished some of them with paper and watercolors, and encouraged them to make pictures for him and for Prince Maximilian. In the collections belonging to the estate of Prince Maximilian zu Wied are no less than nine original Indian drawings on paper, collected during Maximilian and Bodmer's trip to the Upper Missouri in 1833-34.

THE CHANGING ART STYLE OF FOUR BEARS, MANDAN CHIEF

Both Catlin and Prince Maximilian considered Four Bears the most remarkable man in the Mandan tribe. Although he held the rank of second chief, he was his people's most popular leader. He was the son of a prominent warrior, Handsome Child. Four Bears himself, though of slight build and medium stature, claimed to have killed 5 enemy chiefs and to have taken 14 scalps. Upon his return from a coup-counting session in the Mandan village of Ruhptare in January 1834, Four Bears told his white friends "with great satisfaction and self-complacency, that he had enumerated all his exploits, and that no one had been able to surpass him." (Maximilian, 1906, vol. 24, p. 58.)

Four Bears also was a leader in Mandan ceremonies. Prince Maximilian saw him lead a dance of the Dog Society, and learned that he had been selected as director of the great tribal religious festival, the Okipa, to be held the following summer (1834).

Four Bears' services to the traders and to visiting whites were many. Mr. Kipp relied upon him to protect the trading post at Fort Clark from the petty thievery of Mandan women and children. Maximilian found him to be his best authority on the language and religion of the Arikara, a tribe the scientist had no opportunity to visit. He observed that Four Bears spoke Arikara "fluently" (Maximilian, 1906, vol. 24, p. 73).

The active, versatile Four Bears was also an artist. This handsome, stout-hearted, friendly Mandan leader completely captivated George Catlin as did no other Indian among the more than 40 tribes Catlin visited. Catlin devoted a full chapter of his book to this warrior's exploits and frequently referred to him elsewhere. He painted two portraits of Four Bears (his Mah-to-toh-pa), both of which are preserved in the collections of the U. S. National Museum (Nos. 386128 and 386131). One portrait shows Four Bears in mourning, bare to the waist, with scars on his breast, arms, and legs evidencing his past submission to the excruciating self-torture of the Okipa. The other (see pl. 5, fig. 1), painted in a day-long session, presents Four Bears at full length in his finest dress costume. Catlin collected this costume and displayed it for many years in his traveling exhibition. The handsomely quilled and painted shirt is preserved in the U. S. National Museum (No. 386505). This shirt provides excellent examples of the art style Four Bears employed in depicting his war exploits in 1832 or earlier. On the right side of the shirt front he simply recorded his victims by painting their heads and upper bodies (pl. 6). On the back of the shirt he portrayed one of his coups (pl. 7). Note the very close similarity of this style to that of the painting on the buffalo robe collected by Lewis and Clark a quarter century earlier. Except for the crude representation of the features (two marks for eyes and one for the mouth), the rendering of the human figure is almost identical. It is definitely in the tradition of aboriginal Mandan picture writing.

Shortly before Catlin left the Mandan, Four Bears invited him to a feast in his earth lodge and presented him with a robe bearing a representation of his most important coups. The chief had spent two weeks painting this robe during Catlin's residence in the village. Unfortunately, the original of this robe is lost, and Catlin's copy of the specimen, reproduced in his book and in one of his paintings in the American Museum of Natural History (pl. 8), appears to be an untrustworthy interpretation of the Indian artist's style. Catlin adopted conventions of his own for rapidly rendering his copies of Indian pictographs. They appear to be more Catlin than Indian in style. Yet there is one detail in these paintings that Catlin surely did not invent—the hooklike hoofs of the horses, just like the horse hoofs portrayed by the unnamed Mandan artist prior to 1805. (See pl. 3.)

Prince Maximilian and Bodmer came to know Four Bears (their Mato-Tope) even better than had Catlin. They first met him at Fort Clark in June 1833, on their way upriver, and the Prince bought from him "his painted buffalo dress," suggesting that the clever Indian was adept in dealing with white collectors. On their return to Fort Clark in November, Four Bears came to visit them in their studio. Prince Maximilian's journal tells of his repeated visits to his quarters during their long stay at Fort Clark. Sometimes he spent the night on the floor before their fire. Four Bears exhibited an unusual interest in Bodmer's art. He brought other Indians to the studio to be painted and remained to watch the proceedings. He himself posed for two portraits by the Swiss artist, one of which is reproduced as plate 5, figure 2. (The other, a full-length view in dress costume, is published as plate 46, in Maximilian's *Atlas*). He also prevailed upon Bodmer to paint for him a white-headed eagle holding a bloody scalp in his claws. In return Four Bears painted for Maximilian a representation of his principal coups on a buffalo robe, and a separate rendering of one of his exploits, the conquest of a Cheyenne chief in hand-to-hand combat, apparently executed on paper. Although I have not been able to locate the originals of these works, they undoubtedly are reproduced with fidelity in Maximilian's *Atlas,* plates 51 and 55. I include them here as plates 9 and 10. Comparison of the style of painting illustrated by the picture on plate 10 with that of the painting on Four Bears' shirt (pls. 6 and 7), clearly reveals the great change in this Mandan artist's style that took place during the period 1832-34. Gone were the knoblike heads, the stick figures, the crude proportions, the lack of detail. Heads were now painted in profile, the features sharply defined. Great care was taken in drawing a realistic human eye. The arms, legs, and bodies were well proportioned, and the details of headgear, ornaments, and body costume, and the moccasined feet were delineated with painstaking care. Even though the colors of the original drawing are not known, some attempt at color modeling is suggested on the face and upper body of the warrior on the right. Can there be any doubt that this marked change in the painting style of Four Bears in the direction of a much more realistic treatment of the human figure should be attributed to the example of the white artists George Catlin and Carl Bodmer, whose artistic methods Four Bears had observed closely over a total period of several months?

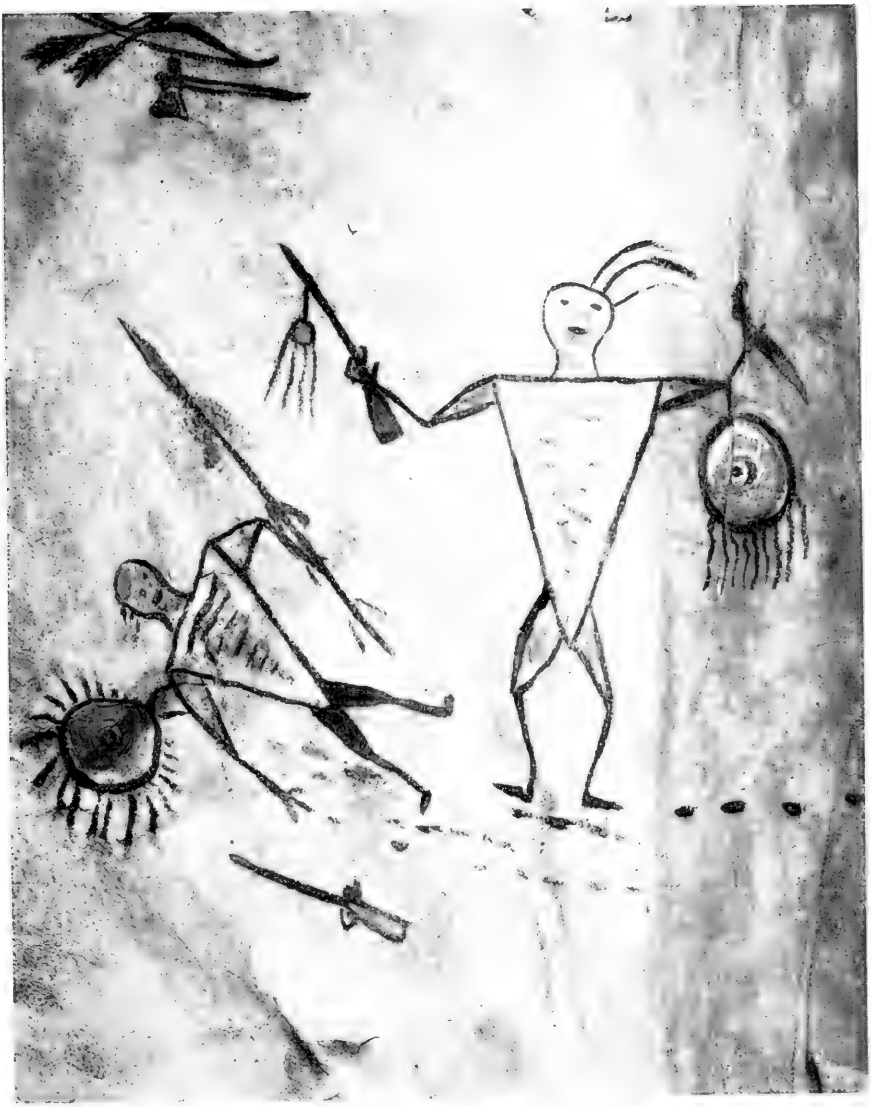
INFLUENCE UPON THE ART STYLE OF YELLOW FEATHER

Next to Four Bears, the most frequent Mandan Indian visitor to Bodmer's studio at Fort Clark during the winter of 1833-34 was a young warrior named Sih-Chida, The Yellow Feather. He was the son of a deceased Mandan head chief. Yellow Feather proudly showed Maximilian the Indians' copy of the first treaty between his tribe and the United States, signed by his father and General Atkinson in the year 1825.

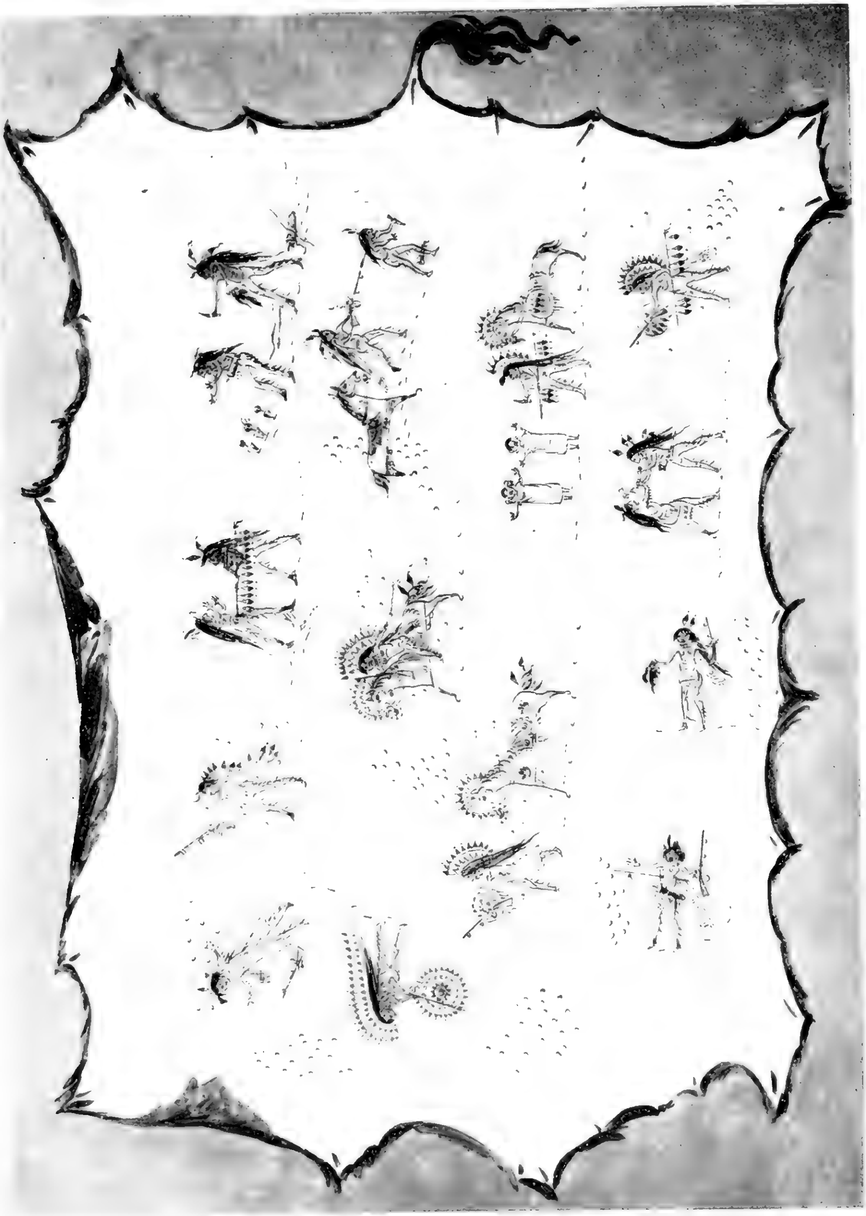
Bodmer executed a full-length portrait of Yellow Feather in December 1833 (plate 11, fig. 2, man on the left). Almost certainly this young man also posed for Catlin a year and a half earlier, although Catlin rendered his name "Seehk-hee-da, the Mouse-coloured Feather." (See pl. 11, fig. 1.) Not only are the facial features of the Bodmer and Catlin portraits similar but the sitter wears a pair of long pendants of dentalia and large trade beads which appear to be identical.

Maximilian wrote, "Sih-Chida, a tall, stout young man, the son of a celebrated chief now dead, was an Indian who might be depended on, who became one of our best friends and visited us almost daily. He was very polished in his manners, and possessed more delicacy of feeling than most of his countrymen. He never importuned us by asking for anything; as soon as dinner was served he withdrew, though he was not rich, and did not even possess a horse. He came almost every evening, when his favorite employment was drawing, for which he had some talent, though his figures were no better than those drawn by our children." (Maximilian, 1906, vol. 24, pp. 15-16.)

Yellow Feather spent several nights in Maximilian's quarters, sleeping on the ground before the fire. On one occasion he recovered Maximilian's thermometer which he found concealed under the robe



Detail of paintings on back of Four Bears' shirt, collected by George Catlin in 1832.



Catlin's facsimile of Four Bears' painted robe. (American Museum of Natural History.)

of a woman who had stolen it. On April 10, Yellow Feather left to join a large Hidatsa and Mandan war party against an enemy tribe. But sometime before his leavetaking, Yellow Feather painted at least two pictures in watercolors on paper for the Prince's collection. One of these I here reproduce as plate 12, with the very kind permission of Karl Viktor Prince zu Wied. The style of painting the human and animal figures exhibited by this picture, though crude, is a far cry from the simple figures of traditional Mandan picture writing. The rider sits astride his horse rather than on top of it. His face is shown in profile and considerable emphasis is given to a realistic representation of the human eye. The eye of the horse, both the white and the ball, are shown with an equal concern for detail. The ears, nostril, and mouth are delineated. There is some grace in the entire horse figure. The hoofs are realistically formed in contrast to the hooklike conventionalized hoofs of traditional Mandan pictography. The figures have some degree of roundness achieved by elementary color modeling which is less apparent in the photographic reproduction than in the full-colored original. Although we have no earlier example of Yellow Feather's art with which to compare this painting, I believe the influence of the white artists Catlin and Bodmer is reflected in this example of the effort of a young Mandan artist to portray details and to achieve realism in his figure painting.

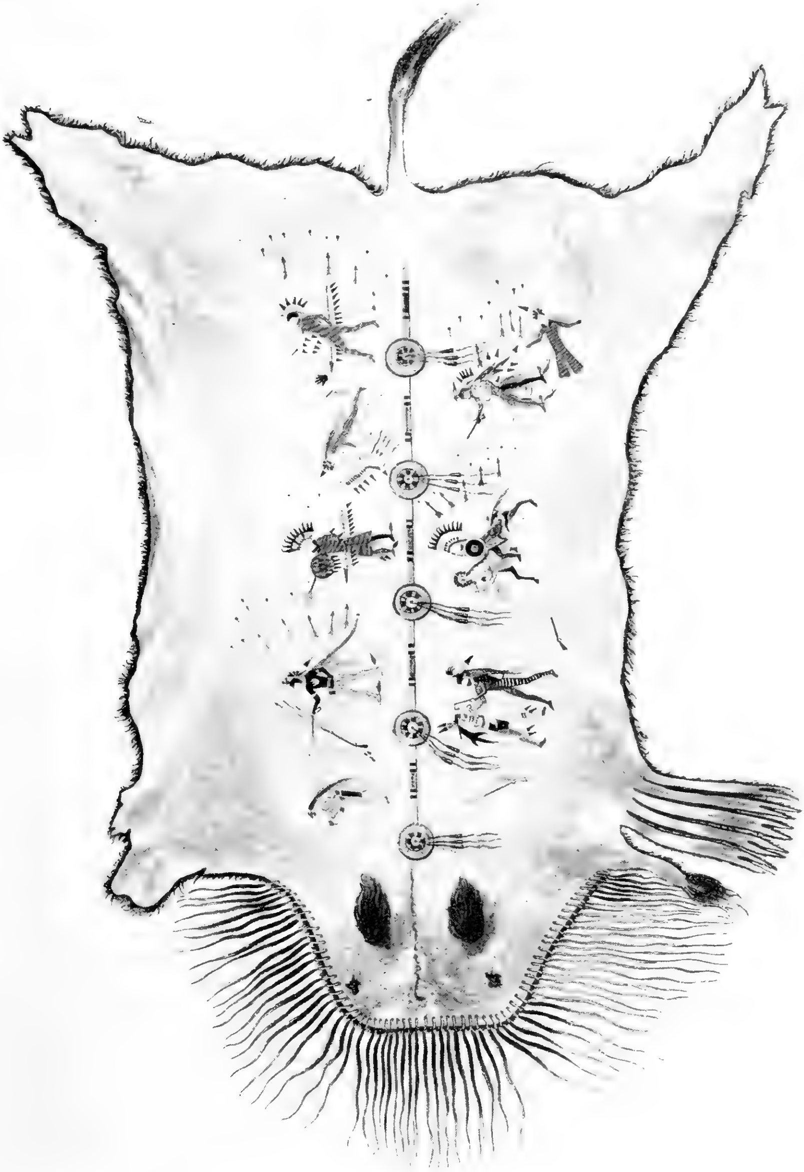
CONCLUSIONS

The foregoing data provide perhaps the best documented case history of the influence of the European artistic tradition of realism upon the painting style of primitive American Indian artists of a century and a quarter ago. The details of this documentation are indeed remarkable. We know the characteristics of traditional Mandan Indian picture writing as it was practiced prior to and at the time of these Indians' introduction to the European art tradition. We know who the missionaries of the European tradition were (George Catlin and Carl Bodmer), and when they were active among the Mandan (1832-34). We know that these white men demonstrated the objectives and methods of realistic drawing and painting to the Mandan, and that they actively encouraged the efforts of native artists. We know who two of those artists were (Four Bears and Yellow Feather). We know that these Indians posed for both white artists a total of six times and that they watched the white men paint numerous portraits of other Indians. We have examples of the painting of one native artist prior to the visits of Catlin and Bodmer, and examples of the work of both artists, executed before Bodmer departed from Fort Clark, which clearly reveal the influence of European realism upon their painting styles.

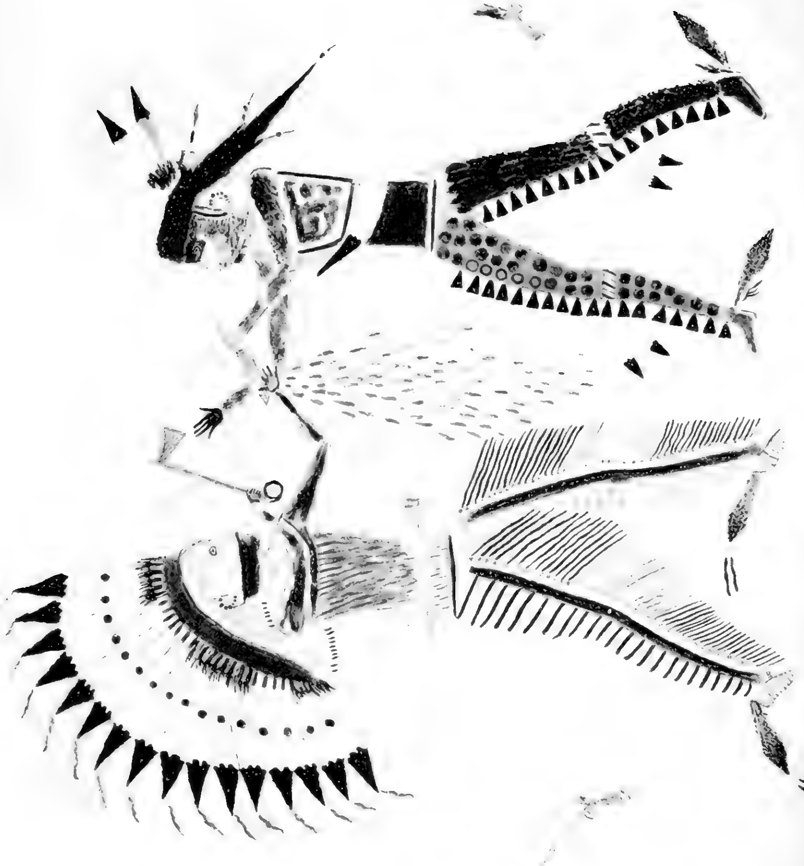
It is not possible or necessary to distinguish the separate influences of Catlin and Bodmer upon the work of these artists. Probably the cumulative effect of the examples and encouragement of two white artists, who visited the Mandan within a period of a little over a year, was important in impressing upon the native artists' minds the possibilities of realistic representation of men and horses which found expression in their own later work.

Significant, too, were the character and position of the two Indian artists who fell under the spell of the white artists' realism. Both Four Bears and Yellow Feather were sons of prominent men in their tribe. They were not idle dreamers but active warriors, versatile, gregarious fellows. Certainly Four Bears was a decided extrovert, who numbered painting among his many interests and accomplishments. He was the antithesis of the American artist James A. McNeill Whistler's conception of the primitive artist as a "man who took no joy in the ways of his brethren, who cared not for conquest, and fretted in the field—this designer of quaint patterns—this devisor of the beautiful—who perceived in Nature about curious curvings, as faces are seen in the fire—this dreamer apart, was the first artist." (Whistler, 1916, p. 8.) Rather, the example of Four Bears would suggest that the artist in a primitive hunting culture was more apt to have been an active hunter and warrior, a fierce competitor, a wide-awake, keen participant in the affairs of his tribe, who enjoyed picturing the most exciting, heroic, and memorable of his rich experiences.

There remains the problem of the relative permanence of Catlin's and Bodmer's influence upon Mandan Indian art. This is difficult to answer. Examples of Mandan painting in the late 1830's and the 1840's are lacking. Unfortunately, neither Four Bears nor Yellow Feather long survived Bodmer's sojourn among the Mandan. Catlin claimed that "Seehk-hee-da was killed by the Sioux, and scalped, two years after I painted his portrait." (Catlin, 1848, p. 19.) The journal of Francois Chardon, who succeeded Kipp in charge of Fort Clark, repeatedly mentioned Four Bears' activity as a warrior during the middle '30s, but said nothing of his artistic endeavors. In the summer of 1837 a disastrous smallpox epidemic decimated the Mandan tribe. Late in July of that year, Four Bears contracted that dread disease. He died a few days later. But before his death this courageous leader delivered a speech to his people denouncing the whites as



Bodmer's facsimile of Four Bears' painted robe. (Maximilian's *Atlas*.)



Facsimile of Four Bears' painting of his victory over a Cheyenne chief. (Maximilian's *Atlas.*)

1. Portrait by Catlin, 1832.

2. Portrait by Bodmer, 1833. (Yellow Feather at left.)

Yellow Feather, artist and son of Mandan head chief.

Reproduction of a watercolor by Yellow Feather. Original owned by the Estate of Prince Maximilian zu Wied.

black-hearted dogs who had repaid his long and faithful friendship with a pestilence which was causing him to "die with my face rotten, that even the wolves will shrink with horror at seeing me." Chardon wrote Four Bears' brief obituary in his journal under the date Sunday, July 30, 1837: "One of our best friends of the Village (Four Bears), died today, regretted by all who knew him." (Chardon, 1932, pp. 44-45, 50, 123-125.)

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A SKULL OF THE BRIDGER MIDDLE EOCENE CREODONT, PATRIOFELIS ULTA LEIDY

(With 4 Plates)

By

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INTRODUCTION

Discovery of a remarkably well preserved skull and lower jaws of the Bridgerian creodont carnivore *Patriofelis* was made by Golden York for the University of Utah. Not only is this by far the most nearly complete known for *Patriofelis,* but almost certainly belongs to the heretofore very poorly represented genotypic species, *P. ulta.* The specimen was found in 1953 while prospecting [1] Bridger exposures about 20-25 miles east of Kemmerer, Wyo., north of Granger and not far from the Green River. Mr. York's description of the location would place it in or near T. 22 N., R. 111 W. The exact horizon is not certain but the specimen is reported to have come from near the top of the section as exposed locally in the hill or bench. The exposures in this general area are of the Bridger formation as shown on the 1955 edition of the Geologic Map of Wyoming. Moreover, there seems no doubt but that only the lower part of the Bridger is represented in this portion of the basin.

I am greatly indebted to Dr. William Lee Stokes, head of the department of geology at the University of Utah, for giving me the opportunity of examining and describing this unusual specimen. Dr. Joseph T. Gregory at Yale University, Dr. Glenn L. Jepsen at Princeton University, and Dr. George G. Simpson at the American Museum of Natural History aided significantly in permitting examination and study of type and related materials in collections under their care. The specimen was skillfully prepared, removing it from the much-

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[1] Mr. York's fieldwork was supported by a grant from the Research Fund of the University of Utah.

indurated nodule in which it was found, by Franklin L. Pearce. The wash drawings accompanying this paper were made by William D. Crockett.

PREVIOUS STUDIES

Matthew has briefly outlined the history of investigation relative to *Patriofelis* up to 1909. A recapitulation, however, with additional details, and comments on more recent studies, may not be unwarranted.

Patriofelis was first described by Leidy in 1870 from a pair of lower jaws (U.S.N.M. No. 105) collected by Hayden in 1869 near Fort Bridger. A major portion of both rami are represented, including alveoli for all the cheek teeth, but portions of the crowns of P_4-M_2 are preserved only on the left side. Leidy did not so indicate, but it is evident from his illustrations of the right ramus published in 1873 (pl. 2, fig. 10) that the tooth portions shown were drawn in reverse from the opposite side. Leidy first regarded his new form, *Patriofelis ulta,* as probably belonging to the cat family, but in 1873 regarded it as "perhaps intermediate to the feline and canine animals."

In the meantime (1872) Marsh described the new genus, *Limnofelis,* with two new species, *L. ferox* and *L. latidens,* based essentially on a lower jaw portion with M_2 (Y.P.M. No. 11865) from Henry's Fork and a last upper premolar (Y.P.M. No. 10904) from the Grizzly Buttes respectively. Later in the same year, with additional material at hand, he proposed the new generic name *Oreocyon* for *Limnofelis latidens.* Marsh did not discuss the possible relationships of these animals, other than to compare their size with that of a lion and to state that the lower canine and premolars of *O. latidens* "somewhat resemble those in the Hyaena." He later concluded, however, that *Limnofelis* was apparently related to the cats, but nowhere did he discuss the possible relationship to Leidy's *Patriofelis* from the same beds.

Although rather generally ignoring Marsh's names, Cope worked out a rather orderly arrangement of the creodonts and in 1880 (figured in 1884a) described as new the form *Protopsalis tigrinus* on the basis of two lower molars (A.M.N.H. No. 4805), a canine and certain bone elements from the lower Eocene Wind River beds. He included this genus tentatively, as he had earlier allocated *Patriofelis,* in his family Oxyaenidae, which he regarded (1884a) as ancestral to the Felidae. The same year (1884b), however, he abandoned this idea in favor of the Miacidae as the ancestral group.

In 1892, Wortman, in a part of a joint paper with Osborn on the

Wasatch and Wind River fauna, discussed and refigured the type of *Patriofelis ulta* and named as new the species *?Patriofelis leidyanus,* based on a jaw portion in the Princeton collections (No. 11375) including, as was later shown, only deciduous teeth. Although uncertain as to the generic reference for his new species, he believed that it indicated for *Patriofelis,* along with *Palaeonictis,* an ancestral position with respect to the true felids. Scott in his revision of the creodonts in 1892 also included *Patriofelis* in the Palaeonictidae, but placed *Protopsalis* along with *Oxyaena* in the Hyaenodontidae! He recognized, however, that *Oreocyon* Marsh, and hence that part of *Limnofelis* which had been named *L. latidens,* was a synonym of *Patriofelis,* but tentatively placed *Limnofelis* in synonymy with *Protopsalis.* Nevertheless, he followed Cope's later thinking in deriving the Felidae as well as other modern Carnivora from the Miacidae.

Wortman's most significant contribution to the study of *Patriofelis* appeared in 1894 and included a detailed description of the mounted skeleton and other newly acquired materials in the American Museum. He placed both *Limnofelis* and *Protopsalis* in synonymy with *Patriofelis,* concluded that only two species were represented, the large *P. ferox* and smaller *P. ulta,* and transferred the group to the Oxyaenidae. No reference was made to Marsh's *Oreocyon latidens;* presumably he regarded this as something different. Furthermore, the species that he had earlier named *?Patriofelis leidyanus* was bebelieved not to represent *Patriofelis,* but a form which might be the forerunner of the Nimravidae. Adams, in 1896, following Wortman's suggestion, gave *?P. leidyanus* the new generic name *Aelurotherium,* and because of it regarded the Felidae as polyphyletic. Wortman, in 1899, placed this genus in the *Palaeonictidae,* separate from the Oxyaenidae, and in 1901 placed his species *A. leidyanum* in synonymy with Marsh's *Limnofelis latidens* as *Aelurotherium latidens.* This procedure, however, was in error as the immature lower jaw of *Limnofelis latidens,* with which comparison was made and which he figured as a type, was not the type but a referred specimen, and hence could not carry the name. The actual type of *Limnofelis latidens,* and hence of *Oreocyon latidens,* was a P^4 which Wortman in a later part of the same paper referred to *Patriofelis ferox,* clearly listing *Limnofelis latidens* as a synonym of *Patriofelis ferox.* Also in 1901 he described the new species *Aelurotherium bicuspis* on the basis of a lower cheek tooth, which he regarded as M_1 (Y.P.M. No. 11755). Although now recognizing that the known lower premolars of *Aelurotherium* were deciduous, he defended his 1892 conclusions as to the ancestral position of *Aelurotherium* with respect to the Oligocene felids, resting them rather largely on his interpretation of M_1 as essentially the carnassial tooth of the lower series.

Osborn (1907, fig. 95, E) reillustrated the teeth in the type of *A. leidyanum* indicating that all were deciduous and belonged to *Patriofelis,* but Matthew, in 1909, demonstrated the synonymous position of *Aelurotherium,* as well as *Limnofelis, Oreocyon,* and *Protopsalis,* with *Patriofelis,* correctly identifying the various teeth in the types. As to whether all the species that he placed in synonymy with *P. ferox,* however, represent that species and none *P. ulta,* may be doubted.

In addition to describing the skeleton of *Patriofelis ferox,* Wortman, in his 1894 paper, pointed out a number of characters that he believed indicated that *Patriofelis* or a closely related form gave rise to the pinnipeds. This suggestion was criticized by Osborn in 1900, and in 1902 Wortman defended his conclusion, taking a strong stand against Osborn's views, but was again refuted, this time by Matthew in 1909. Kellogg, in 1922, discussed at length such evidence as had been presented on the origin of the pinnipeds, but deduced that a case for the Oxyaenidae had not been demonstrated, nor had Matthew's suggestion of an arctoid fissiped ancestry solved the problem.

Matthew's (1909) monographic study of the Bridger carnivores and insectivores included a review and restudy of the known material of *Patriofelis,* as well as a taxonomic revision. The four species that he recognized are indicated as representing four distinct stratigraphic units and include as the oldest *Patriofelis tigrinus* (Cope) from the Wind River beds; a species from the Huerfano B beds originally referred by Osborn (1897) to *P. ulta,* but named *Patriofelis coloradensis* by Matthew; the genotypic species *Patriofelis ulta* Leidy from Bridger B; and Marsh's *Patriofelis ferox* from the upper Bridger levels. In 1915 he decided that *P. coloradensis* represented *Ambloctonus* rather than *Patriofelis.*

Later discussions of *Patriofelis* included a review by Thorpe (1923) in which an attempt was made to revive *Patriofelis latidens.* Thorpe recognized the error in Wortman's taxonomic procedure in arriving at the name *Aelurotherium latidens,* but seems to have committed a similar error in regarding the lower jaws, Y.P.M. No. 10940, as the type of *Oreocyon latidens,* whereas the holotype of *Limnofelis latidens* is No. 10904, a last upper premolar. Although Marsh's characterization of the genus *Oreocyon* was based on referred materials, the type species was clearly that which he originally described as *Limnofelis latidens* and hence cannot have a different type specimen.

In his revision of the "Pseudocreodi," Denison (1938) revived

Protopsalis for the Wind River form *P. tigrinus* Cope because he felt that the carnassial construction exhibited had not attained the *Patriofelis* stage, and restored Huerfano B *Ambloctonus coloradensis* to *Patriofelis,* largely on the basis of characters of the lower jaw proper. A new species, *Patriofelis compressa,* was described, characterized by slender premolars, on a lower jaw (A.M.N.H. No. 17017) also from the Huerfano B stage in Colorado.

P. M. Butler (1946) in a discussion of the evolution of carnassial dentitions in certain creodont subfamilies indicated the changes that took place in the development of the Oxyaeninae, culminating in *Patriofelis.* In his treatment of the various subfamilies he gave no preferred arrangement of these into families, but did discuss the general characteristics of the superfamilies or tribes as named by Matthew.

TAXONOMIC SUMMARY

The taxonomic arrangement adopted here is essentially that of Matthew, modified by Denison, but with minor differences and a corrected synonymy as far as known material can be interpreted. Although species are not redescribed, annotations are included where pertinent and a key is added.

OXYAENIDAE Cope, 1877

OXYAENINAE Trouessart, 1885

PATRIOFELIS Leidy, 1870

Synonyms.—Limnofelis Marsh, 1872.
Oreocyon Marsh, 1872.
Protopsalis Cope, 1880.
Aelurotherium Adams, 1896.

Type.—Patriofelis ulta Leidy, 1870.

Discussion.—The number of incisors above and below for the middle Eocene or Bridger members of this genus is two in the material at hand, although Matthew has indicated (1909) that the number is three in the lower jaw, based partly on the appearance of alveoli in A.M. No. 12078. If Matthew has correctly interpreted No. 12078, the number of lower incisors in *Patriofelis* is variable as in *Oxyaena.* Moreover, *Patriofelis* has been characterized as lacking the second upper molar. Its presence, however, is variable, as a vestigial M^2 may occur, possibly characterizing lower Bridger *P. ulta* (and Huerfano species ?).

PATRIOFELIS ULTA Leidy, 1870

Synonyms.—*Limnofelis latidens* Marsh, 1872; *Oreocyon latidens* (Marsh), 1872.

Type.—Lower jaws with P_4-M_2 (incomplete) in left ramus (U.S.N.M. No. 105).

Referred material.—The upper premolar (P^4 according to Marsh, Wortman, and Thorpe, but P^3 according to Matthew) upon which Marsh based the species *Limnofelis latidens* is decidedly smaller than either P^3 or P^4 in A.M. No. 13145—the skull material described by Matthew as *Patriofelis ferox.* Its length is about intermediate between that of P^3 and P^4 in the skull of *P. ulta* described in this paper. Moreover, this premolar is reported to be from the Grizzly Buttes and hence lower Bridger, the horizon which seems characterized by *P. ulta.* Hence, *Limnofelis latidens* and *Oreocyon latidens* are more likely synonyms of *Patriofelis ulta* rather than, as Wortman (1902) and Matthew (1909) indicate, of *P. ferox.*

Besides the University of Utah skull and jaws (No. B50) belonging to *Patriofelis ulta,* there is in the U. S. National Museum (No. 21365) a right mandibular ramus of this species, with P_2-P_4 partially erupted, Dp_4 loose, and M_1 and M_2 but little worn. The lower molars are only slightly smaller than in the type, but the horizon represented is believed to be very low in Bridger C, immediately above the Green River shale just to the northeast of Twin Buttes.

PATRIOFELIS FEROX (Marsh), 1872

Synonyms.—*Patriofelis leidyanus* Wortman, 1892; *Aelurotherium leidyanum* (Wortman), see Adams 1896.
Aelurotherium latidens Wortman (not Marsh), 1901.
Aelurotherium bicuspis Wortman, 1901.
Patriofelis latidens Thorpe (not Marsh), 1923.

Type.—Fragment of left ramus of mandible with M_2 (Y.P.M. No. 11865).

Referred material.—Included among the materials referred to *Patriofelis ferox* are the type specimens of the above species placed in synonymy. These are the immature lower jaw with Dp_2-Dp_4 (P.U. No. 11375) of *P. leidyanus;* the lower jaw with a canine, Dp_3, Dp_4, and M (Y.P.M. No. 11756), which was "another specimen" in Marsh's description of *Limnofelis latidens,* but which Wortman indicated as a type for *Aelurotherium latidens;* the lower cheek tooth regarded by Matthew Dp_4 (Y.P.M. No. 11755) of *Aelurotherium bicuspis;* and the symphysial portion of a pair of lower jaws with

C–P_4 (Y.P.M. No. 10940) which was among the "additional remains" Marsh had when he proposed *Oreocyon* for *L. latidens,* and which Thorpe regarded as the type of *O. latidens* when he attempted to preserve the species name *Patriofelis latidens.*

Additional materials of *Patriofelis ferox,* including the mounted skeleton composed of A.M. Nos. 1507 and 1508 in the American Museum, are listed by Matthew (1909, p. 420). In the National Museum, besides the unused portions of A.M. No. 1508 (U.S.N.M. No. 5916) received in an early exchange, there are several parts of a comparatively large skull (U.S.N.M. No. 21364) obtained in the upper Bridger, probably C, to the north of the saddle between Sage Creek Mountain and Cedar Mountain, and the right ramus of a lower jaw, mentioned by Denison (p. 173) as exhibiting Dp_2–Dp_4 with M_1 erupting (U.S.N.M. No. 13318), from the upper part of Bridger C between Sage Creek and Hickey Mountain. M_1 in the latter specimens is not completely exposed, but its size is clearly much greater than in *P. ulta.*

PATRIOFELIS (PROTOPSALIS) TIGRINUS (Cope), 1880

Type.—Two lower molars, a lower canine, and certain bone elements (A.M.N.H. No. 4805).

Discussion.—The type of this species is reported by Matthew (1915) to be from the Lost Cabin beds of the Wind River series. No additional specimens are known. I have retained *Protopsalis* as a subgenus rather than completely suppressing it in *Patriofelis* as Matthew did in 1909, and in preference to recognizing full generic rank as Denison did in 1938. *Protopsalis* appears to be structurally intermediate between *Oxyaena* and typical *Patriofelis,* but possibly a little closer to *Patriofelis,* although there is greater difference between it and *Patriofelis* than between the middle Eocene species of *Patriofelis.* This can perhaps be best represented by regarding it as a distinct subgenus. Nevertheless, *P.* (*Protopsalis*) *tigrinus* is a rather gigantic form and surely is not the species which gave rise to the comparatively small lower Bridgerian forms of *Patriofelis.*

?PATRIOFELIS COLORADENSIS Matthew, 1909

Type.—Left ramus of mandible with C–P_4 and M_2 (A.M. No. 2691).

Discussion.—I suspect, as did Denison (1938), that this species belongs to *Patriofelis* rather than *Ambloctonus* where Matthew placed it in 1915. In addition to characters cited by Denison, I note that

Osborn's (1900, fig. 8) illustration of the jaw shows the interval for missing M_1 smaller than would seem possible for this tooth in *Ambloctonus.* Moreover, *Ambloctonus* is not otherwise known from beds as late as Huerfano B or lower Bridger.

PATRIOFELIS COMPRESSA Denison, 1938

Type.—Left ramus of mandible with C–M_2 (A.M. No. 17017).

Discussion.—Slightly larger, though close to ?*P. coloradensis* in size, this form is apparently distinguished by relatively slender premolars. No information is available on the extent to which this character is variable in *Patriofelis.* It comes, moreover, from the same beds as ?*P. coloradensis.*

KEY TO SPECIES OF PATRIOFELIS

M_2 with small talonid	
Very large	*P.* (*Protopsalis*) *tigrinus*
M_2 without talonid	
Large (P_2-M_2, 78-84 mm.)*	*P. ferox*
Intermediate size (P_2-M_2, 75.5-76.0 mm.)*	
Vestigial M_2	*P. ulta*
Small	
Lower premolars robust (P_2-M_2, 60 mm.)*	?*P. coloradensis*
Lower premolars slender (P_2-M_2, 65 mm.)*	*P. compressa*

* Measurements according to Denison, except second specimen of *P. ulta.*

DESCRIPTION OF THE SKULL AND JAWS OF PATRIOFELIS ULTA

Attention was called by Scott (1913) to the resemblance in relative body proportions of *Patriofelis* to an otter. The short, broad, and low snout of the skull is perhaps even more otterlike than he had realized. The general appearance of the skull was not hitherto known, as that of *Patriofelis ferox* which Wortman (1892) described (A.M. No. 1507) was considerably restored and the portions of the top of the skull were evidently placed too high, so that the rostrum has the appearance of much greater depth than in the University of Utah specimen. The latter shows a small amount of crushing dorsoventrally below the frontal region, but it is so nearly complete that the extent of deformation is evident and would in no way account for the depth indicated in the larger animal.

Dorsal aspect.—In dorsal view (pl. 1) the remarkable shortness and breadth of the rostral portion of the skull is clearly evident. The nasals are broad forward but taper posteriorly to near the frontomaxillary sutures on either side where they abruptly widen and then taper to a point between the frontals, producing a pattern resembling an arrowhead pointing posteriorward. The frontals are decidedly broad forward but taper posteriorly toward the parietals. Between the postorbital processes the frontal area or plateau is slightly concave, a condition that I do not attribute to the compression which has taken place between this surface and the posterior part of the palate. At the position of the postorbital processes the frontals are bluntly inflated, and moderately prominent temporal ridges extend posteriorly to their union forming the sagittal crest at about the juncture of the frontal and coronal sutures. The parietals are elongate and slender, and support a moderately well developed sagittal crest that slopes downward and backward, although increasing in depth toward the supraoccipital. The supraoccipital is missing from the *P. ulta* skull, but from other material of the genus it is known to extend far backward and a little upward, forming a remarkably developed inion. The greatest constriction of the slender braincase is across the parietals between the temporal part of the frontals and the anterior margin of the squamosals where these pairs approach each other closest. Posterior to the constriction the superior and lateral surface of the cranium formed by the squamosal sweeps widely out onto the broad and massive zygomatic processes. At the deepest part of the temporal fossa, a very large vascular foramen penetrates the parietals on each side of the sagittal crest. This is accompanied by a smaller foramen posterolateral to it on each side close to the squamosal but also within the parietal.

Lateral aspect.—In lateral view (pl. 2) the premaxilla is seen to rise as a narrow rim of bone along the anterior margin of the maxilla and form the lateral rim of the broad but possibly somewhat depressed anterior narial aperature. The premaxilla is rapidly pinched out posteriorward between the nasal and maxilla. The maxilla as exposed laterally is anteroposteriorly short, although the nasal process extends posteriorly above the lachrymal as it rises onto the dorsal surface, and the malar process extends prominently backward beneath the malar or jugal. The large infraorbital foramen penetrates the maxilla above the anterior root of P^3, well forward of the orbital rim and about midway dorsoventrally. The lachrymal bone is prominently displayed on the dorsolateral surface of the rostrum anterior to the orbital rim and forms the anterior margin of the orbit. Extending downward to the anterior extremity of the jugal and separated from it by a marked notch, it almost or quite excludes the maxilla from participation in the formation of the rim. The lachrymal foramen is concealed just within the orbital fossa posterior to a small process on the lachrymal bone formed by the above notch. The jugal is comparatively deep and strong, articulates in a much-extended contact with the maxilla below and inward, and shows almost no evidence of a postorbital process. Posteriorly, the squamosal portion of the zygoma is particularly deep and sturdy. The transversely elongate postglenoid process extends strongly downward and forward, forming with a prominent process on the outer part of the anterior margin of the glenoid fossa a combination which almost locks the condyle of the lower jaw in place. Unfortunately the mastoid and exoccipital portions of the skull are incomplete; however, sufficient remains to note that the posterior profile of the occiput is nearly vertical beneath the inion.

The orbits of *Patriofelis ulta* are not large but are decidedly dorsal in their position on the face. This is effected by the flattened to concave frontal area between them and by the deep zygomae below. Not only are the orbits high but the plane of the orbital rim faces decidedly upward because of the outward sweep of the jugal. The anterior margin of the orbit is well forward, about over the middle or anterior portion of P^4.

It is only in the orbital fossa that there is any evidence of dorsoventral compression of the skull; nevertheless, the noticeable fracturing and distortion are not so severe that details of the foramina penetrating bone in this area cannot be determined, although certain of the sutures are obscured. The large posterior opening of the infraorbital canal is just below and slightly median to the lachrymal foramen, at the anterior apex of the orbital plate of the maxilla. Posterior to the infraorbital opening, a little over 2 centimeters, and about on the same level, there is a large, anteroposteriorly elongate sphenopalatine foramen, and immediately below the latter is a much smaller, though prominent, posterior palatine foramen.

In the posterior portion of the orbital fossa, a separate optic foramen seems indicated by an opening about 1½ centimeters anterior and dorsal to the sphenoidal fissure. The large sphenoidal fissure, directly below the most constricted portion of the cranium, evidently transmitted not only the third, fourth, first branch of the fifth, and sixth cranial nerves as customary, but also the second branch of the fifth or trigeminal, inasmuch as the foramen rotundum does not appear to have become separated from the sphenoidal fissure (Wortman believed them separate), at least not externally, in this group of animals. Moreover, the sphenoidal fissure must also have transmitted the external carotid artery, as the anterior opening of the alisphenoid canal, which, when present as in modern bears and dogs, opens into the foramen rotundum, was evidently confluent anteriorly with the sphenoidal fissure. The posterior opening of the alisphenoid canal is surely represented by the clearly defined foramen immediately anterior to the foramen ovale (agreeing here with Wortman's interpretation).

Ventral aspect.—In the over-all appearance of the skull in ventral view (pl. 3), one notes the short, broad palate, elongate mesopterygoid and basicranial portion, and widely swinging, massive zygomae. The palate in greater detail shows the premaxillae not much extended forward of the canines and nearly straight across the front of the incisors. The anterior palatine foramina are close to the incisors and median to the canines. They appear nearly circular when viewed from somewhat forward of the palate. The posterior palatine foramina are on the forward portion of the suture between the maxillae and palatines, medial to the fourth premolars. The posterior nares are covered beneath by the palate to a point farther back than the posterior border of the orbital plate of the maxilla on either side, about medial to the posterior margin of the carnassials. The mesopterygoid fossa is extremely elongate anteroposteriorly and the forward portion is partially constricted below by inwardly directed lower margin of the ascending plate of the palatines. Posteriorly the fossa is more open as the pterygoids along their lower margins diverge toward the hamular processes. The posterior margin of the pterygoids, above the hamular process, sweeps abruptly upward and posterolaterally just inward of the foramen ovale, apparently extending almost to the notch representing the foramen lacerum medius. Particularly noteworthy is the union of the pterygoids across the roof of the mesopterygoid fossa, concealing the presphenoid and the anterior portion of the inferior surface of the basisphenoid. Anterior to this the evidence is not so clear, but there seems no doubt but that the palatines are also united through a median suture completely removing the presphenoid from participation in the mesopterygoid fossa, not, however, the vomer, the median ridge of which can be seen emerging from the nasal cavity.

In the basicranial area only the basisphenoid, basioccipital, and periotics are preserved posteromedial to the squamosals and alisphenoids. The basioccipital is broad as well as elongate, evidently occupying a relatively large area of the basicranial region. The basilar tubercles for the *recti capitis* muscles on the forward portion of this bone are elongate and well developed, reaching their greatest prominence forward at the suture between the basioccipital and basisphenoid. Posterolaterally, the basioccipital is perforated by a broad and flattened condylar or hypoglossal foramen which joins a prominent vascular canal before entering the foramen magnum. Medial to the hypoglossal foramen and extending ahead to the lateral margin of the basioccipital, a broad and distinct anterolaterally directed groove, evidently occupied by the internal carotid, as suggested by both Wortman and Matthew, rises into the large aperture representing the foramen lacerum medius just ahead of the medial portion of the petrosal. The exposed surface of the basisphenoid is triangular in shape with the anterolateral sides bound in part by the alisphenoids and forward by the V-shaped margin of the pterygoids. About midway forward on the anterolateral margin on each side, at the anterior extremity of a shallow groove from the foramen lacerum medius, there is a foramen which extends forward above the pterygoid, eidently the pterygoid canal for the *Vidian* nerve. Parallel and lateral to this on the surface of the alisphenoid are two or three sharp grooves or striae, extending between the posterior margin or lip of the foramen ovale to the position on the margin of the aperture corresponding to the eustachian foramen. Still more lateral and nearly parallel to the foregoing, but on the squamosal, is the straight and deeply impressed fissura Glaseri, for the chorda tympani nerve, sharply limiting the glenoid surface and postglenoid process medially and extending backward to a recess in the squamosal directly opposite the fenestra ovalis. The posterior surface of the postglenoid process shows a number of dorsoventral ridges and grooves near the lower margin, and a very broad and shallow depression near its medial margin extends upward and is confluent with a comparatively large postglenoid foramen (Wortman thought this to be absent) close to the fissura Glaseri.

Petrosal.—The petrous portion of the periotic is exhibited in the anterolateral portion of the large otic fossa lateral to basioccipital. It does not appear to separate completely the foramen lacerum medius from the foramen lacerum posterius as the medial margin of the petrosal shown on the left side approaches close but does not touch the basioccipital. The outline of the petrosal as exposed ventrally cannot be fully determined because the margin is somewhat damaged and incomplete; nevertheless the most conspicuous feature of this element is the downward- and forward-directed buttonlike promontorium. A fairly large fenestra rotunda faces backward and slightly outward. An elongate groove on the petrosal extending backward from a position immediately outward from the lateral margin of the fenestra rotunda is not explained but suggestion is made that this may have covered the stapedial muscle dorsally, or possibly the stapedial artery. The slightly smaller fenestra ovalis is forward and a little above the fenestra rotunda and faces laterally and somewhat forward.

The ventral aperture of the stylomastoid foramen is destroyed on both sides but sufficient remains of the walls of the foramen to indicate that it may not have been completely closed medially. A small portion of the mastoid projects medially, in front of the stylomastoid foramen and beneath its continuation as the facial canal, almost to the petrosal posterolateral to the fenestra rotunda. Immeditely lateral to the stylomastoid foramen and confluent with it, as exposed in the broken section, is a larger cavity (or canal?) that may have contained the stylohyal. The facial canal is open anteriorly at least as far as a point just ahead of the fenestra ovalis. Here the facial nerve may have entered the petrosal, although slight damage obscures the relationship. On the other hand, a large aperture on the dorsal surface of the petrosal, posteromedial to the promontorium, may have conducted the facial nerve, in which case it was uncovered ventrally through most of its course. The large aperture referred to is not otherwise accounted for. A prominent epitympanic recess is noted, apparently in the squamosal, opposite the fenestra ovalis and at the posterior extremity of the fissura Glaseri.

Upper dentition.—In a superficial way the teeth (pl. 3) of *Patriofelis,* as noted by Marsh, show an interesting resemblance to those of the hyena. Although the form of the palate is rather like that in *Crocuta,* the pattern of the upper teeth is perhaps less hyena-like than it is in the lower series. The carnassials in each, of course, are not homologous. The upper cheek tooth series in *Patriofelis ferox* was described by Matthew (1909), but the anterior part of the dentition was not known. The University of Utah specimen demonstrates that there are only two upper incisors and that M^2 may be present so that the formula for the genus may be written

$$I\frac{2}{2\text{-}3?},\ C\frac{1}{1},\ P\frac{3}{3},\ M\frac{1\text{-}2}{2},$$

with M^1 and M_2 as carnassials.

The upper incisors are simple teeth with conical crowns exhibiting enamel distributed a little higher on the outer side, and a prominent lingual cingulum that is carried nearer the apex of the crown medially. The median incisor is comparatively small with a transversely flattened root, whereas the lateral of the two is decidedly large and more caninelike in appearance. Its root is more nearly circular in cross section, but with the posterolateral surface somewhat flattened. The canine is very robust and heavy rooted, approximately oval in cross section—not flattened or saberlike. These teeth have been much blunted by wear.

There is no P^1. P^2 is simple and two rooted with a very broad posterior portion. There is a small posterior cusp placed buccally and a brief shelf posterolingually, but without a deuterocone. P^3 is three rooted with a small anterior cuspule and a large tritocone not as high as the primary cusp. The deuterocone, though damaged, is seen to be well developed and about median in position. In P^4 the small anterior cusp is higher or nearer the apex of the primary cusp and the tritocone is about as large as the primary cusp but more bladelike in appearance. The talon carries a well-developed crestlike deuterocone and is anteroposteriorly broader and more anterior in position than that of P^3. M^1, the carnassial, has been converted entirely to a shearing blade. This tooth is rather worn lingually, but it is apparent that the anterointernal root did not support a talon or deuterocone. M^2 is a small peglike tooth anterolingual to the posterior margin of M^1.

An interesting feature of the *Patriofelis* upper dentition is the extent to which it is carried outward and posteriorly on the strong zygoma as in cats and hyenas, and the fossil form, *Hyaenodon*—quite unlike the bears, and possibly dogs. Also, as noted by Matthew (1909), the upper cheek teeth are inclined inward, very much so in the posterior part of the series, so that the shearing surface, particularly of M^1, is vertical. The outer wall of M^1 is nearly horizontal and the angle that it makes with the shearing surface is, in consequence, not particularly acute. Also, as a result of this, the vestigial M^2 is implanted at an angle, dorsal to the crown of M^1, so that it is almost concealed in the ventral view. Its small crown scarcely reaches the plane of shear on M_1 immediately ventral to it.

Mandible.—The *Patriofelis* jaws (pl. 4), as Matthew (1909) has noted, are deep and massive. The symphysis is deep and elongate, and although Matthew considered it as not co-ossified, I find the two rami are firmly united. When it was necessary to separate the jaws so as to remove them from the skull during preparation, breakage for the most part occurred to one side through the canine alveolus. The anterior margin of the symphysis is a little less abrupt than Matthew has shown for *P. ferox,* curving gently into the comparatively straight lower margin of the horizontal ramus. The depth of the jaw beneath the tooth row is nearly uniform, though a little shallower beneath the posterior root of P_4 as shown for *P. ferox*. The mental foramina are variable and on the right side two are located one above the other beneath the anterior part of P_2, and two side by side beneath the posterior root of P_3 and the anterior root of P_4. On the left side two slightly larger foramina are located, one beneath P_2 and the other beneath P_3. There is also an irregular display of foramina beneath the incisors close to the anterior margin of the symphysis.

Neither the angle nor the top of the coronoid process are complete on either side of the *P. ulta* mandible, but it is seen that the slope of the anterior margin of the ascending ramus is not so steep as shown for *P. ferox*. The condyle is transversely very elongate and carries the articular surface well forward along the inferior as well as the superior surface. The outer portion of the superior surface extends down on the anterior part of the condyle where articulation occurs with the well-developed process anterior to the glenoid surface of the squamosal, almost locking the lower jaw in place, as in some mustelids. The masseteric fossa would appear to be weakly defined near the lower margin of the jaw but is deeply impressed in the upper portion. The deeper part of the fossa is limited downward by a ridge which extends forward from just below the condyle. The crest bounding the fossa anterodorsally extends downward and forward from the anterior margin of the coronoid process, but disappears upon reaching a position almost below the posterior margin of M_2.

On the medial surface of the jaw it is seen that the symphysis extends posteriorly to a position below about the anterior margin of P_4 and exhibits a deep pit forward near its posterior limit for certain muscles, including the geniohyoid and probably a part of the digastric. The inferior dental foramen is located above the shallow vascular notch in the lower border of the jaw and about opposite the ridge on the outer surface that limits the deeper part of the masseteric fossa ventrally. Posterior and ventral to the inferior dental foramen the medial surface of the jaw is distinctly concave. There is no particular indication of a sulcus mylohyoideus.

Lower dentition.—As noted above, the hyena-like appearance of the teeth (pl. 4) in *Patriofelis* is most noticeable in the lower series, particularly the premolars. The resemblance in the molar series is between nonhomologous carnassials and is upset by the presence of the small M_1 in *Patriofelis*.

The number of lower incisors is clearly two in the University of Utah specimen. The smaller, medial incisor is distinctly posterior to the lateral tooth and rather flattened transversely. The lateral incisor is less procumbent and shows a relatively broad anterior surface. The crowns of both are blunt with wear. The canines have massive roots and are comparatively close together, much crowding the incisors. Their crowns are likewise considerably worn.

P_2 is neither crowded nor oblique as in *P. ferox*. It shows a short diastema between it and the canine, and though small, is relatively broad and two rooted. It carries a minute cuspule anterior to the principal cusp and a low, blunt cusp on the talonid. P_3 is similar but much larger and broader, with a relatively larger and transversely flattened talonid cusp. Like P_4, this tooth shows a distinct backward tilt. P_4 is larger than P_3 and has higher cusps, also the talonid shows a more pronounced crest on its lingual margin. The backward tilt of this tooth is rather pronounced, so that the outer margin of the talonid is much lower than that of the trigonid, or than any of the other teeth. M_1 is small and crowded with a comparatively large paraconid portion, although this part of the tooth is rather obscured by wear. The metaconid is developed as an upward and posterolingually directed spur from the protoconid. The talonid is low, much worn, and almost completely hidden lingually by the anterior root of M_2. M_2, of course, is the shearing tooth and possibly a trifle longer than P_4. It lacks any trace of a talonid. The posterior blade along its cutting edge is longer than the anterior, and projects backward and upward rather strikingly.

In addition to the backward tilt noted for P_3 and P_4, all the cheek teeth, as noted by Matthew (1909), tilt distinctly outward. As with the inward tilt of the upper teeth, this orients the shearing surface of P_3 and P_4, as well as that of the carnassial, nearly vertical. It is noted also that the outer shearing surfaces are dorsoventrally more elongate than the lingual walls. The crown of each tooth has a noticeably greater buccal than lingual height.

MEASUREMENTS IN MILLIMETERS OF SKULL AND MANDIBLE OF
Patriolefis ulta LEIDY, UNIV. UTAH NO. B50

Skull:

Greatest length from anterior margin of premaxillae to two small processes on superior margin of foramen magnum......	248.
Length from anterior margin of nasals to vertical portion of occiput above foramen magnum..........................	227.
Length from anterior margin of premaxilla to posterior wall of glenoid surface medially..................................	178.
Length of palate from anterior margin of premaxilla to anterior margin of posterior narial aperture........................	100.5
Greatest length of nasals....................................	78.0
Distance between lateral margin of anterior narial aperture and anterior margin of orbit....................................	52.5
Greatest width across zygomae..............................	183.
Width across nasals anteriorly..............................	40.
Width between orbits dorsally..............................	76.
Width across postorbital processes of the frontals..............	70.
Width of cranium at constriction............................	38.
Width of palate between canines............................	31.
Width of palate posteriorly, between M^2's at alveoli...........	81

Upper dentition:

Over-all length of dentition from anterior surface of lateral incisor to posterior margin of M^1.........................	105.

Length of cheek tooth series, P^2-M^1, inclusive	68.5
I^2 (at alveolus), anteroposterior diameter: transverse diameter	9.0 : 4.0
I^3 (at alveolus), anteroposterior diameter: transverse diameter	13.0 : 10.0
C (at alveolus), anteroposterior diameter: transverse diameter	23.0 : 16.0
P^2, anteroposterior diameter: transverse diameter posteriorly	11.2 : 8.0
P^3, anteroposterior diameter externally: transverse diameter perpendicular to outer wall	17.8 : 19.0[a]
P^4, anteroposterior diameter externally: transverse diameter perpendicular to outer wall	18.5 : 22.0[a]
M^1, anteroposterior diameter	21.5
M^2, greatest diameter	4.0

Mandible:

Length from anterior margin of symphysis to posterior surface of condyle medially	177.
Length of symphysis	60.
Posterior margin of M_2 (at alveolus) to posterior surface of condyle medially	76.

Lower dentition:

Anterior margin of lateral incisor to posterior margin of M_2 (at alveoli)	103.
Length of cheek tooth series, P_2-M_2 (at alveoli) inclusive	76.
I_2 (at alveolus), anteroposterior diameter: transverse diameter	6.5 : 3.0
I_3 (at alveolus), anteroposterior diameter: transverse diameter	7.8 : 5.0
C (at alveolus), anteroposterior diameter	21.0
P_2, anteroposterior diameter: transverse diameter at talonid	10.5 : 7.2
P_3, anteroposterior diameter: transverse diameter at talonid	13.3 : 9.5[a]
P_4, anteroposterior diameter: transverse diameter at talonid	17.8 : 11.6
M_1, anteroposterior diameter: transverse diameter at trigonid	16.0 : 8.5
M_2, anteroposterior diameter: transverse diameter	18.6 : 10.0

[a] Approximate.

SUMMARY OF RELATIONSHIPS

The position of *Patriofelis* in the Oxyaenidae, as the culminating stage of the Oxyaeninae in North America, seems firmly established, although it should be noted that a later survival of the subfamily is believed represented by the genus *Sarkastodon* (Granger, 1938) in the upper Eocene of Asia. The genus *Oxyaena* is first recognized in the Clark Fork Paleocene and carries through the lower Eocene represented by several species. An intermediate form, *Protopsalis,* here regarded as a subgenus of *Patriofelis,* is known from the Lost Cabin level of Wasatchian time and *Patriofelis* proper characterizes the upper Huerfano as well as both upper and lower levels of Bridger Middle Eocene. The lower Bridger species *Patriofelis ulta* may well be the forerunner of larger *Patriofelis ferox,* and although in turn evidently derived from *Oxyaena* through the *Protopsalis* stage, the known species *P.* (*Protopsalis*) *tigrinus* was clearly not in the direct line of development.

Wortman (1894, 1902, and 1906) was strongly convinced that *Patriofelis* was aquatic or semiaquatic in habit and in or near the line of descent of the pinnipeds. He also advanced the idea that *Patriofelis* may have "preyed on numerous species of turtles that inhabited the Bridger lake." While his reasoning and analysis of the possibilities are thought provoking, as far as the position of the Oxyaenidae with respect to the pinnipeds is concerned, I am unable to agree. Nevertheless, there would seem from Wortman's argument some justification for believing that *Patriofelis* may have been partially aquatic in habit. I am particularly impressed by the over-all otterlike body proportions and the rather otterlike structure of the rostrum of the skull. On the other hand, the teeth are basically so very much like those of a hyena that I greatly suspect a carrion-feeding habit, if this can be reconciled with the foregoing, or, as Wortman has postulated, a diet of fresh-water turtles.

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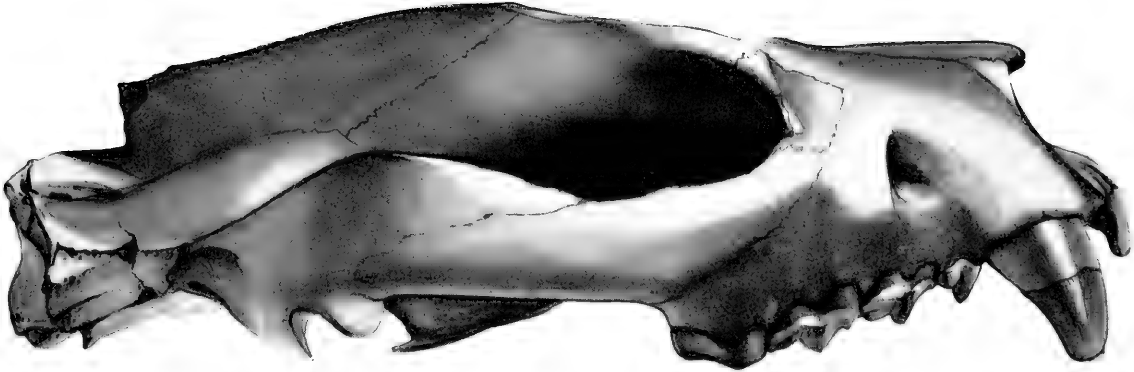
PATRIOFELIS SKULL FROM THE BRIDGER MIDDLE EOCENE

Patriofelis ulta Leidy: Skull (Univ. Utah No. B50), dorsal view. Approximately three-fifths natural size.

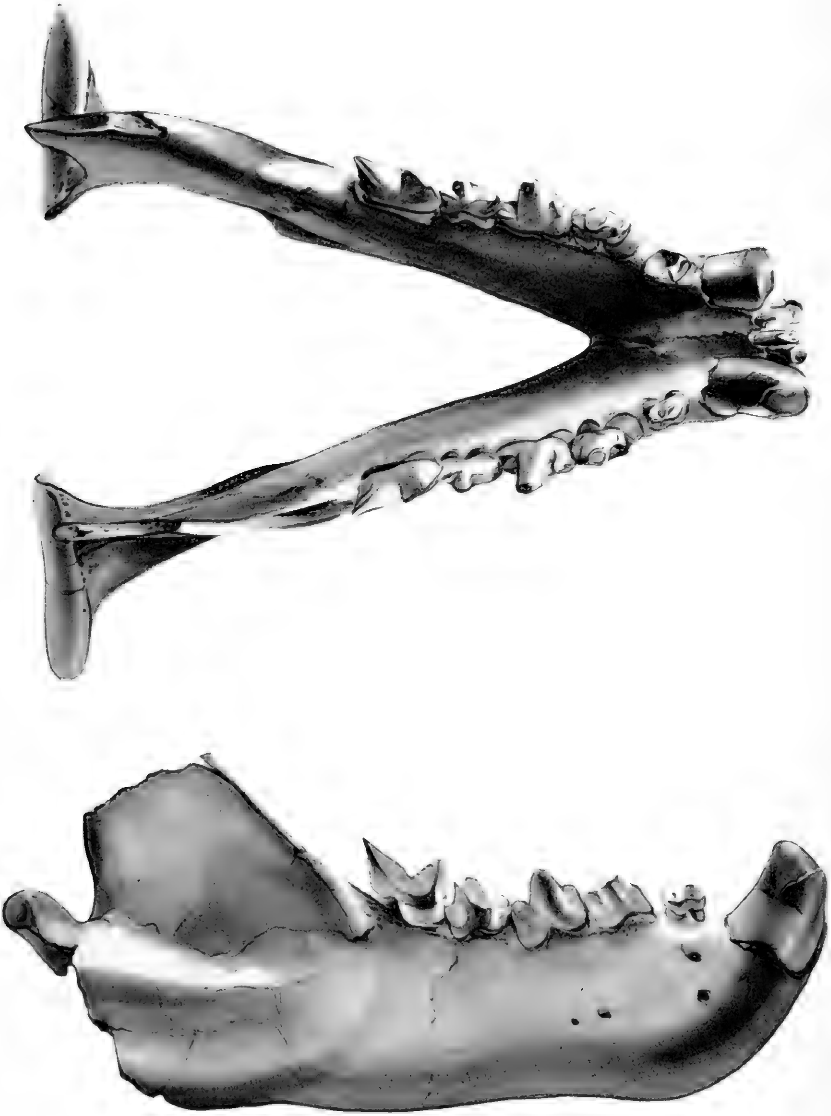


PATRIOFELIS SKULL FROM THE BRIDGER MIDDLE EOCENE

Patriofelis ulta Leidy: Skull (Univ. Utah No. B50), lateral view. Approximately three-fifths natural size.

PATRIOFELIS SKULL FROM THE BRIDGER MIDDLE EOCENE

Patriofelis ulta Leidy: Skull (Univ. Utah No. B50), ventral view. Approximately three-fifths natural size.



PATRIOFELIS MANDIBLE FROM THE BRIDGER MIDDLE EOCENE

Patriofelis ulta Leidy: Mandible (Univ. Utah No. B50), dorsal view (above), lateral view of right ramus (below). Approximately three-fifths natural size.

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THE BIRDS OF ISLA COIBA PANAMÁ

(With Four Plates)

By
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(Publication 4295)

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INTRODUCTION

Isla Coiba, largest island on the Pacific coast of Central America, lies well at sea to the west of the lower end of the Azuero Peninsula, at lat. 7°20′ to 7°40′ N. and long. 81°36′ to 81°54′ W. The island trends northwestward and southeastward, with a length of 21½ miles and a greatest width of 13 miles. It is well watered, with numerous small streams running down from the rough, broken interior, where two separated high points near the center rise to about 1,400 feet above the sea. A lower hill, about 1,150 feet high, stands in the center of the northern end, while the southern end is mainly lower ground. The island bulges to the westward, while on the eastern side there is the large indentation of Bahía Damas, and the smaller one of Ensenada Arenosa. A broad valley, now mainly cleared to form cultivated fields and pastures, lies back of the large bay mentioned. It is drained by the parallel streams of the Río San Juan and Río Catival, which are actually a single river system, separated in their lower ends only by swampy land.

The entire island is covered with heavy virgin forest, except along the lower courses of the larger streams where there are swampy woodlands, succeeded to seaward by stands of mangroves. In the San Juan area these are of considerable extent. Rocky headlands project along the coast, with sand beaches, some of considerable extent, between them, broken by mangroves at the river mouths. The land rises back of the shore rather steeply to elevations of 80 to 250 feet, and then slopes back to the interior ridges, which in many places are steep-sided and much broken.

Near the projecting point on the western side of Boca Grande, at the extreme southern end of Bahía Damas I noted many fragments of coarse-grained sandstone, wave-worn into flattened, lenticular form, piled up on the beach. Elsewhere the numerous exposures along the eastern shore of Coiba and on Isla Ranchería are an altered igneous rock, in places associated with beds of white chert. These three types of rock presumably belong to the pre-Tertiary basement complex of Panamá. At Punta Damas small, roughly circular, iron manganese concretions (perdigones) are extraordinarily abundant on partly eroded surfaces, particularly over the small landing field for airplanes, where, at a casual glance, the appearance of the ground in places was that of a goat corral. There is a small thermal spring, with water the temperature of a very hot bath, at the base of the hill above the swampy woodland on the southern side of the Río San Juan.

Isla Coiba, because of its size and location, was well known in the early days of the Spanish settlement in Panamá. The first white man to visit it was Bartolomé Hurtado, a lieutenant of Gaspar de Espinosa, who came to the island in 1516 during an exploration of the coast to the west of the Azuero Peninsula. Hurtado, and those who followed, found on Coiba Indian inhabitants of powerful physique, speaking a Guaymí dialect. They were armed with heavy spears, set at the tip with shark's teeth, and wore corselets made of cotton thick enough to turn a bullet, but of no avail against Hurtado's cannon. Some gold was obtained from them, which probably aided in their undoing. They were exterminated early, the final remnant being taken as laborers to Darién, probably about 1550. In historic accounts the name of the island is called variously Cabo, Cobaya, Quibo, and Coiba, apparently all variations of the name of the Indian chief in control at the time of the Spanish discovery.

Spanish settlement in Panamá during the latter part of the sixteenth century spread to the west beyond Natá, through the great Province of Veragua, which in that day extended to what is now Costa Rica. The Carmelite friar Vásquez de Espinosa, writing of the Pacific side of Veraguas, apparently from information gathered between 1612 and 1620, speaks of sawmills and shipyards employing 4,000 workmen. He mentions Remedios with about 80 houses, Montijo, and Chiriquí which had 80 Spanish residents. Since transport of products from these western outposts would have been by boat, Coiba must have been seen and visited regularly, but I have found no record of early settlement there. The operations of buccaneers along these coasts in early years may have been a deterrent to permanent residence on islands so remote.

Capt. William Dampier in his travels writes that he came to Coiba on June 15, 1685. He refers to it as the "isle of Quibo or Cobaya" and remarks on the forests, the deer, the monkeys, the iguanas, and the snakes. Among details concerned with fresh-water supply, navigation, and dangers, of interest to mariners, he mentions that the "isle of Quicarra is pretty large" which is an early reference to Isla Jicarón. He makes no reference to human habitation on Coiba, but this must have come soon after, if not already in existence, through the pearl fishery which later was pursued through the annual period of good weather. From June to November, the season of the "vendevales," strong winds blowing from unfavorable quarters were too frequent to make pearl diving profitable or safe.

Capt. George Shelvocke of the British Navy, in his account of his voyage around the world, came to Coiba on January 13, 1720, anchored off the northeast point, and found two or three deserted huts that he supposed were used by pearl fishermen, as there were heaps of pearl shell around them. During his stay two large piraguas landed on adjacent Isla Ranchería (which he calls Quivetta), and he learned from prisoners that he took of another Spanish ship laden with provisions that had passed during the night. Shelvocke came again to Coiba about the first of May 1721, and then gives a considerable description of it, in which he mentions "the great variety of birds, which the woods would not permit us to follow," and the abundance of black monkeys and igaunas.

George Anson, on another British expedition around the World, stopped at Coiba on December 3, 1741. As the expedition included several vessels, and was therefore in strong position, they anchored in Bahía Damas, off the present location of the Colonia Penal, as indicated on the map that Anson made of the eastern side of the island. Anson mentions parrots and parakeets, and especially great flights of macaws. Like his predecessors, he writes of monkeys and deer, which, however, could not be hunted because of dense forest. He discredited reports from prisoners he had taken of "tigres," since he saw no tracks or other sign of them. These same prisoners described in detail a highly dangerous poisonous snake of which they were much in fear. Pearl oysters were reported in greater abundance here than anywhere else in Panamá. Anson was impressed by the great number of turtles, and includes an account of the pearl fishery, and of the divers who obtain the shells. Only a few unoccupied huts were found.

Coconut plantations were established in due time, but there seems never to have been any extensive settlement on Coiba. At the opening of the present century, the pearl fishery was in operation, with a store, cantina, and other buildings located, in part at least, near Punta Observatorio in the southern section of the bay, the site of the present convict camp at María. Other fishing went on also, but all this activity lessened with the depletion of the shell beds. Private holdings finally were acquired by the Government of Panamá, and the island was set aside as the penal colony of the country. A plaque on the main guardhouse and cellblock at the headquarters records that this was done by President Porras in November 1919. The location of the headquarters, known as the Central, is below the base of Punta Damas in the northern rim of Bahía Damas. The seven outlying work camps are spread along the eastern side of the island from Aguja at the north end, opposite Isla Ranchería, to Playa Blanca at the southern end, a short distance west of Boca Grande. Only two, Catival and San Juan, located on the rivers of the same name, are inland. Extensive clearings for pasture and the planting of food crops have been made adjacent to these camps, the largest of these, embracing many hundred acres, extending from Punta Damas south to the Río San Juan, and inland over the broad valley of that section. The cleared areas in general rise from the beaches back to the crest of the slopes of low hills, so that most of their area is visible from the sea, except for the interior of the San Juan Valley. Behind these there has been some logging for timber, but the great interior forests have not been touched.

Trails, mainly near the shore, for travel on foot or by horse, connect the outlying camps with the Central, and pass back through the broad San Juan Valley. There is also one across to the opposite side of the island from María and Playa Blanca, traversing the lower elevation at the southern end of the island. During World War II radar detectors were installed on a 1,400-foot hill back of the San Juan Valley, with a camp located near Playa Hermosa. The tower was still visible at the time of my visit but the camp had been long abandoned.

The impressive vegetative cover of Coiba is not appreciated until it is penetrated. I found an extensive stand of red mangroves at the mouths of the Catival and San Juan Rivers, and lesser tracts elsewhere. Behind these, at the rivers mentioned, there was swampy woodland, one of the common interesting trees being the alcornoque (*Dimorphandra megistosperma*) whose huge flattened, beanlike seeds measure up to 180 mm. in length. Near Playa Blanca I noted considerable numbers of manchineel growing in low, open groves along the beach. Plantings of coconut palms are extensive.

Inland from the clearings the forest is unbroken, the great trees rising to such heights that loads for my shotgun, suitable for the largest birds, failed to reach hawks and pigeons in the higher branches. Only on the upper Río Jaque in eastern Darién have I seen similar stands of trees. Below the high crown were the tops of lower trees, a stratum of branches and then undergrowth, usually fairly open and easy of penetration. Through this there are scattered thickets of bamboo that are too dense for passage except by cutting trail with a machete.

On days of sunshine the masses of leaves and vines stood out clearly in silhouette in the high summits of the trees, with small birds moving actively through them. Below, the forest floor was dark and shadowed, so dimly lighted in many places that clear vision was difficult. On occasional cloudy days many areas in the heavy forest were too obscure for successful hunting.

Isla Ranchería, distant 2 miles from the northern end of Coiba, about 1¾ miles long by a mile wide, of irregular shape, rises to an elevation of nearly 500 feet. I visited this on one occasion, landing on a sandy beach midway of the southern side. A wooded swamp lay behind, and above this were fairly steep, well-forested slopes, but with trees of lesser height than those on Coiba. Many seemed stunted by the thin soil overlying the mass of altered igneous rock that is the core of the island. Ranchería long has been private property, and at one time considerable activity is reported in pearl and other fisheries. Of the store, the houses, and the clearings in which they stood there is now no evident trace, except for coconut palms and a lemon tree back of the beach, and a scattered growth of succulent bryophyllum, grown commonly as a decorative plant in gardens.

This island is known universally in Panamá as Isla Coibita, a name that is applied on current charts and maps to an outlier in the groups of islets known as the Aaron Rocks, a mile to the northwest of the western point of Ranchería. Shelvocke, in 1720, called the island Quivetta, and Anson, in 1741, varied this to Quiveta, both these names being diminutives of Quibo, the name these travelers applied to the large island. Dampier, in 1685, used the name Ranchería, which is the one cited for records in the following report since the island is so called on current charts and maps.

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For permission to visit Isla Coiba I have to thank Coronel Bolívar Vallarino, Comandante Jefe de la Guardia Nacional, who issued the necessary instructions. It was his assistance and personal attention that assured the success of the undertaking. Throughout my detailed studies of the ornithology of the Republic of Panamá I have had the friendly cooperation of Dr. Alejandro Méndez Pereira, Director of

the Museo Nacional in Panamá, who in the present instance rendered major assistance in communicating my plans to Sr. Don Alejandro Remón C., Ministro de Gobierno y Justicia, in introducing me personally to Coronel Vallarino, and in numerous other ways. Dr. Pedro Galindo, of the Gorgas Memorial Laboratory in Panamá, also assisted in my plans with friendly courtesy. For transportation to and from the island I am deeply indebted to officers of the U. S. Air Force at Albrook Air Base, Canal Zone, particularly in this instance to Col. J. W. Oberdorf, Commanding Officer, and Lt. Col. D. L. Peck and Lt. Col. R. T. Lively of his staff. On my arrival at Isla Coiba I was met by Capitán Juan A. Souza, Director de la Colonia Penal, who received me in most friendly manner, and did all that was necessary to insure the success of my work, as did his assistant, Teniente Valenzuela, and other officers and members of his staff.

In making my arrangements, I was much indebted to Capt. Gordon Field, and Marvin Keenan of the 25th Medical Detachment, U. S. Army, for friendly help in numerous details concerned with preparations for the work.

I have to thank also Duncan Alexander Duff Mackay, Second Secretary, and Mr. R. A. Acley, Counselor, at the American Embassy in Panamá, for courteous assistance relative to papers for the Coiba trip, as well as for the arrangement with the Ministerio de Relaciones Exteriores of Panamá, under which my scientific work has been done. The expedition has been one of the most successful in scientific result that I have made.

ORNITHOLOGICAL STUDIES

The first birds collected for scientific purposes on Isla Coiba of which I have record were obtained by the taxidermist and preparator J. H. Batty, who was on the island from April to June 1901. Following this work Batty proceeded to the Province of Chiriquí, where he located for some time at Boquerón, and seems also to have worked for a brief period at Boquete. His final collections, dated January and February 1902, before his return to Panamá, contain specimens labeled from Insolita, Gobernadora, Sevilla, Brava, and Cebaco islands, with a scattering of other island localities along the Pacific coast of Panamá. A specimen of *Buteo magnirostris,* dated February 5, 1902, from Iguana Island, north of Punta Mala, must have been obtained during his return journey to Panamá. The itinerary outlined is not complete, the only data available being the labels on his specimens. Part of this collection, sold to the Tring

1. Headquarters of the Colonia Penal, Isla Coiba.

2. Hauling a seine in Bahía Damas; Punta Damas in background.

1. Pastures at the Juncal work camp; Isla Canal de Afuera in the background.

2. Southern shore of Isla Rancheria.

Museum, was shipped from the field, probably on the collector's arrival in Chiriquí, since Rothschild described the wood pigeon, and Hartert a hummingbird and the pepper-shrike of Coiba, in the Bulletin of the British Ornithologists' Club for December 30, 1901. At the close of the Panamanian work sets of the skins were purchased by the American Museum of Natural History, where they were cataloged in July 1902. The Chicago National History Museum also has a small lot of specimens from this collection, presented by Batty, and entered on the Museum records on January 4, 1906. The remainder came to the American Museum, apparently as a gift from the collector, where they were cataloged in March 1910, nearly four years after Batty's accidental death in Chiapas, on May 26, 1906. A few of the skins have gone in exchange to other institutions, but with the accession of the Rothschild collection, the American Museum of Natural History now houses the greater part of this material. The Coiba material has been mentioned from time to time by Griscom, Hellmayr, and Zimmer in various studies, and Eugene Eisenmann in 1950 described the white-throated robin from the island as a distinct subspecies.

In my work on Panamanian birds over a period of years I have examined Batty's specimens from Coiba from time to time and have been puzzled occasionally by discrepancies apparent in dates and other details. These could not be explained until I began the identification of my own collection. As this work has progressed, it has become clearly evident that some of the field labels for Batty's skins must have been made later, after the work was completed, and that there was a certain amount of mixing through which a number were marked with the wrong localities. This I have been able to determine because of the considerable differences that exist between various of the mainland birds and their representatives on Coiba. For example, in the series of the woodpecker *Centurus rubricapillus,* there are six specimens marked "Coiba" of which five are obviously the peculiar subspecies found on the island, and one as obviously represents the mainland race. Among the skins of the wood pigeon *Leptotila plumbeiceps battyi,* restricted to Coiba, there is one immature bird of the distinct species *Leptotila v. verreauxi* also labeled "Coiba," an obvious error as only *L. p. battyi* occurs on the island. Similar mixing is evident in the crimson-backed tanager, where 20 skins labeled "Coiba" in major part represent *Ramphocelus dimidiatus pallidirostris* of Chiriquí, and only a few the Coiba subspecies.

The pepper-shrike of Coiba, described by Hartert, is a very distinct form, with clearly marked characters. The Batty collection, in addition to the type series from Coiba, contains one skin labeled "Hicaron" (intended for Isla Jicarón) which is a typical example of *Cyclarhis gujanensis subflavescens* of the hill country of the mainland. Isla Jicarón, a small island, lies immediately south of Coiba, with its larger neighbor between it and the distant isthmian shore. It would be most remarkable to have the mainland race on Jicarón, and a completely different one on Coiba. Batty's "Coiba" specimens also include a juvenal sparrow of the species *Zonotrichia capensis,* which is resident in Panamá only in the mountains from Chiriquí eastward, mainly above 3,000 feet elevation, occasionally somewhat lower, but never in Panamá near sea level.

It is undoubtedly this mixing of localities in the Batty material, aided by the fact that the collection runs largely to the more easily found and conspicuous species, that has caused the considerable degree of endemism in the resident birds to be overlooked by the careful systematists who have handled the skins.

Among the few other naturalists who have visited the island, a party of British scientists traveling on the yacht *St. George* came to Bahía Damas on the afternoon of August 31, 1924, and remained for five days to make shore collections. Lt. Col. H. J. Kelsall, the ornithologist, with his assistant Cullingford, obtained a small lot of birds which are now in the British Museum (Natural History). Collecting was confined to the vicinity of the headquarters of the Penal Colony, with one trip by cayuco along mangroves and past a low bluff to a small stream, where Kelsall shot a few birds.[1] Apparently this was near Bajo España at the mouth of the Río Catival. No published report was made on the specimens obtained, which include a few of the forms peculiar to the island. Dr. Alejandro Méndez, Director of the Museo Nacional of Panamá, visited Coiba in 1932, when he made observations in various branches of natural history, including the birds.

The only other ornithologist known to me to have visited Coiba is William Beebe, who was there for a day while on Templeton Crocker's yacht *Zaca* in 1938. On March 19 the ship crossed from Bahía Honda, on the coast of Veraguas, to Ensenada Hermosa, a bay on the western side of Isla Coiba. The following night while they were collecting with lights on Banco Hannibal to the west a

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[1] For accounts of this expedition see Douglas, A. J. A., and Johnson, P. H., The South Seas today, being an account of the cruise of the yacht *St. George* to the South Pacific, London, 1926, pp. 73-81; and Collenette, C. L., Sea-girt jungles, the experiences of a naturalist with the "St. George" Expedition, London, no date [1926], pp. 186-195.

storm petrel came on board.[2] This was the only bird specimen recorded.

My own studies of the birds of Coiba extended from January 6 to February 6, 1956. I had with me two assistants, Armaguedón Hartmann of Chiriquí, who had been my helper for the two previous field seasons in Panamá, and Vicente Álvarez, technician of the Malaria Control Force of the U.S. Army, assigned for special work by Capt. Gordon Field, 25th Medical Detachment (Preventive Medicine Survey), and Marvin Keenan, Chief, Mosquito Control Force, attached to the Survey mentioned. Through the friendly interest of Col. J. W. Oberdorf, Commanding Officer at Albrook Air Base, transportation was provided on an Air Force crash boat, which made a journey that otherwise would have been difficult, not only rapid, but comfortable. Our field equipment and supplies were delivered and stowed on board on the afternoon of January 5, under the direction of Chief Warrant Officer Claude H. Drake, Commanding Officer, Crash Boat Detachment, who commanded the boat on the following day. We left the crash boat base at Fort Rodman, C.Z., at 3:50 a.m., January 6, passed out of the Canal, and at 8:30 a.m. were abreast of Cape Mala. At 1:30 p.m. we dropped anchor in Bahía Damas, Isla Coiba, off the Penal Colony Headquarters, after a pleasant and interesting journey of 220 miles.

Capitán Juan A. Souza, Director de la Colonial Penal de Coiba, came off to greet me, and we were soon ashore and established in two rooms in a new hospital building. The captain assigned a trusty as our cook, regularly supplied us with fresh meat, vegetables, oranges, and plátanos, and assisted us throughout the work effectively and courteously.

During the following month I was out in the field daily, having boat transportation whenever needed by cayuco driven by an outboard motor, handled competently by a convict skilled in such craft. On foot and by boat I was thus able to cover the entire shoreline of Bahía Damas, from Punta Fea at the entrance of Boca Grande, beyond the southernmost convict work camp at Playa Blanca, to Punta Damas on the north. Farther north we worked along the Ensenada Arenosa to the work camp at Juncal. On February 4 I went by cayuco to Isla Ranchería off the northeastern end of Coiba, a journey I had attempted on an earlier day, but had been driven back by suddenly rising seas. In addition we opened a hunting trail

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[2] See Beebe, Zoologica, vol. 28, 1932, pp. 297-298; Book of Bays, 1942, pp. 280, 297.

through the forest from the end of the paths back of the Colonia Central inland for a distance of 5 miles, and to an elevation of about 700 feet, along the slowly rising ridges leading to a high point in the center of the northern end of the island. The mangroves at the mouths of the Río Catival and the Río San Juan, and the swampy woodland bordering them, were productive, as was the low second growth (known locally as rastrojo) in areas of abandoned fields.

The only bird reported that I did not actually see and identify was a hawk, an example of which had been killed the week before my arrival. The partly decomposed feet, preserved as curiosities, shown to me by Capitán Souza, had the tarsi completely feathered. Because of their condition I was not able to identify them certainly, but I believed at the time that they came from a species of *Spizaëtus*.

Heavy rain had fallen the night before our arrival, but the weather then remained clear and pleasant until January 14. Clouds began to gather, and two days later there was a heavy shower before dawn, with mist the following morning. On January 25 there came a heavy downpour before sunrise, and rains continued at intervals until our departure. This, however, did not interfere with our fieldwork. Daily Fahrenheit temperatures for the first eight days ranged from 70° to 72° at dawn to 82° to 85° at midday, with the trade wind tempering the heat. With the return of the rains this changed to 74° to 76° at dawn, and 84° to 89° at midday, with uncertain breezes and high humidity.

There was constant talk among the convicts of the dangers attendant on entering the forests because of the great abundance of poisonous snakes, a belief that was so prevalent even in Panamá that a trip to Coiba was discussed as a definitely perilous adventure. It was my experience, however, and that of my two assistants, all of us accustomed to jungle work, that the snake population appeared to be the same as that of similar woodland throughout the Pacific slope of the mainland. We practised the usual precautions in working through areas suitable for snakes, particularly when hunting at night, and actually saw few since they tend to keep hidden, and to move aside when they have warning. Laborers engaged in clearing land are in a different situation, since the removal of cover destroys the usual hiding places, and danger from snakebite is inevitable. Several men have died from this cause on the island, one not long after our departure.

My last trip in the field came on February 4, and the day following was devoted to packing, in readiness for departure. At 5:00 p.m. as this work was finished word came that the crash boat was in sight, and soon it was at anchor. Since the tide was full, we went on board that evening in readiness for an early start. At 5:20 a.m. on February 6 we were underway, and I watched the lights of the Colonia Penal and the dark shoreline at either side recede, well satisfied with the results of my work, and with many pleasant thoughts of the friendly assistance that I had received at the hands of Capitán Souza and his staff of guards. We were delayed somewhat by headwinds after rounding Cape Mala, but were at the dock at Fort Rodman at 3:50 p.m. The entire expedition is one that remains most pleasantly in memory.

THE BIRD LIFE

The annotated list that follows these introductory paragraphs covers 133 species and subspecies of birds that are recorded from Isla Coiba, with remarks on 4 additional (a skua, a gull, and 2 terns) noted in the Gulf of Panamá en route to and from the island. Of the total as given, 36 are migrants, one, the small Galápagos storm petrel, coming from Peruvian waters to the south, another, a subspecies of the yellow-green vireo (*Vireo flavoviridis hypoleucus*), found en route from winter quarters in South America to nesting grounds in northwestern México, and the remainder kinds that nest in the United States and Canada, present for the period of the northern winter. Plovers, sandpipers, and related shorebirds, 10 species in all, were the most common, with scattered individuals of 6 wood warblers and the summer tanager standing next in abundance.

Kinds that are resident in Panamá as a whole number 97, a few of these like the black jaçana, the white-collared swift, and the fork-tailed flycatcher, being merely wanderers from the mainland. Among the resident kinds the amount of endemism that is found is quite remarkable, in part for the number of species concerned, and in part for the fact that its extent has gone unnoted for so long. Four well-marked subspecies had been described from Batty's collections prior to my visit—the wood pigeon by Rothschild, the Cuvier's hummingbird and pepper-shrike by Hartert, and the white-throated robin by Eisenmann. These four I recognized easily, and in addition, from my first day afield I observed differences among a number of others, sometimes on my first view of the bird in life, sometimes after specimens were in hand, even though no comparative material was available.

In the following report I have described 16 races that are new to science, in addition to the 4 mentioned, several of them so well marked that they are treated as geographic races only under present-day concepts, since 20 years ago they would have been considered distinct species. There are also several others that undoubtedly will be named later when further specimens corroborate differences now discernible in the few examples at hand. Thus of the 97 kinds among the tropical residents of the island more than 20 percent are distinct subspecies. Among these the most surprising is the race of the rusty spinetail (*Cranioleuca vulpina*), a species of South America not previously found north of the valley of the Orinoco River in southern Venezuela and southeastern Colombia. It represents an avian element previously unknown in the avifauna of Central America.

The differences that mark the resident races are mainly heavier, darker pigmentation, which may be explained in terms of more abundant rainfall, indicated by the considerable drainage system seen in the numerous rivers of the island. There is also a tendency in some to large bills, which is not unusual in isolated islands.

The great forests that clothe Isla Coiba, still practically unbroken except for a relatively small area, offer habitat suitable for any of the birds that exist in such abundance as to kinds and individuals in the vast lowland area between southern México and northern Argentina. When we note those that are lacking in the island environment, we find a matter for astonishment equal to that experienced with the amount of endemism among the kinds that do occur. The following list of families of birds of regular occurrence on the nearby mainland but not found on Coiba is noteworthy:

Tinamous (Tinamidae)
Curassows and guans (Cracidae)
Trogons (Trogonidae)
Motmots (Momotidae)
Jacamars (Galbulidae)
Puffbirds (Bucconidae)
Toucans (Ramphastidae)
Woodhewers (Dendrocolaptidae)

In addition to these eight prominent families, there is no record of the wood-quails (*Odontophorus*), the long-tailed squirrel cuckoo (*Piaya cayana*), or the large forest woodpeckers (*Dryocopus* and *Phloeoceastes*). Ovenbirds (*Furnariidae*), except the rusty spinetail (*Cranioleuca vulpina*), are missing, as are antbirds, except the barred antshrike (*Thamnophilus doliatus*), manakins, except the lance-tailed manakin (*Chiroxiphia lanceolata*), many common genera of forest-loving tyrant flycatchers, wrens, except the house wren, and resident orioles and blackbirds, except the boat-tailed grackle. The common jay of the mainland (*Cyanocorax affinis*) does not occur, and there are none of the true forest tanagers (*Tangara*) so abundant as to kinds, or of the widespread euphonias.

The northern end of Isla Coiba is separated from Punta Jabalí, marking the southern side of the entrance to Bahía Honda, the nearest point on the mainland of Veraguas, by a little more than 15 miles. From the southern end of the island to Punta Brava, at the western side of the Golfo de Montijo, the distance is about 32 miles. The depths separating the island from the mainland range from 240 to 330 feet. Coiba is seen thus to be fairly remote in miles, and also to be cut off by a fair depth of water. Current geological theory is to the effect that the present Isthmus of Panamá was considerably wider in earlier times than at present. If earth movement during the subsidence that has molded the present outline of the land proceeded in a fairly regular and evenly distributed manner, then Coiba may have been separated early in the history of the Isthmus. If the separation came sufficiently early, it may have been established before the growth of forests to provide suitable ecological habitat for the spread of true woodland inhabitants. Or, the formation of the island may have come before the missing groups of birds had begun their movement between the northern and southern continents. The third obvious explanation would be that Coiba at no time was connected with the mainland.

While birds are readily mobile because of their powers of flight, it is an accepted fact that, although many are venturesome, there are many others that avoid crossing wide expanses of water. The avian colonists of Coiba in the main appear to be either those that are known to make extensive flights, or others—for example, the flycatchers—that may be assumed to have been blown across from the mainland by violent winds of tornado force.

These are purely speculative hypotheses, but it seems difficult except in some such fashion to explain the condition as it actually exists.

ANNOTATED LIST

Details of occurrence and other information concerned with the kinds of birds at present known from Isla Coiba are given, species by species, in the pages that follow, with descriptions of the forms that are new to science. With each form there is included the scientific name with its reference, and a common name in English and in Spanish. These common names in the two languages are intended to be used for the species as a whole, regardless of geographic race, and thus cover all of the subspecies of the particular kind of bird concerned. In numerous cases the scientific name is that of a subspecies, but this does not in any way indicate that the common names that follow cover that species alone. They are not so intended. The English names, with a few exceptions follow those given in the recent useful and important paper by Dr. Eugene Eisenmann entitled "The Species of Middle American Birds".[3]

Selection of the Spanish names has been made with care, and in some cases after considerable thought. Some conspicuous birds are well known, so that their Spanish names are matters of common knowledge. Where several terms are in local use for the same bird, choice has been made of the one that seems most general, in some cases extending beyond Panamá to other countries in Central America or the West Indies, for example, alcatraz, rather than cuáco, for the brown pelican. The list of names given by Señor Alberto Frederico Alba in his book "Algunas Aves de Panama," published in 1946, in a number of cases has been helpful. In numerous instances with small, inconspicuous kinds, where no local name is available, one that seems properly applicable has been selected, sometimes from usage in other countries, sometimes from a descriptive term that seems appropriate, and sometimes by a translation of the name in English. In some instances the name in Panamá refers to quite a different bird elsewhere, as ruiseñor for the house wren, but this term is so universal in the country that it would be wholly inappropriate to attempt to change it.

The black-and-white illustrations drawn by Walter Weber are from a series intended for a volume on the birds of the Republic of Panamá, for which I have been gathering data for several years. They are intended to represent the species depicted as a whole, and not any particular subspecies from Coiba or elsewhere.

Mention is made above, in the account of my fieldwork, of the crested hawk (apparently a *Spizaëtus*), of which I saw only the feet, killed by a hunter. There is also a specimen in the Batty collections that should be recorded, a skin of Gould's manakin (*Manacus vitellinus vitellinus*) labeled "Coiba, J. H. Batty, Jun. 23, 1901 ♀." This manakin, widely distributed in Panamá from the lower mountains of Veraguas east to Darién, is a conspicuous bird, and one readily found, of which I encountered no trace on Coiba during the month in which I was daily afield. Possibly it may occur, but I feel there is only a slight probability that it does. The "make" of this specimen

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[3] Published in Trans. Linn. Soc. New York, vol. 7, Apr. 1955, pp. i-iv, 1-128.

appears somewhat different from Batty's usual preparation so that he may have obtained it from some other source, perhaps from the collector Enrique Arcé, with whom Batty must have had contact.

The forests of the western side of Coiba have still to be examined for their birds. There is a possibility that there may be further resident species in that area.

Family Podicipedidae: Grebes

PODICEPS DOMINICUS BRACHYPTERUS (Chapman): Least Grebe, Tigua

Colymbus dominicus brachypterus Chapman, Bull. Amer. Mus. Nat. Hist., vol. 12, Dec. 23, 1899, p. 256. (Lomita Ranch, lower Rio Grande, Tex.)

On January 13 a prisoner brought me a live young least grebe that he had captured on a small lagoon beyond Catival. The following day we visited this locality and found several of these birds floating about on a small pond in which there was considerable aquatic growth. Adept at concealment, they dived and disappeared, but by careful watching we were able to get an occasional glimpse of one under the cover of the taller water plants.

I have realized for several years that these grebes fly about a good deal from one body of water to another, probably at night, but this occurrence on Coiba was a definite surprise. It is probable that the lagoon in which they lived would be dry before the end of the summer season so that they might be under necessity of crossing to the mainland. We secured an adult female, one young fully grown but with the throat and lines on the side of the head white, and another half grown. The adult, in full breeding plumage, agrees in color and size with birds from Central America and México. Its measurements are as follows: Wing 90.0, culmen from base 22.7, tarsus 33.8 mm.

Countrymen in Panamá usually call any species of grebe a patico.

Family Hydrobatidae: Storm Petrels

OCEANODROMA TETHYS KELSALLI (Lowe): Galápagos Petrel, Golondrina de Mar Galapagueña

Thallassidroma tethys kelsalli Lowe, Bull. Brit. Orn. Club, vol. 46, Nov. 4, 1925, p. 6. (Pescadores Islands, off Ancón, Perú.)

William Beebe informs me that he secured one of these petrels that came on board ship at night on March 20, 1938, while on Banco Hannibal, west of Coiba. The bird was attracted by lights that he was using to lure and collect marine life.[4] There are three specimens

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[4] See Beebe, Book of Bays, 1942, pp. 280, 297.

of this petrel in the British Museum (Natural History) taken in Panamanian waters out from Balboa August 22, and 20 miles south of Panamá, September 9, 1924, by Lt. Col. H. J. Kelsall in whose honor this race is named.

Family PELECANIDAE: Pelicans

PELECANUS OCCIDENTALIS CAROLINENSIS Gmelin: Brown Pelican, Alcatraz

Pelecanus carolinensis GMELIN, Systema naturae, vol. 1, pt. 2, 1789, p. 571. (Charleston Harbor, S. C.)

Brown pelicans were to be found daily over Bahía Damas, shifting about to some degree, so that the number present varied. Those observed were mainly immature, or adults with the white necks that mark the postbreeding stage, though occasionally individuals in full breeding dress were seen. No nesting colonies were recorded, though undoubtedly their rookeries were not far distant. When the tide was high they cruised about as usual in line, diving whenever fish were sighted. At low water groups of the great birds rested in the mangroves and on rock exposures on the beach. I saw one fishing after dark on one occasion, sighting it as it passed the electric lights at the Colonia Central.

Two adults were prepared for specimens, a male with white neck, and a breeding female with the larger ovaries developed to a diameter of half an inch. Measurements are as follows: Male, wing 518, tail 136, culmen from base 327, tarsus 79.4 mm.; female, wing 507, tail 131, culmen from base 290.0, tarsus 74.7 mm. In coloration these two agree with birds from Taboga Island in the northern sector of the Gulf of Panamá. The brown of the hindneck in the female is very dark, like that of Taboga birds, being darker than the average in pelicans of the southeastern United States. The Coiba birds however are within the limits of variation of the race *carolinensis,* and are identified as that subspecies. I watched particularly for individuals with exceptionally long bills but saw none that could represent the large-billed subspecies *californicus* of the coasts of California and northwestern México.

The usual name for the alcatraz in these waters is cuáco.

Family SULIDAE: Boobies

SULA LEUCOGASTER ETESIACA Thayer and Bangs: Brown Booby, Piquero Moreno

Sula etesiaca THAYER and BANGS, Bull. Mus. Comp. Zoöl., vol. 46, June 1905, p. 92. (Gorgona Island, Colombia.)

Single birds or couples cruised regularly over the sea, sometimes near the shore but more often half a mile or more from land. Usually they coursed with set wings in the stiff breeze, low over the water, rising at intervals to 30 or 40 feet in the air. It was usual to have them approach our cayuco when we crossed the bays, but then to veer away to continue their fishing. All those observed were in adult plumage.

They were noted commonly over the sea between Taboga Island and Punta Mala during the journeys to and from Coiba. Fishermen and boatmen in these waters usually called this bird piquero, a name that applies properly to another species of the family, *Sula variegata,* which is one of the important species of the guano islands of Perú. They are also known as bobito.

Family PHALACROCORACIDAE: Cormorants

PHALACROCORAX OLIVACEUS OLIVACEUS (Humboldt): Olivaceous Cormorant, Pato Cuervo

Pelecanus olivaceus HUMBOLDT, *in* Humboldt and Bonpland, Recueil d'observations zoologie et d'anatomie comparée, vol. 1, livr. 1, 1805, p. 6. (El Banco, Magdalena River, Colombia.)

Birds, mainly in immature dress, were present daily along the shores of Bahía Damas, where they fished in little groups in the shallows bordering the beach when the tide was full, or joined the pelicans farther out when schools of fish appeared. Otherwise they rested on the rock exposures near the waterline. Few adult birds were recorded.

When Dr. Charles W. Richmond established the scientific name of this bird, he was under the impression that the citation above was a later print of the work concerned, and that the description of this cormorant was to be listed from the same title with the same year, but on page 47 instead of on page 6. In this he was in error as the listing given is the original that immediately seems to have been included, with a few modifications, in the great series of 24 volumes covering the voyage and observations of Humboldt and Bonpland.

Family FREGATIDAE: Frigate-birds

FREGATA MAGNIFICENS Mathews: Magnificent Frigate-bird, Tijereta de Mar

Fregata minor magnificens MATHEWS, Austr. Avian Rec., vol. 2, Dec. 19, 1914, p. 120. (Barrington Island, Galápagos Islands.)

Frigate-birds were noted regularly, but usually only one or two per day. On February 4 I saw one at Isla Ranchería, and on the journey to Coiba and return I observed them in numbers off Punta Mala. On one occasion I watched for several minutes as one pursued an agile royal tern over Bahía Damas, without making the smaller bird disgorge.

Family ARDEIDAE: Herons

ARDEA HERODIAS Linnaeus: Great Blue Heron, Garzón Cenizo

Ardea Herodias LINNAEUS, Systema naturae, ed. 10, vol. 1, 1758, p. 143. (Hudson Bay.)

These large herons were seen feeding or flying along the beach near the Headquarters, or in a wet meadow inland, on four occasions between January 11 and February 3. All were wary and remained in the open where they had a clear view for some distance around. From their rather casual occurrence it appeared that they had reached Coiba by chance while in flight along the mainland coast. I watched three for some time and observed that they were decidedly dark-colored, indicating that they were probably of the typical race *Ardea herodias herodias,* which is the one to be expected.

CASMERODIUS ALBUS EGRETTA (Gmelin): Common Egret, Garza Blanca

Ardea Egretta GMELIN, Systema naturae, vol. 1, pt. 2, 1789, p. 629. (Cayenne.)

These large egrets were seen regularly along the beach or occasionally in wet meadows inland. Larger size and yellow bill distinguish them from the other white herons. This species is called garza real, also.

LEUCOPHOYX THULA (Molina): Snowy Egret, Garceta Blanca

Ardea Thula MOLINA, Saggio sulla storia naturale del Chili, 1782, p. 235. (Chile.)

This egret was recorded in the small flocks of white herons that were common along the beaches, being marked by its black legs, yellow feet, and black bill. On January 30 I identified a dozen.

FLORIDA CAERULEA (Linnaeus): Little Blue Heron, Garceta Azul (adults), Garceta Blanca (immature birds)

Ardea caerulea LINNAEUS, Systema naturae, ed. 10, vol. 1, 1758, p. 143. (South Carolina.)

The immature birds in white plumage, with dark gray-green legs and bills, were common along the beaches of Bahía Damas, where they often gathered in little flocks. When small fishes came into the shallows with the incoming tide the herons often became quite active, dancing about gracefully in pursuit of this food. Occasionally I noted a bird in slate-blue adult dress, rarely one pied variously in slate and white, but most were immature individuals in white plumage. About January 20 there was a considerable increase in their numbers, and they remained in this greater abundance until the close of my stay. January 27 I recorded 50 congregated on the flats near Hato, with others scattered along the water beyond.

BUTORIDES VIRESCENS MACULATUS (Boddaert): Green Heron, Martinete

Cancroma maculata BODDAERT, Table des planches enluminéez, 1783, p. 84. (Martinique.)

January 20 I shot a female in the mangroves at the mouth of Río Catival, the only one recorded on Coiba. The bird is adult as shown by the pointed wing coverts and their buffy edgings, and has the wing in partial molt. The next to the outermost primary, somewhat worn at the tip, is still in place in each wing, allowing a fairly accurate wing measurement of 166 mm. The brown on the side of the neck is quite dark, which, in conjunction with the short wing, places it in the subspecies *maculatus,* it being too small for migrant *virescens* of the north. The fact that the color of the under surface of the body is pale like that of mainland birds suggests that it may be a wanderer from some point on the Isthmus. It would be expected that a resident population on Coiba, if there is one, would have darkened coloration, on the order of that found in the subspecies *Butorides v. margaritophilus* of the Pearl Islands in the Gulf of Panamá.

NYCTANASSA VIOLACEA CALIGINIS Wetmore: Yellow-crowned Night Heron, Garzota de Corona Amarilla

Nyctanassa violacea caliginis WETMORE, Proc. Biol. Soc. Washington, vol. 59, Mar. 11, 1946, p. 49. (San José Island, Archipiélago de las Perlas, Panamá.)

Near the mouth of the Río Catival we obtained an adult male January 27, and saw several others. Apparently they are not common here, though it was difficult to judge their number accurately because of the difficulty in penetrating the extensive mangrove swamps.

The bird taken is typical of the resident race of Panamá, being dark in color, with a heavy bill that measures 22.8 mm. in depth through the nostril. Another common name for this species is yaboa coronada.

HETEROCNUS MEXICANUS (Swainson): Bare-throated Tiger Bittern, Jorrálico

Tigrisoma mexicanus SWAINSON, *in* Murray, Encyclopedia of geography, July 1834, p. 1383. (México.)

This curious heron, now rare in many parts of mainland Panamá, was fairly common on Coiba where it lived in the mangrove swamps. Morning and evening these birds came out on the open flats or on areas of mud left by the receding tide, sometimes far from any cover. It was possible to approach them without much precaution, and undoubtedly it is this lack of wariness that has destroyed them in more settled areas, since they are easy marks for a gun, or, for that matter, for a well-aimed stone. They move quietly in feeding, often remaining motionless for long periods. Crabs seemed to be a principal source of their food.

On January 21 as my cayuco, driven by an outboard motor, entered the mouth of the Río San Juan, I saw four, evidently two pairs, engaged in a display in which they swelled out the breast and neck, showing a prominent orange streak down the sides. At the same time the bill, with the long neck fully extended, was pointed directly upward. As their legs are short they presented a most unusual, almost grotesque appearance.

An adult female taken January 14 has a wing measurement of 350 mm.

Family THRESKIORNITHIDAE: Ibises

EUDOCIMUS ALBUS (Linnaeus): White Ibis, Coco Blanco

Scolopax alba LINNAEUS, Systema naturae, ed. 10, vol. 1, 1758, p. 145. (South Carolina.)

Small bands frequented the extensive swamps, particularly where the Río San Juan entered Bahía Damas. From here they ranged out to feed, as twice, at sunset, I saw a flock of a dozen flying low over the water of the bay past the Colonia Central bound for a roost in the distant mangroves.

Family ANATIDAE: Ducks

ANAS DISCORS Linnaeus: Blue-winged Teal, Cerceta

Anas discors LINNAEUS, Systema naturae, ed. 12, vol. 1, 1766, p. 205. (South Carolina.)

On January 14 I saw a flock of a dozen on the small lagoon back of Catival, and I was told that teal came regularly to the Río San Juan in its lower section above the wooded swamps. On January 23, as we crossed in a cayuco to the western side of Bahía Damas, a teal flew low over the sea in front of us.

On February 6, off Punta Mala, one rose from the sea before our boat and flew away through a host of circling terns.

CAIRINA MOSCHATA (Linnaeus): Muscovy Duck, Pato Real

Anas moschata LINNAEUS, Systema naturae, ed. 10, vol. 1, 1758, p. 124. (Brasil.)

On January 23, at sunrise, half a dozen of these ducks, of maximum size, flew past the Colonia Central over the sea on a course that led past Punta Damas toward the distant mainland. These were evidently wild birds, and quite different from the domestic stock, with plumage partly pied with white, that flew about regularly between the stream at headquarters and that at Hato a mile south.

AYTHYA AFFINIS (Eyton): Lesser Scaup, Pato Pechiblanco

Fuligula affinis EYTON, Monograph of the Anatidae or duck tribe, June 1838, p. 157. (North America.)

On January 14 five rested on the small lagoon back of Catival. Such an occurrence on this small body of water in its remote location is interesting evidence of the broad line of flight through which these ducks perform their migrations.

Family CATHARTIDAE: American Vultures

CORAGYPS ATRATUS (Bechstein): Black Vulture, Gallinazo

Vultur atratus BECHSTEIN, *in* John Latham, Allgemeine Uebersicht der Vögel, Bd. 1, Anhang, 1793, p. 655. (Florida.)

Gallinazos were in constant attendance about the buildings at headquarters and the work camps—scavengers in search of any source of food. While waiting at the abattoir for some scrap of refuse it was amusing to see them running and hopping about, fighting among themselves, often with the tail erect like a rail. Once I saw one try to drive a laughing gull from a bit of food on the open beach, but the gull held its ground, and the vulture finally gave up the attempt. Prisoners in charge of the vegetable gardens told me that the vultures were nesting during the middle of January.

CATHARTES AURA (Linnaeus): Turkey Vulture, Noneca

Vulture aura Linnaeus, Systema naturae, ed. 10, vol. 1, 1758, p. 86. (Veracruz, México.)

Turkey vultures were seen daily in flight over the island though never in large numbers. About January 12, with a change in weather conditions, the northeast trade wind blew steadily throughout the day, which made soaring easy, and immediately there was an increase in the prevalence of these birds. While I noted them regularly above the high forest, where occasional openings in the treetops gave a view of the sky, they were more often seen over the open pastures and along the beaches.

Most of those that I observed near enough at hand to give me a clear view with binoculars, had the bare skin of the head dull red, indicating that they were migrants from the north, in Panamá for the winter season. But on January 8 I noted one with the definite yellow lines across the back of the red head that identified it as the race *Cathartes aura ruficollis* Spix, which I have found to be the breeding bird of the Pacific slope of Panamá, west to Chiriquí.

SARCORAMPHUS PAPA (Linnaeus): King Vulture, Cacicón

Vultur Papa Linnaeus, Systema naturae, ed. 10, vol. 1, 1758, p. 86. (Surinam.)

The king vulture appears to be fairly common on Coiba Island though I recorded it on only three occasions. At Salinas January 23 three adults soared high in air. Three days later near Punta Damas several turkey vultures flew out of the brush back of the beach, and when I walked in to see what had attracted them I found a great king vulture, in fully adult feather and color, peering down with its light-colored eyes from a low branch barely 40 feet away. I watched it for some time, and then moved along without disturbing it. It did not seem desirable to kill it for a specimen as I was 3 miles from our quarters! (There are several available from Coiba, viz, two adult and two immature in the Chicago Natural History Museum, collected by J. H. Batty May 21 to 26, 1901.) I saw another in a tree in an open pasture at Punta Damas February 1, and approached it closely, but it showed no apparent fear of me.

Family Accipitridae: Hawks, Eagles

HARPAGUS BIDENTATUS FASCIATUS Lawrence: Double-toothed Kite, Gavilán Dentado

Harpagus fasciatus Lawrence, Proc. Acad. Nat. Sci. Philadelphia, December 1868 (1869), p. 429. (Guatemala.)

On January 13, when I was calling small birds, a female kite alighted overhead on a limb so large that the bird was completely hidden from view. Presently it moved to another tree and began to climb through the branches. It is a specimen in which the lower surface is strongly chestnut, with the barring broad and the gray much reduced.

ACCIPITER BICOLOR BICOLOR (Vieillot): Bicolored Hawk, Gavilán de Dos Colores

Sparvius bicolor Vieillot, Nouveau dictionnaire d'histoire naturelle, nouv. éd., vol. 10, June 21, 1817, p. 325. (Cayenne.)

On January 17 when we were in tall forest one of these hawks came dashing through the branches to a perch a few feet away, attracted by the calls of a thrush. It proved to be an adult female, and one that probably was feeding young. On January 23, a prisoner brought me an immature male from San Juan. Hawks of this species are decidedly uncommon in Panamá, being found only where there is heavy forest.

The adult female had the following colors in life: Base of maxilla below nostril and base of mandible neutral gray; rest of bill black; cere dusky neutral gray; edge of the eyelids honey yellow; rest of the bare skin about the eye and on the loral area dull yellowish green; iris orange; tarsus and toes yellow; claws black. The double ovary, usual in hawks of this genus, was present, the right one about one-third the size of the one on the left. The appearance on the left side indicated that the bird had laid rather recently. This bird has the abdomen paler than the breast and the under wing coverts partly rufous, both indications that remain from the immature dress.

The second specimen is cinnamon-buff below, with gray feathers of the adult dress beginning to appear on the throat, foreneck, and in a ring around the hindneck.

BUTEO PLATYPTERUS PLATYPTERUS (Vieillot): Broad-winged Hawk, Gavilán Aliancho

Sparvius platypterus Vieillot, Tableau encyclopédique et méthodique des trois règnes de la nature, vol. 3, 1823, p. 1273. (Philadelphia, Pa.)

The broad-winged hawk, migrant from the north, is common on the mainland, but during my entire stay on Coiba I recorded only half a dozen or so. The species apparently is averse to long flights over water. An immature male was taken on January 28.

BUTEO MAGNIROSTRIS PETULANS van Rossem: Large-billed Hawk, Cuiscuí

Buteo magnirostris petulans VAN ROSSEM, Condor, vol. 37, No. 4, July 15, 1935, p. 215. (Lion Hill, Canal Zone.)

This hawk undoubtedly is more common on Coiba than any of the other species of its family. I saw it at first in small trees along the fences in pastures, and then more commonly in the second-growth brush that covered old fields in which cultivation had been abandoned. As I became more familiar with the island I found that it also ranged inland over the high forest crown, where apparently the undulating surface of the leaf canopy and the smaller branches immediately below, lying in the sun, afforded as favorable hunting ground as the old

FIG. 1.—Large-billed Hawk, Cuiscuí.

fields and the rastrojo where these birds are usually observed in more settled areas.

Though they shun deeply shaded forest areas, they usually rest on perches that are protected from the sun but that are sufficiently open to afford a view. Often they call querulously, when they are easily located. Usually, also, it is easy to approach them as they have little fear. On January 21 I recorded a nest, with birds about it, 40 feet from the ground in a tree of moderate size, rising above a thicket of second growth, but was not able to examine it closely.

The six specimens prepared agree in general with those from the Pacific slope of Panamá. The breast and foreneck average very faintly darker gray than most, but are equaled in this by occasional mainland specimens. The common name is given in imitation of the call.

MORPHNUS GUIANENSIS (Daudin): Crested Eagle, Águila Moñuda

Falco guianensis DAUDIN, Traité élémentaire et complet d'ornithologie, vol. 2, 1800, p. 78. (Cayenne.)

An occasional view of one of these great eagles soaring high in air over the forest is one of my stirring memories of Isla Coiba. The long tail and broad but blunt-pointed wings present a curious outline when seen in the air so that for a time, viewing them from a considerable distance, I was not wholly certain of their identity. One day the sharp eyes of Vicente saw one resting quietly on a high upper branch in an enormous forest tree, where its background at first view dwarfed it in such proportion that, until my eye had noted the long central feathers of the erected crest, the bird appeared to be some smaller kind of hawk. On several occasions two, obviously a pair, were observed soaring together.

There have been relatively few observations of this species in Panamá.

BUTEOGALLUS ANTHRACINUS SUBTILIS (Thayer and Bangs): Common Black Hawk, Gavilán de Ciénaga

Urubitinga subtilis THAYER and BANGS, Bull. Mus. Comp. Zoöl., vol. 46, June 1905, p. 94. (Gorgona Island, Colombia.)

A few of these hawks lived in and near the tidal swamps at the mouths of the San Juan and Catival rivers, and I saw others occasionally on the uplands back of the beach at Punta Damas. They do not enter the heavy inland forests, but prefer areas of more open growth along the borders.

The two adult females shot at Salinas January 23 and 28 have the following measurements: Wing 357, 365; tail 210, 206; culmen from cere 27.4, 26.6; tarsus 89.8, 86.2 mm.

Family PANDIONIDAE: Ospreys

PANDION HALIAETUS CAROLINENSIS (Gmelin): Osprey, Águila Pescadora

Falco carolinensis GMELIN, Systema naturae, vol. 1, pt. 1, 1788, p. 263. (South Carolina.)

Ospreys were observed daily along the shore, usually alone, but occasionally two in sight at the same time. One was recorded carrying a fish at Isla Ranchería February 4.

Family FALCONIDAE: Falcons

FALCO PEREGRINUS ANATUM Bonaparte: Peregrine Falcon, Halcón Cazapatos

Falco Anatum BONAPARTE, Geographical and comparative list of the birds of Europe and North America, 1838, p. 4. (Egg Harbor, N. J.)

Peregrines were observed occasionally but appeared to be casual in occurrence. On the afternoon of January 21 a large one, evidently a female, dropped on a laughing gull resting on the beach in front of the guardhouse, crippled it, and then began to circle over it. The tide was out, exposing a broad expanse of sand and rock, and presently the falcon alighted briefly at the edge of the water. Apparently it was not hungry, as, though it returned several times, it did not pick up the gull. While it seemed to pay little attention to the crowd of men watching, it was careful not to come within gun range.

FALCO ALBIGULARIS ALBIGULARIS Daudin: Bat Falcon, Halcón Cazamurciélagos

Falco albigularis DAUDIN, Traité élémentaire et complet d'ornithologie, vol. 2, 1800, p. 131. (Cayenne.)

January 13 I shot the female of a pair flying about at the edge of the forest back of the pastures at Punta Damas. Ten days later one soared in rising air thermals in company with several vultures near the shore at Salinas. Another was recorded at Punta Damas January 26. These falcons are graceful on the wing and soar regularly, evidently for pleasure. At rest they perch on dead branches or stubs where they have a clear view. Small birds in their haunts seem to continue their activities without fear while the falcons are about.

It is probable that they were more common on Coiba than these few notes indicate, as in these heavy forests they must often be hidden from view to one on the ground.

FALCO SPARVERIUS SPARVERIUS Linnaeus: Sparrow Hawk, Cernícalo

Falco sparverius LINNAEUS, Systema naturae, ed. 10, vol. 1, 1758, p. 90. (South Carolina.)

Occasionally during January I saw a sparrow hawk in the pastures above the Colonia Central, a migrant individual here for the northern winter. They flew immediately when men come in sight, and seemed quite wild.

Family RALLIDAE: Rails, Coots, and Gallinules

ARAMIDES CAJANEA CAJANEA (Müller): Gray-necked Wood Rail, Cocaleca

Fulica Cajanea P. L. S. MÜLLER, Vollständigen Natursystems, Supplements- und Register-Band, 1776, p. 119. (Cayenne.)

The wood rail ranged in two quite different habitats on Coiba, being fairly common in the mangrove swamps at the mouths of the rivers, and found also in more open forest areas in the uplands. In

FIG. 2.—Gray-necked Wood Rail, Cocaleca.

early morning we sometimes saw them along the small streams running through the pastures, but it was more usual to hear their curious calls from dense cover where they remained hidden, except perhaps for a brief impression of movement as one stirred behind leafy cover in dense shadows. They call frequently at night. The country name is given in imitation of their calls, and curiously, is used for other rails, regardless of their size.

In the swamps they appear to feed largely on crabs, and their flesh has a definitely rank odor. One shot in the forest lacked this entirely and I found the body, saved from the skinning table, excellent eating.

The three taken—two males and a female—are very slightly darker, more reddish brown on the breast and sides when compared with mainland skins, being in fact decidedly darker than the average bird from Panamá proper. Occasional mainland specimens, however, approach them so closely that it does not seem appropriate to try to separate the Coiba population under a distinct name, particularly in view of the considerable individual variation found among these rails.

PORZANA CAROLINA (Linnaeus): Sora, Cocalequita Migratoria

Rallus carolinus LINNAEUS, Systema naturae, ed. 10, vol. 1, 1758, p. 153. (Hudson Bay.)

On January 14 we secured a male from the dense cover of water plants growing in knee-deep water in a small lagoon back of Catival. It was my first personal observation in Panamá of this northern migrant.

LATERALLUS ALBIGULARIS ALBIGULARIS (Lawrence): White-throated Rail, Charrasqueadora

Corethrura albigularis LAWRENCE, Ann. Lyc. Nat. Hist. New York, vol. 7, 1861, p. 302. (Atlantic side of the Isthmus of Panamá along the line of the Panama Railroad.)

These little rails were found, few in number, around a small lagoon back of Catival and in a marshy place at San Juan, to my definite interest, as I had not expected birds of this type on Coiba Island. They were recorded most frequently through their rattling, chattering calls, given rapidly from the depths of the thick vegetation standing in water that they frequent. They range in pairs, and by patient stalking and watching it is sometimes possible to have a glimpse of one moving about in the dark shadows, but ordinarily it is difficult to secure them. My three specimens, a male and two females taken January 14, 17, and 19, agree in color with our series from the Pacific slope of Panamá.

LATERALLUS EXILIS (Temminck): Gray-breasted Rail, Cocalequita Pechiceniza

Rallus exilis Temminck, Nouveau recueil de planches coloriées d'oiseaux, livr. 88, 1831, pl. 523. (Cayenne.)

On January 28 a convict brought me one alive, captured in marshy ground near the Catival work camp. The bird, an adult female, is the first record of the species from Panamá. The nearest locality at which it has been found to the north is on the Río Escondido, 50 miles above Bluefields, Nicaragua, and to the south at the Laguna Guájaro, near La Peña, Atlántico, Colombia.

The specimen has the following measurements: Wing 74.2, tail 29.7, culmen from base 16.8, tarsus 24.8, middle toe with claw 33.8, middle toe without claw 30.0 mm.

Family Jacanidae: Jaçanas

JACANA JACANA HYPOMELAENA (Gray): Wattled Jaçana, Gallito de Ciénaga

Parra hypomelaena G. R. Gray, Genera of birds, vol. 3, 1846, p. 589, pl. 159. ("Bogotá.")

A black jaçana seen near the river at San Juan, was probably a stray from the mainland, as there would not appear to be suitable habitat on the island for permanent residence. These birds apparently wander extensively over the Pacific slope of Panamá during the dry season.

Family Charadriidae: Plovers, Turnstones

CHARADRIUS SEMIPALMATUS Bonaparte: Semipalmated Plover, Chorlito Semipalmado

Charadrius semipalmatus Bonaparte, Journ. Acad. Nat. Sci. Philadelphia, vol. 5, August 1825, p. 98. (Coast of New Jersey.)

These plovers were common on the beaches, one being taken January 18. Shortly after the middle of January there was a considerable increase in their number, dozens being recorded where only one or two had been noted earlier. This status continued to the end of the month when their abundance was reduced to the earlier level.

CHARADRIUS WILSONIA BELDINGI (Ridgway): Wilson's Plover, Chorlito Piquigordo

Pagolla wilsonia beldingi Ridgway, U. S. Nat. Mus. Bull. 50, pt. 8, June 26, 1919, p. 112. (La Paz, Baja California.)

At Juncal on January 30 I shot one as it ran across the broad sand beach. This bird, a female with undeveloped ovaries, was the only one seen.

SQUATAROLA SQUATAROLA (Linnaeus): Black-bellied Plover, Chorlo Gris

Tringa Squatarola Linnaeus, Systema naturae, ed. 10, vol. 1, 1758, p. 149. (Sweden.)

The black-bellied plover fed regularly on the beaches in groups of 3 or 4 to 25. One was taken January 12.

ARENARIA INTERPRES MORINELLA (Linnaeus): Ruddy Turnstone, Vuelvepiedras

Tringa Morinella Linnaeus, Systema naturae, ed. 12, vol. 1, 1766, p. 249. (Coast of Georgia.)

Turnstones ranged daily over the broad flats of Bahía Damas when these were laid bare by low water, or ran along the sandy margins when the tide was full. It was amusing to see how expertly they flipped over small stones or shells to search underneath, and also to hear their low chattering calls when feeding in close company during rain. At low water they came back among the mangrove roots at the mouths of the rivers.

Two birds, male and female, were taken January 11 and 27.

Family Scolopacidae: Snipe, Woodcock, Sandpipers

EREUNETES PUSILLUS (Linnaeus): Semipalmated Sandpiper, Playerito Gracioso

Tringa pusilla Linnaeus, Systema naturae, ed. 12, vol. 1, 1766, p. 252. (Hispaniola.)

These small sandpipers scattered far out over the bare flats at low tide, where they often passed unnoticed until driven in to the beach at high water. They seemed to vary in abundance; many were recorded January 18 and 20.

EREUNETES MAURI Cabanis: Western Sandpiper, Playerito Occidental

Ereunetes Mauri Cabanis, Journ. für Orn., vol. 4, 1856 (1857), p. 419. (South Carolina.)

On January 18 I recorded four western sandpipers among the many semipalmated and shot one, a female, for a specimen. Several were seen two days later. The longer bill serves to identify them when they are feeding with the other species. It is probable that they were much more common than these two observations indicate.

EROLIA MINUTILLA (Vieillot): Least Sandpiper, Playerito Menudo

Tringa minutilla Vieillot, Nouveau dictionnaire d'Histoire naturelle, nouv. éd., vol. 34, December 1819, p. 466. (Halifax, Nova Scotia.)

Specimens were taken on January 14 and 18 from among the abundant semipalmated sandpipers.

CATOPTROPHORUS SEMIPALMATUS INORNATUS (Brewster): Willet, Playero Aliblanco

Symphemia semipalmata inornata Brewster, Auk, vol. 4, No. 2, April 1887, p. 145. (Larimer County, Colorado.)

This migrant from the north apparently is of casual occurrence on Coiba. January 8 I noted a number along the beach, but did not see them again until January 20, when I shot one of several seen at María.

CROCETHIA ALBA (Pallas): Sanderling, Playero Arenero

Trynga alba Pallus, *in* Vroeg, Catalogue raissonné d'oiseaux. Adumbratiunculae, 1764, p. 7. (Coast of the North Sea.)

Occasionally at high tide sanderlings appeared on the beach at the Colonia Central, sometimes alone, sometimes two or four together. Here they ran back and forth, as usual following the receding waves and then retreating quickly as the water returned. Two were taken for specimens February 3.

TOTANUS FLAVIPES (Gmelin): Lesser Yellowlegs, Playero Chillón Chíco

Scolopax flavipes Gmelin, Systema naturae, vol. 1, pt. 2, 1789, p. 659. (New York.)

I saw one near the mouth of Río Catival on February 2.

ACTITIS MACULARIA (Linnaeus): Spotted Sandpiper, Playerito Coleador

Tringa macularia Linnaeus, Systema naturae, ed. 12, vol. 1, 1766, p. 249. (Pennsylvania.)

This bird of the north is so prevalent on beaches and around more open bodies of water in Panamá, many nonbreeding individuals remaining throughout the year, that it is almost a native species. On Coiba spotted sandpipers were scattered singly along the shore, or along the inland streams where these ran past open banks in cleared areas. Usually from one to a dozen were seen daily, teetering ahead of me, or flying with quick, short wingbeats low over the water. At high tide, when much of their normal feeding ground on the beaches was under water, I saw them perched on the gunwales or prows of boats anchored in the bay, or on logs and rocks above the water, where they rested quietly with none of the nervous body movements that normally draw attention to them. At the convict camps located near the shore, they came familiarly along the paths and about the houses in search of food.

NUMENIUS PHAEOPUS HUDSONICUS Latham: Whimbrel, Zarapito Trinador

Numenius hudsonicus LATHAM, Index ornithologicus, vol. 2, 1790, p. 712. (Hudson Bay.)

These large curlews were scattered along the beaches everywhere, regardless of whether the surface was the edge of a rocky reef, or a smooth stretch of sand. As they are hunted to a certain extent, they were rather wild, flying out ahead of me with the loud calls that give them their Spanish name of trinador. Occasionally I found one in the marshy open pastureland at Baja España, near the mouth of the Río Catival, but the shore, even among the mangroves, was the normal habitat.

Family STERCORARIIDAE: Skuas, Jaegers

CATHARACTA SKUA CHILENSIS (Bonaparte): Skua, Salteador Grande

Stercorarius antarcticus b. *chilensis* BONAPARTE, Conspectus generum avium, vol. 2, 1857, p. 207. (Chile.)

On the return trip to Balboa on February 6 I recorded between 15 and 20 skuas at sea between Punta Mala and the area where the islands of Otoque and Bona were barely in sight to the north. All were flying low above the water among the terns and other sea birds. None were recorded on January 6 when I crossed these same waters on the voyage to Coiba.

While these records, like my earlier observations of skuas in the Gulf of Panamá in 1944, are placed under the subspecies *chilensis* on the basis of probability, it must be noted that no specimens have been taken as yet in these waters. One or two seen near at hand seemed to show the characters of *chilensis,* so far as could be told without the bird in hand. I was interested, however, to have a brief, distant view of one that appeared very light in color.

Family LARIDAE: Gulls, Terns

LARUS HEERMANNI Cassin: Heermann's Gull, Gaviota de Heermann

Larus Heermanni CASSIN, Proc. Acad. Nat. Sci. Philadelphia, vol. 6, Dec. 31, 1852, p. 187. (San Diego, Calif.)

On February 6, when the crash boat was about 3 miles south of Otoque, three of these gulls rose from the water near at hand, giving me a clear view of their colors and color pattern. The species has been recorded south in winter only to Champerico and San José on the Pacific coast of Guatemala, so that it was a distinct surprise to see them in the Gulf of Panamá.

LARUS ATRICILLA Linnaeus: Laughing Gull, Gaviota Reidora

Larus atricilla LINNAEUS, Systema naturae, ed. 10, vol. 1, 1758, p. 136. (Bahama Islands.)

On January 6 I recorded Laughing Gulls at sea throughout the journey from Balboa, and at Coiba one or two came daily to the beach in front of the Colonia Penal. I was interested to see one that was tearing at a small bird body on the beach stand its ground and drive off a black vulture that attempted to crowd it away from the food. As related above, on one occasion a laughing gull was killed rather wantonly by a peregrine falcon.

A male taken January 9 had begun to molt on the back, scapulars, and wing coverts, but in the main was still in worn winter dress.

THALASSEUS MAXIMUS MAXIMUS (Boddaert): Royal Tern, Gaviotín Real

Sterna maxima BODDAERT, Table des planches enluminéez, 1783, pl. 58. (French Guiana.)

Scattered royal terns fished daily over the bay, or gathered in little groups to rest on the beaches. In journeys by boat I saw them standing on drift floating on the water, often on bits of stick or board barely large enough to support them. One day I watched with interest while a frigate-bird pursued one of these terns for five minutes, but was so completely outmaneuvred that finally it gave up the chase. A female tern in winter plumage was taken January 18.

STERNA ANAETHETUS NELSONI Ridgway: Bridled Tern, Gaviotina Monja

Sterna anaetheta nelsoni RIDGWAY, U. S. Nat. Mus. Bull. 50, pt. 8, June 26, 1919, pp. 487 (in key), 514. (Sihuatanejo, Guerrero.)

On February 6, as our boat passed the two rocks of Frailes del Sur, off Punta Mala, suddenly scores of terns appeared, wheeling over the sea, and looking back I saw hundreds more, circling in apparent confusion but in their usual manner over the barren summit of the larger of the two islets. They continued in numbers until we were opposite Isla Iguana, and an occasional one was sighted farther north to within 15 miles of Isla Otoque. None was seen when we passed on January 6, and apparently they had arrived only recently at their nesting grounds at the Frailes, to judge from their actions. The presence of this large tern colony here has not been reported so far as I am aware.

A few that came near appeared to be the present species, an identification that is probable because of the immature specimen in the National Museum collections captured by Charles L. Fagan on September 24, 1922, aboard a ship when the vessel was abeam of Punta Mala.[5]

CHLIDONIAS NIGER SURINAMENSIS (Gmelin): Black Tern, Gaviotina Negra

Sterna surinamensis Gmelin, Systema naturae, vol. 1, pt. 2, 1789, p. 604. (Surinam.)

On January 6, while passing Punta Mala I noted two flocks of about 40 each resting on the sea 3 miles offshore.

Family Columbidae: Pigeons, Doves

COLUMBA CAYENNENSIS PALLIDICRISSA Chubb: Pale-vented Pigeon, Torcaza Común

Columba pallidicrissa Chubb, Ibis, ser. 9, vol. 4, January 1910, p. 60. (Costa Rica.)

The torcaza was present in fair numbers, scattered singly through the forest, where for most part they remained in the tops of the taller trees, so high as to be beyond gunshot. While we heard their guttural calls daily, it took careful stalking and watching to see them, and then usually they were out of reach. Finally we secured a male on January 28, and a female two days later.

COLUMBIGALLINA TALPACOTI NESOPHILA (Todd): Ruddy Ground Dove, Tortolita Colorada

Chaemepelia rufipennis nesophila Todd, Ann. Carnegie Mus. vol. 8, May 8, 1913, p. 590. (Isla El Rey, Archipiélago de las Perlas, Panamá.)

The ruddy ground dove was found in the pastures where I saw them daily, feeding in little groups on the ground where the grass

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[5] See Wetmore, Condor, vol. 25, Oct. 3, 1923, p. 171.

was short, or where it grew in scattered tufts on stony soil. As I approached the doves crouched motionless until I had passed; or if I came too near, they rose quickly with a flash of bright reddish brown from their wings, often to perch on shaded branches in the small, scattered trees in these locations. I heard them calling occasionally, and January 11 flushed a female from a nest placed 6 feet from the ground on the summit of a tree stump standing in the border of swampy woodland. The nest was a flat, fairly well-built platform of twigs, hidden among tall, green shoots sprouting from the top of the stump. The two eggs were white, bluntly ovate in form, and measured 22 x 16.9 and 22.2 x 16.9 mm. The following day a convict brought me another nest with two eggs that he had found in the top of a palm while gathering coconuts, but these were nearly ready to hatch, and could not be saved.

On the Pacific slope of Panamá these doves prefer open lands. They enter thickets or groves readily, but usually do not penetrate forested areas beyond the immediate borders. The pastures cleared around the convict camps are definitely favorable to them so it is apparent that they must be more common now than formerly, when they were restricted to the borders of the swamps and the shoreline. At present this species is the only common bird in the man-made environment of these pasturelands, which are frequented otherwise only by kingbirds except along their borders. Two males and two females were prepared for specimens.

On comparing these birds with others, it was noted immediately that the females were definitely darker on the lower surface than the mainland series; and also that they agreed in this darker color with skins from San José and Pedro González Islands in the Archipiélago de las Perlas, which represent the race named *nesophila* by Todd. It is highly interesting to note this resemblance between the Coiba population and that of this other island group. Bangs[6] stated that Todd's type of *nesophila,* from "San Miguel" (Isla El Rey) was an immature male with the sex wrongly marked as female by the collector, and therefore placed *nesophila* in the synonymy of *C. t. rufipennis,* in which he has been followed by Peters and by Hellmayr and Conover. However, in 1944 when I secured four females from the Perlas Islands I found that these clearly upheld the validity of Todd's race.[7] An occasional immature bird from the mainland, freshly molted from juvenal plumage, may approach *nesophila* in

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[6] Bull. Mus. Comp. Zoöl., vol. 70, 1930, p. 165.

[7] See Wetmore, Smithsonian Misc. Coll., vol. 106, No. 1, Aug. 5, 1946, pp. 36-37.

depth of color, but in a considerable series I have seen only one that could not be separated easily on close examination, and that single specimen does not agree entirely with the island series.

CLARAVIS PRETIOSA (Ferrari-Pérez): Blue Ground Dove, Tortolita Azul

Peristera pretiosa Ferrari-Pérez, Proc. U. S. Nat. Mus., vol. 9, Oct. 2, 1886, p. 175. (Brasil.)

These handsome little doves, of shy and retiring habit, were found sometimes in swampy woodland, as in the area near Catival, and sometimes along the more open trails on the upland where the larger trees of the forest had been cut. In early morning they were encountered in plantations of plátanos and yuca. Occasionally, while moving quietly, I had brief glimpses of them as they walked on the ground under the shelter of leaves and branches, but more often they were not observed until they flushed and flew with swift, direct flight, traveling low down, usually to drop in some spot that was difficult of access. Three males were taken on January 11, 25, and 31.

LEPTOTILA PLUMBEICEPS BATTYI Rothschild: Gray-headed Dove, Paloma Cabeciceniza

Leptoptila battyi W. Rothschild, Bull. Brit. Orn. Club, vol. 12, Dec. 30, 1901, p. 33. (Coiba Island, Panamá.)

The gray-headed dove was one of the common birds in the forests of Coiba Island, so abundant in fact that in spite of their secretive habits I saw them nearly every day, sometimes in the swampy woodlands back of the mangroves near the river mouths, sometimes in the great forest of the interior. They live and feed on the ground, usually two or three together, rising to low perches on logs or branches when flushed if not too badly frightened, or, if startled, flying swiftly to secure cover. Occasionally I had random glimpses of them walking with bobbing heads among the shadows, or standing completely motionless, when it was difficult to distinguish them in the dim light of their haunts. In early morning they came out into the open trails, but when startled darted at once to cover.

Some of the males were calling, a single hooting note, so highly ventriloquial that we never succeeded in following it to see the actor perform, though we were certain of the source. Usually the birds when calling appeared to rest on low perches near the ground, where they were completely concealed; when we came too near they became silent and flew or walked away. But always the impression was that the sound came from the trees rather than from the undergrowth near at hand.

The flesh of these doves was esteemed highly for the table and the convicts trapped many and sold them alive, the usual price being 60 cents a dozen.

This is the most handsomely marked of the races of this species, the darker colors, in contrast with the paler hues of the other subspecies, following the characteristic pattern of increased depth in color found in the other forms that are peculiar to Coiba Island. Until now this race has been represented in collections by a male and two females (the type series) in the American Museum of Natural History, and a female in the British Museum (Natural History) taken on Coiba by H. J. Kelsall Sept. 4, 1924.

Following are measurements of eight skins that I prepared: Males (2 specimens), wing 139.2-143.5, tail 89.2-89.4 (89.3), culmen from cere 8.5-8.9 (8.7), tarsus 31.2-32.6 (31.9) mm. Females (6 specimens), wing 134.0-142.2 (138.2), tail 82.5-90.2 (86.0), culmen from cere (5 specimens) 8.0-9.0 (8.6), tarsus 29.9-33.2 (32.1) mm.

The soft parts in a female taken January 17 were colored as follows: Bill black; bare loral area dull red; rest of bare skin on side of head dull neutral gray; iris dull yellow; tarsus and toes dull red; claws wood brown. The sexes are alike in color and in size, the resemblance extending to the incised tip of the outermost primary, which averages very slightly broader in the females than in the males, but varies in length of the attenuated portion apparently without regard to sex. Immaturity in age may be a factor among those in which it is shortened, since in one bird that had just attained adult body plumage this feather is only slightly narrowed toward the end.

An immature specimen in the American Museum of Natural History, collected by J. H. Batty, May 11, 1901, has a few feathers of the juvenal plumage remaining on the forehead, crown, neck, and upper breast that are wood brown edged with cinnamon. The greater wing coverts have an indistinct subterminal bar of dark neutral gray and a narrow tip of cinnamon.

GEOTRYGON MONTANA MONTANA (Linnaeus): Ruddy Quail-Dove, Paloma Montañesa

Columba montana LINNAEUS, Systema naturae, ed. 10, vol. 1, 1758, p. 163. (Jamaica.)

This quail-dove, widely distributed in the American Tropics, was fairly common in the heavy forests where, as usual, it lived on the ground in the shadows of the undergrowth. Occasionally one flushed ahead of me, when it was readily identified by its shorter tail and general form, even when the colors were not clearly seen; but when

I detected a dove walking amid the low cover below the undergrowth I was often uncertain which of the two forest-inhabiting species was before me. Two males in adult plumage and two females in immature dress were taken. One of the latter, collected February 4, was shot on Isla Ranchería as it walked along a steep, fairly open slope back of the beach.

Family PSITTACIDAE: Parrots, Macaws

ARA MACAO (Linnaeus): Scarlet Macaw, Guacamayo Rojo

Psittacus Macao LINNAEUS, Systema naturae, ed. 10, vol. 1, 1758, p. 96. (Lower Amazonas, Brasil.)

Each morning, when the sun was above the horizon, groups of macaws, traveling in pairs, came flying over the forest and the pasturelands from the southern part of the island, and each evening as sunset was near they returned. Often the low-lying sun was at a proper angle to light their brilliant colors, and always whether

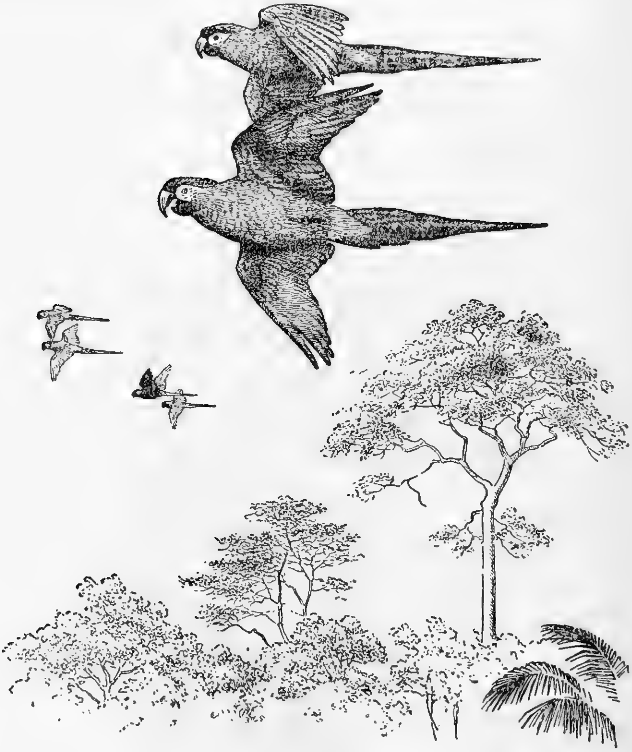

FIG. 3.—Scarlet Macaw, Guacamayo Rojo.

near or far, they made an attractive sight as they crossed the sky with steady wing beat, and long tail streaming behind. During the day I encountered them about fruiting trees of various kinds, feeding usually high above the ground, sometimes wary and sometimes quite tame, usually calling raucously whenever I came near. At the beginning of February the pairs were often increased to trios as young birds, with the longer tail feathers not quite grown, began to accompany their parents. Though they appeared to gather at night to roost in some special area in the southern end of the island, during the day they scattered to the farthest forests. On February 4 I saw several on Isla Ranchería. Male and female were collected January 8 and 15 for specimens.

The restricted type locality, "Baixo Amazonas" designated by Pinto,[8] is to be accepted (Linnaeus having written only "America meridionali"), rather than the proposal of Hellmayr [9] who selected Pernambuco, as in Brasil the bird is found only in the northwestern section, in Amazonas, Pará, and northern Mato Grosso.

AMAZONA FARINOSA INORNATA (Salvadori): Mealy Parrot, Loro Verde

Chrysotis inornata Salvin, Cat. Birds Brit. Mus., vol. 20, 1891, pp. 269 (in key), 281. (Veraguas, Panamá.)

These, the conspicuous parrots on Coiba, ranged in pairs and flocks everywhere through the forest. Their calls greeted me constantly, and at times, when fruiting trees caused them to congregate, their noise was such that few other bird sounds could be heard above it. In early morning they were active in flying about until they had located a feeding area for the day, when they tended to move only through limited areas. The guards responsible for the work camps often stationed men around fields of ripening corn for two hours or so after sunrise, when the parrots were flying from their roosts, to move the birds along to the forests by shouting and making other noise, as if not driven away the birds caused much damage. Several were heard and seen on Isla Ranchería February 4.

The four prepared for specimens all agree with skins from the mainland from Veraguas eastward in having the crown clear green with the back of the head and upper hindneck rather dark blue. The edge of the wing (the carpal area) in all four shows the line of red usual in this race, though in one it is reduced in extent. They show no resemblance therefore to *Amazona farinosa virenticeps* which is

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[8] Catalogo das aves do Brasil, pt. 1, 1938, p. 182.

[9] Abh. Kon. Bayerischen Akad. Wiss., Kl. 2, vol. 22, pt. 3, 1906, p. 577.

found in the lowlands of western Chiriquí (Bugaba, Divalá) and Bocas del Toro (Almirante), which has the crown bluish green, the hindneck lighter blue, and the edge of the wing marked with yellow, only rarely with a tinge of red.

AMAZONA AUTUMNALIS SALVINI (Salvadori): Red-fronted Parrot, Loro Frentirojo

Chrysotis salvini Salvadori, Cat. Birds Brit. Mus., vol. 20, 1891, pp. 271 (in key), 300, pl. 7, fig. 3. (Lion Hill Station, Canal Zone.)

I was certain that this species was present on Coiba as at times I believed that I could distinguish the notes of these birds among the myriad parrot calls of the forest, but in spite of much scanning of feeding and flying birds I was not able to find them. The only one identified was a captive bird that had been taken on the island. The Batty collection in the American Museum of Natural History includes eight skins labeled Coiba Island, taken May 5, 11, and 14, 1901, in which the locality given is assumed to be correct.

PIONUS MENSTRUUS (Linnaeus): Blue-headed Parrot, Casanga

Psittacus menstruus Linnaeus, Systema naturae, ed. 12, vol. 1, 1766, p. 148. (Surinam.)

Blue-headed parrots were as common on Coiba as the larger species, but were less conspicuous because of their smaller size and less raucous voices, their higher-pitched calls being lost on many occasions amid the shrieks and gutturals of the loro verde. Where casangas found an abundant supply of food they tended to remain quietly through the day, being conspicuous only when disturbed, or during their morning and evening flights to their roosting places. Often they relied on their green coloration for concealment, allowing me to pass close at hand, even when they were low down in banana plantations. They did much damage in the cornfields, so that it was necessary frequently to drive them out by shooting. Sometimes I found them feeding alone, but where food was abundant, 40 to 50 congregated in scattered flocks. Two males were preserved for specimens on January 7 and 19.

BROTOGERIS JUGULARIS JUGULARIS (Müller): Orange-chinned Parakeet, Perico Común

Psittacus jugularis P. L. S. Müller, Vollständigen Natursystems, Supplements- und Register-Band, 1776, p. 80. (Bonda, Magdalena, Colombia.)

This small parakeet, familiar as a household pet throughout the Republic, is fairly common on Coiba, though not nearly so abundant as in many mainland localities. Occasionally I heard them calling from the high forest crown, where they were hidden from view by the screen of leaves, or saw little groups in flight near the work camps. But it was not until the guayabo trees scattered through the pastures came into blossom that I recorded them regularly, as then they came in bands of a dozen to 25 to feed at the blossoms. Three that I shot for specimens on January 26 at one of these trees had the throat completely filled with nectar.

Family Cuculidae: Cuckoos, Anis

CROTOPHAGA ANI Linnaeus: Smooth-billed Ani, Garrapatero Común

Crotophaga Ani Linnaeus, Systema naturae, ed. 10, vol. 1, 1758, p. 105. (Jamaica.)

Anis in the usual little groups of 6 to 12 or so were found in the low thickets in abandoned fields, or around the borders of the pastures. They were restricted to the cleared areas, and, though only fairly common, probably were more abundant now that some of the land has been cleared than they were formerly when the island was completely forested. Two were taken for specimens January 21 and 26.

Family Strigidae: Owls

BUBO VIRGINIANUS MAYENSIS Nelson: Great Horned Owl, Gran Buho Cornudo

Bubo virginianus mayensis E. W. Nelson, Proc. Biol. Soc. Washington, vol. 14, Sept. 25, 1901, p. 170. (Chichén Itzá, Yucatán.)

On February 4, on Isla Ranchería, I came on one of these birds resting in a large-limbed, open tree standing at the edge of a swamp. The bird was only a short distance from me, as at the time I was climbing along the face of a steep bank, high above the muddy, level ground. While I had a clear view of the owl for a minute or so, I failed to secure it for a specimen owing to one of those mishaps that torment the naturalist when a quick snap shot is necessary, since my footing on the slippery bank was treacherous. My disappointment was the greater since I knew at the moment that the only record of this species for Panamá was that of a bird taken by Enrique Arcé at Chitrá, Veraguas, in 1868. As the bird was near at hand I could see that it was quite dark in general coloration.

From examination of available material, including that in the British Museum (Natural History), I agree with Griscom[10] that the

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[10] Ibis, 1935, pp. 546-547.

great horned owls of southern México and Central America include only one race, to be called *mayensis*. Under these circumstances I have listed this observation under the subspecific name though it is only a sight record.

Owls were reported as occasional on Coiba, but search for them by day and by night was unsuccessful. Whether the present species or others were involved is therefore unknown.

Family CAPRIMULGIDAE: Goatsuckers

CAPRIMULGUS RUFUS MINIMUS Griscom and Greenway: Rufous Nightjar, Chotacabras Morena

Caprimulgus rufus minimus GRISCOM and GREENWAY, Bull. Mus. Comp. Zoöl., vol. 81, May 1937, p. 424. (Panamá City, Panamá.)

It was a pleasant experience to find this interesting goatsucker fairly common on Coiba, particularly since the omnipresent *Nyctidromus* encountered throughout the lowland coverts of the mainland, was entirely absent. In traversing the forest I came across them resting on the ground, usually in sections where the surface was somewhat hilly or undulating. They rose on noiseless wings and flew swiftly through the undergrowth where, in the dim light, it was difficult for the eye to follow them. I soon learned to move quietly ahead in the general direction that they had taken, and by watching carefully often saw them perched on a log or a low vine, where it was easier to see them than when they were on the ground. In flying they did not rise more than 10 to 20 feet, and usually traveled at a much lower level. In the evening I heard them calling in the distance from the forest border above the pastures, *whit-wit-we-oo,* uttered rapidly, repeated after a slight pause, and continued steadily for several minutes. The sound was low but resonant, so that the notes carried for a considerable distance. Male and female shot in company on January 10 were not in breeding condition, but on January 19 a female taken in the forest near the Punta Damas trail was nearly ready to lay. January 29 I shot another female that flew up to perch on a log, and then discovered that she had risen from her nest. This was on the ground, in a little space free of undergrowth beside a fallen log. A single egg was placed in the center of a thick, brown-colored dead leaf that measured 4 by 7 inches. On this dark background the light-colored egg stood out clearly with no semblance of concealment. Two small, freshly plucked green leaves had been laid alongside on the larger leaf, apparently as decorations. The egg, oval in shape, measures 30.8 x 23.5

mm. The general ground color is somewhat glossy white, marked irregularly over the entire surface with spots of French gray to lilac gray, with a lesser number that are cinnamon drab, some of these scattered over the surface, but most of them grouped as a poorly outlined wreath around one end. Many of the spots are highly irregular in outline. On skinning the parent I found that she contained a second egg ready for the shell, so that the complete set is two, as it is in the related chuck-will's-widow (*Caprimulgus carolinensis*) that nests in the southeastern United States.

The five skins from Coiba Island probably represent a race peculiar to the island, since they are definitely brighter, more rufescent brown on the crown and hindneck than four others, two from the Province of Panamá, and two from northern Colombia, that are at the present moment available. The Coiba series includes specimens in the two color phases, one grayer and one browner, usual in this species, and the difference indicated holds in both. However, in view of the considerable individual variation in the rufous nightjar it seems desirable to see further mainland specimens before reaching final decision on the Coiba series.

Family APODIDAE: Swifts

STREPTOPROCNE ZONARIS ALBICINCTA (Cabanis): White-collared Swift, Vencejo Cuelliblanco

Hemiprocne albicincta CABANIS, Journ. für Orn., vol. 10, May 1862, p. 165. (Junction of Haiama Creek and the Demerara River, British Guiana.[11])

On January 14 I shot two from a small flock that came to drink at the little fresh-water lagoon at Catival. As no others were seen, this occurrence may be taken as an example of the wide range of territory covered by the fast-moving flocks of swifts, since it is assumed that they had crossed from the mainland. Both of the specimens are immature. One, a male, has the breast band restricted in size and dull white. In the other, in which I was not able to determine the sex, the feathers of the upper breast are tipped so lightly and so narrowly with white that the band seems to be completely lacking until the bird is examined closely.

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[11] In the original description Cabanis proposed this name for the birds found from "Mexico bis Guiana" without selecting a type. Zimmer, Amer. Mus. Nov., No. 1609, Feb. 25, 1953, p. 3, has designated the type locality as given above. It is to be noted in this connection that Ridgway, U. S. Nat. Mus. Bull. 50, pt. 5, 1911, p. 698, in discussion of this race had already suggested "Guiana."

CHAETURA VAUXI OCHROPYGIA Aldrich: Vaux's Swift, Vencejo Oscuro Común

Chaetura vauxi ochropygia Aldrich, Sci. Publ. Cleveland Mus. Nat. Hist., vol. 7, Aug. 31, 1937, p. 68. (Paracoté, 1 mile south of the mouth of the Río Ángulo, Montijo Bay, Veraguas, Panamá.)

These small swifts were seen constantly over the open pastures and around the groves of coconut palms, usually in groups of a dozen or more. They ranged over the entire island, as I saw them also flying high over the unbroken forest. Hundreds of them were present on Coiba. February 4 I recorded many along the shores of Isla Ranchería.

Fig. 4.—Vaux's Swift, Vencejo Oscuro Común.

While on many occasions they flew high in air, near the shores and over the pastures they circled lower, sometimes quartering like swallows barely above the ground. From the regularity with which small groups flew around the coconut palms after the sun had set I had the impression that they sought roosting places in these trees, but this I was not able to ascertain with certainty. Sometimes as they passed I heard low, wheezy, chattering calls that had little volume or carrying power, but ordinarily the only impression of them was of their angular wings, beating rapidly as they passed at high speed.

Three taken on January 10 and 15 are typical of the present race, marked by light-colored rump and upper tail coverts.

Family TROCHILIDAE: Hummingbirds

PHAEOCHROA CUVIERII SATURATIOR (Hartert): Cuvier's Hummingbird, Colibrí de Cuvier

Aphantochroa cuvieri saturatior HARTERT, Bull. Brit. Orn. Club, vol. 12, Dec. 30, 1901, p. 33. (Coiba Island, Panamá.)

This large species was found only in the stand of white mangroves in the swampy area bordering the mouths of the San Juan and Catival Rivers. They came so quietly among the other hummers to feed at flowering trees that, with their dull coloration, they attracted little attention, and it was only when they were in clear view that they were distinguished by their size. They were not common, and it required much watching to collect the two males and two females that I obtained.

These four bear out fully the characters assigned in the original description, being decidedly darker both above and below when compared with the two races of this species known respectively from eastern and western Panamá. Measurements are as follows: Males (2 specimens), wing 78.7, 75.8, tail 45.5, 45.0, culmen from base 24.7, 25.6 mm. Females (2 specimens), wing 70.2, 74.1, tail 46.7, 45.2, culmen from base 25.9, 24.7 mm.

Hartert believed that a longer bill might be one of the characters of this race but this is not true.

CHLOROSTILBON ASSIMILIS Lawrence: Allied Emerald, Colibrí Esmeraldino

Chlorostilbon assimilis LAWRENCE, Ann. Lyc. Nat. Hist. New York, vol. 7, January 1861, p. 292. (Atlantic side of the Isthmus of Panamá, along the line of the Panama Railroad.)

This was the least prominent of the hummingbirds, the few noted being found in the forest, or at the forest border. The three males and two females secured do not differ from mainland specimens. On January 16, when I obtained a pair in swampy woods along the Río Catival, I found that the female was laying.

LEPIDOPYGA COERULEOGULARIS COERULEOGULARIS (Gould): Sapphire-throated Hummingbird, Colibrí Zafirino

Trochilus coeruleogularis GOULD, Proc. Zool. Soc. London, pt. 18, 1850 (Feb. 28, 1951), p. 163. (Near David, Chiriquí, Panamá.)

These handsome hummingbirds were encountered only in the borders of the mangrove swamps, where they were feeding at flowering trees. They seemed rather quiet, and also somewhat timid as they fled from the attacks of the more aggressive goldentail, even though that species is smaller. The series of four males and three females from Coiba does not differ from birds taken on the mainland.

HYLOCHARIS ELICIAE (Bourcier and Mulsant): Blue-throated Goldentail, Colibrí Cola de Oro

Trochilus Eliciae Bourcier and Mulsant, Ann. Sci. Phys. Nat. Agr. Ind. Soc. Roy. Lyon, vol. 9, 1846, p. 314. (Type locality unknown.)

This was a common hummingbird, found in small numbers in the lower level of branches in the high forest, and more abundantly in the mangroves and the swampy woodlands bordering the river mouths. Possibly flowering trees were the attraction that drew them to the latter habitat, as toward the end of my stay on Coiba I found them about blossoming guayabo trees that grew scattered through open pasturelands. They seemed more aggressive than other species of the family here, and especially toward other hummers. The light-colored base of the bill, which is pale reddish in life, shows clearly as they move about, even in the dim light of heavy forest. They seemed to seek shaded haunts, except when lured into the open by especially attractive flowers. The series collected includes one bird from Isla Ranchería. A female taken January 24 was laying.

When compared with mainland series the Coiba birds appear to average very faintly darker, but there is no clear-cut distinction between specimens from the two areas.

Carriker[12] suggests that the type locality of this bird, which was not indicated in the original description, may be Guatemala since the authors of this species describe another hummer from that country in the same paper.

AMAZILIA EDWARD NIVEOVENTER (Gould): Snowy-breasted Hummingbird, Colibrí Pechiblanco

Trochilus niveoventer Gould, Proc. Zool. Soc. London, pt. 18, 1850 (Feb. 28, 1851), p. 164. (Near David, Chiriquí, Panamá.)

This handsomely marked hummingbird was one of the least common kinds of the family. I found it mainly at the borders of the swampy woodlands near the river mouths, where one came occasionally, with other species, to the flowers of white mangroves, or was found alone. The bushy growths of old fields, as at San Juan, were also attractive, and when the guayabo trees in the pastures came into

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[12] Proc. Acad. Nat. Sci. Philadelphia, vol. 87, Dec. 27, 1935, pp. 422-423.

bloom the birds congregated about them in some numbers. A female shot January 11 was laying. The three males and three females prepared for specimens agree with mainland examples.

AMAZILIA TZACATL TZACATL (De la Llave): Rieffer's Hummingbird, Colibrí Colimorena

Trochilus Tzacatl De la Llave, Registro Trimestre, vol. 2, No. 5, 1833, p. 48. (México.)

This species, easily identified by the rufous-brown tail, is the most abundant hummingbird, ranging from the open borders of the lowland swamps back into the heavy shade of the high forest. They were especially abundant at the flowers of the white mangroves, and at the blossoms of the guayabo trees growing in the open, but were observed elsewhere at almost any herbaceous plant or shrub that was in bloom. The flowers of the mangroves were so large that to feed on them easily the hummers usually perched on the ends of the petals, or on adjacent blossoms, and then reached over with long bills to probe the centers. In early morning I found this hummingbird in the warm sun on open branches, often in small dead trees along the beaches. Part at least were nesting during January, and I was interested to have one male scold me with loud chirping calls. On January 8 I found a nest in a small, broad-leafed tree growing beside a coconut palm back of the beach. The bird had built on a shaded horizontal branch about 7 feet from the ground, the entire structure being formed of fine shreds of plant fiber, of coarser form exteriorly on the immediate surface, but aside from this quite uniform. The outer surface was light grayish brown, decorated with a few bits of lichen. The nest measured 42 by 44 millimeters externally, being somewhat flattened by the two well-grown young, a week or more old, that it contained. These had two lines of clay-colored down along the dorsal pteryla. The female perched on the edge of the nest beside them, striking steadily with her bill at large ants that ran back and forth along the branch supporting the nest. This hummer was common also on Isla Ranchería.

The series of 12 adult birds, viewed as a whole, averages very faintly darker on the lower breast and abdomen than the excellent representation available from the mainland. None of the Coiba birds is as light as the average from Panamá proper, but numerous specimens from the mainland are equally dark. The island series also is uniformly deep green above, again being equaled by occasional skins from the other series, though most of the latter have a distinctly brassy sheen. There seems to be an incipient difference, but not one that would merit a special name.

Family ALCEDINIDAE: Kingfishers

MEGACERYLE TORQUATA TORQUATA (Linnaeus): Ringed Kingfisher, Martín Pescador Grande

Alcedo torquata LINNAEUS, Systema naturae, ed. 12, vol. 1, 1766, p. 180. (México.)

A few of these kingfishers ranged along the lower courses of the Río San Juan and the Río Catival, where the tidal part of these streams traversed the great lowland swamps.

A male was collected January 12.

CHLOROCERYLE AMERICANA ISTHMICA (Goldman): Green Kingfisher, Martín Pescador Verde

Ceryle americana isthmica GOLDMAN, Smithsonian Misc. Coll., vol. 56, No. 27, Dec. 1, 1911, p. 1. (Río Indio, near Gatun, Canal Zone, Panamá.)

Green kingfishers lived along the lower courses of all the streams, large and small, that flowed into Bahía Damas. In early morning they rested on sticks, or on projecting points of rock exposures where small creeks came down to the beaches, but as soon as the sun was high they retreated inland where the water flowed between shaded banks. Along the larger rivers they ranged through the mangrove swamps. As they fly near the surface of the water in these dimly lighted places it is only the white marking of the tail and lower abdomen that allows the eye to follow them.

CHLOROCERYLE AENEA AENEA (Pallas): Pygmy Kingfisher, Martín Pescador Enano

Alcedo aenea PALLAS, *in* Vroeg, Beredeneerde catalogus, . . . Vogelen, Adumbratiunculae, 1764, p. 1. (Surinam.)

A male, taken low down among the roots of the white mangroves in the swamp at the mouth of Río Catival, was the only one seen.

Family PICIDAE: Woodpeckers

CENTURUS RUBRICAPILLUS Cabanis: Wagler's Woodpecker, Carpintero Rayado

Centurus rubricapillus CABANIS, Journ. für Orn., vol. 10, 1862, p. 328. (Barranquilla, Atlántico, Colombia.)

This is the common woodpecker on the island as it is throughout the Pacific lowlands of mainland Panamá from the Costa Rican border to western Darién. On Coiba I was interested to find it moving regularly over the forest crown throughout the heavy woodland of the interior of the island, in addition to its common mainland habitat of trees in the open pastures and plantations. In the higher branches of the tall forest it finds the same conditions of light and sun that it enjoys around savannas and clearings elsewhere, which suggests that this may have been a considerable part of its original haunt on the mainland, and that because of its life in the open treetops, above the shadowy depths of the lower levels, its manner of living was not unduly disturbed when the great lowland forests of Veraguas and eastern Chiriquí were cut down. The chattering calls and drumming of these birds were a daily accompaniment to my observations, both around our quarters and in the field. In the forests they came down occasionally from the higher levels to scold at me, or to search for food. On February 4 I recorded them on Isla Ranchería.

Fig. 5.—Wagler's Woodpecker, Carpintero Rayado.

I was attracted immediately by the darker color of my first specimens, in comparison with the bird of the mainland, a distinction that has merited description as a race that is new to science.

CENTURUS RUBRICAPILLUS SUBFUSCULUS subsp. nov.

Characters.—Similar to *Centurus rubricapillus rubricapillus* Cabanis,[13] but decidedly darker throughout; blacker above, with the white bars reduced in width, and the black bars correspondingly broader; under surface and side of head definitely darker, more grayish olive; crown in male deeper red; white markings on rectrices somewhat reduced in extent.

Description.—Type, U.S.N.M. No. 460784, male, Isla Coiba, Panamá, collected Jan. 18, 1956, by A. Wetmore (orig, No. 20311): Forehead olive-buff, with the plumes behind the nostrils apricot buff, fading immediately into the background color of the forehead; crown and hindneck slightly darker than spectrum red; back black, barred narrowly with white, the light bars being one-third or less the width of the black ones; remiges dull black, the secondaries and inner primaries notched and barred rather narrowly but prominently with white; three outermost primaries dull black, with the outer webs unmarked; rump and upper tail coverts white, with scattered freckling and spotting of dull black; rectrices black, the central pair barred on the inner webs, and lined broadly on the outer webs, with white; side of head grayish olive; throat citrine-drab, changing to light brownish olive, with an overwash of isabella color, on foreneck, this color continuing over breast and sides; center of abdomen dull nopal red, merging at the sides into isabella color which covers the rest of the abdomen; under tail coverts and lower part of flanks dull white, barred narrowly with dark neutral gray; under wing coverts white, barred irregularly with dark neutral gray; inner surface of remiges dark neutral gray, barred rather broadly with white. Bill dull black; tarsus and toes blackish slate (from dried skin).

Measurements.—Males (11 specimens), wing 101.8-108.5 (105.0), tail 48.7-55.9 (52.0), culmen from base 23.1-27.3 (25.2), tarsus 17.8-20.2 (18.9) mm. Females (4 specimens), wing 99.3-101.8 (100.4), tail 49.2-50.5 (49.4), culmen from base 22.0-23.4 (22.9), tarsus 17.5-18.2 (17.7) mm.

Type, male, wing 103.5, tail 50.0, culmen from base 26.8, tarsus 19.0 mm.

Range.—Isla Coiba and Isla Ranchería, off the Pacific coast of Veraguas, Panamá.

Remarks.—The bird in habits and in actions is the counterpart of *Centurus rubricapillus rubricapillus* of the adjacent mainland. A

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[13] *Centurus rubricapillus* Cabanis, Journ. für Orn., vol. 10, 1862, p. 328. (Barranquilla, Atlántico, Colombia.)

nearer approach in color is found in *Centurus rubricapillus seductus* of Isla El Rey in the Perlas Islands of the Gulf of Panamá, which differs also from the typical form *rubricapillus* in generally darker color above and below, in heavier bill, and in paler red on the crown of the male. The bird of Coiba Island, *C. r. subfusculus* is separated from *seductus* as it is from *rubricapillus* by still darker coloration, the under surface especially being decidedly darker. In addition the crown in the male *subfusculus* is much darker red. It is interesting to observe that there is a general resemblance in the two island forms, which suggests that darker color may be a more primitive stage which has been preserved in the limited confines of offshore islands while modification has come in the extensive mainland range.

The Romans recognized a brunette as "mulier subfuscula." It seems appropriate to use their adjective as the name for the present form, the darkest race of the species.

Study of the bird from Coiba Island has led to an examination of the series of the species that is now available from the entire range. It may be observed in the beginning that the writer believes it useful to treat the *Centurus* group of species as a separate genus, rather than to merge it with the allied *Melanerpes,* as Peters and some others have done. Aside from the pattern conformation found in the regularly barred back, the feathers of the throat are soft and blended, not hairlike as in typical *Melanerpes.*

As another matter, the races of *Centurus rubriventris* Swainson appear specifically distinct from *rubricapillus* in the much narrower barring of the back, and in the proportionately much longer tail. It may be observed in this connection that *Picus flavifrons* Vieillot appears to belong with true *Melanerpes,* so that this genus thus includes *Picus rubriventris* Vieillot (1818) for the race *Melanerpes flavifrons rubriventris.* With *Centurus* recognized as a distinct genus the specific name *rubriventris* of Swainson (1838) remains available for the Mexican species, and the name *rubricomus* Peters (1948), necessary if *Centurus* is united with *Melanerpes,* is not required.[14]

The following summary outline covers the races of *Centurus rubricapillus.*

Centurus rubricapillus rubricapillus Cabanis:

Centurus rubricapillus Cabanis, Journ. für Orn., vol. 10, 1862, p. 238. (Barranquilla, Atlántico, Colombia.)

Centurus terricolor Berlepsch, Ibis, 1880, p. 113. (Orinoco district, or Trinidad.)

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[14] See Peters, Check-list of the Birds of the World, vol. 6, 1948, p. 164.

Melanerpes Wagleri Salvin and Godman, Biologia Centrali-Americana., Aves, vol. 2, 1895, p. 416. (Lion Hill, Canal Zone.)

Melanerpes subelegans neglectus Richmond, Proc. U. S. Nat. Mus., vol. 18, Aug. 12, 1896, p. 668. (Bogotá, Colombia.)

Melanerpes wagleri sanctae-martae Bangs, Proc. Biol. Soc. Washington, vol. 12, June 3, 1898, p. 134. (Santa Marta, Colombia.)

Centurus rubricapillus costaricensis Aldrich, Sci. Publ. Cleveland Mus. Nat. Hist., vol. 7, Aug. 31, 1937, p. 81. (El Pozo, 25 feet, Río Terraba, Puntarenas, Costa Rica.)

Characters.—White and black bars on back nearly equal; under surface pale.

Measurements.—Male, wing 100.8-114.5 (108.2), culmen from base 21.6-27.6 (24.7) mm. Female, wing 95.9-112.6 (105.1), culmen from base 19.8-25.1 (22.5) mm.

Range.—Pacific slope from southwestern Costa Rica (Uvita, and the valley of Río Diquis) across Panamá (in western Chiriquí to 5,000 feet elevation) to the mouth of Río Tuyra (Punta de la Sabana), extending northward through the broad depression traversed by the Panamá Canal to the Caribbean coast between the Río Indio (El Uracillo, Coclé; Chilar, Colón) and Porto Bello including the valley of the Río Chagres (to Madden Dam); northern Colombia from the Río Sinú (Tierra Alta) through the drainage of the Río Magdalena (including the Río Cauca and the Río Cesar), the northern slopes of the Sierra Nevada de Santa Marta, and across Norte de Santander (Convención, Ocaña, Cúcuta); through northern Venezuela (except northern Falcón) south to the Río Orinoco, including Margarita Island; and Trinidad and Tobago.

The series now available in the U.S. National Museum covers this extensive range in sufficient detail to show that none of the supposed races that have been separated may be maintained, as there are no constant color differences. Birds from Colombia average slightly smaller, especially in the females, but local variation in measurements is such that no line of demarcation may be drawn. The range in size is shown by the following summary of wing measurements:

MALES

Costa Rica (11 specimens[15]), 105.0-113.0 (109.7) mm.
Panamá (31 specimens), 105.7-114.5 (110.6) mm.
Colombia (23 specimens), 100.8-111.4 (105.1) mm.
Venezuela (12 specimens), 104.4-113.2 (108.1) mm.

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[15] From the description of *C. r. costaricensis* by Aldrich.

FEMALES

Costa Rica (4 specimens[15a]), 104.5-113.0 (107.5) mm.
Panamá (25 specimens), 103.7-112.6 (105.1) mm.
Colombia (15 specimens), 95.9-106.7 (100.6) mm.
Venezuela (5 specimens), 104.4-108.8 (106.0) mm.

The range in Panamá, from present information, is separated from that in western Colombia by Darién and the lower Atrato basin.

Centurus rubricapillus subfusculus Wetmore:

Characters.—Decidedly darker above, with the white barring reduced; under surface much darker; red on crown of male darker.

Measurements.—Male, wing 101.8-108.5 (105.0), culmen from base 23.1-27.3 (25.2) mm. Female, wing 99.3-101.8 (100.4), culmen from base 22.0-23.4 (22.9) mm.

Range.—Isla Coiba and Isla Ranchería, off the Pacific coast of Veraguas, Panamá.

Centurus rubricapillus seductus (Bangs):

Malanerpes (sic) *seductus* BANGS, Auk, vol. 18, No. 1, January 1901, p. 26. (San Miguel, Isla El Rey, Archipiélago de las Perlas, Panamá.)

Characters.—Similar to *C. r. subfusculus,* but less dark above, and paler below, but darker both above and below than *C. r. rubricapillus;* lower breast and sides of abdomen distinctly light buff; bill averaging slightly longer and definitely heavier than in any of the other races.

Measurements.—Male (8 specimens), wing 101.0-105.0 (103.5), culmen from base 26.0-27.2 (26.6) mm. Female (7 specimens), wing 101.0-104.0 (102.2), culmen from base 22.4-24.7 (23.7) mm.

Range.—Isla El Rey, Pearl Islands, Panamá.

Centurus rubricapillus paraguanae Gilliard:

Centurus subelegans paraguanae GILLIARD, Amer. Mus. Nov., No. 1071, June 5, 1940, p. 7. (Cerro Santa Ana, Paraguaná Peninsula, Venezuela.)

Characters.—Decidedly lighter above than *C. r. rubricapillus,* especially on the upper back and scapulars; red of crown and hindneck in male often broken or completely interrupted across hindneck.

Measurements.—Males (6 specimens), wing 106.5-111.4 (108.3), culmen from base 25.6-28.3 (26.8) mm. Females (3 specimens), wing 101.2-106.0 (103.1), culmen from base 22.4-25.1 (23.6) mm.

Range.—Guajira Peninsula (Riohacha to Nazaret), Colombia; Paraguaná Peninsula and adjacent northern Falcón (Casigua to Cumarebo), Venezuela.

[15a] From the description of *C. r. costaricensis* by Aldrich.

The paler coloration of these birds separates them clearly from the typical form. The tendency toward reduced red on the head of the male is found occasionally in specimens of *C. r. rubricapillus* from the more eastern part of its range in Colombia and from the western section in Venezuela. It seems probable that the area inhabited by *paraguanae* is continuous around the western shore of the Gulf of Venezuela in extreme northern Zulia.

VENILIORNIS KIRKII CECILII (Malherbe): Red-rumped Woodpecker, Carpintero Rabadillaroja

Mesopicos Cecilii Malherbe, Rev. Mag. Zool., ser. 2, vol. 1, November 1849, p. 538. (Colombia.)

As I found these birds on four occasions only it was my assumption that few were present, though this may be erroneous since they live amid leafy branches where it is difficult to see them. The three secured were shot in the lower forest growth near the shore, as they climbed along the smaller branches. Near Catival two were seen in company, but elsewhere the birds appeared to be alone. Probably they range also through the high woodlands inland, as I saw one at the forest edge above the Colonia Central. In such haunts they would escape detection, except occasionally, because of their subdued colors and quiet movements. I was somewhat troubled to find that the crown feathers were so loosely attached that there was some slipping in spite of every care in preparation of my specimens.

The three taken are identified with the form found in Darién and the Comarca de San Blas in eastern Panamá, which ranges south through Colombia to western Ecuador, an interesting fact since the darker-colored *V. k. neglectus* of western Chiriquí and southwestern Costa Rica geographically is a near neighbor, much closer at hand. The Coiba specimens appear to be slightly smaller, with smaller bills, but are not sufficiently different to warrant separation on basis of the present series. One of the three, taken January 11, is a fully grown juvenile with barring on the lower surface averaging faintly narrower than in the other two.

Family Furnariidae: Ovenbirds, Spinetails

CRANIOLEUCA VULPINA (Pelzeln): Rusty Spinetail, Coli-aguda Rojiza

Synallaxis vulpina Pelzeln, Sitzungsb. Kon. Akad. Wiss. Wien, math.-nat. Cl., vol. 20, 1856, p. 162. (Engenho do Gama, Rio Guaporé, Mato Grosso.)

This is a bird of forest tangles and dense undergrowth where it clambers quietly but actively through creepers or matted branches, searching carefully through the leaves for food. I found them in such areas as the border of swampy woods near the lower Río Catival, in the higher, unbroken forest inland, usually ranging from the undergrowth to the lower branches of the trees, and at the borders of thickets. I noted them also at berry-bearing trees, in company with honeycreepers and fruit-eating flycatchers and manakins. They were solitary in habit, and though apparently fairly common, they remained so closely under cover that it was difficult to see them. Their method of progression was by climbing through dense cover, rather than by hopping about in more open branches, a mode of travel for which their large, strong feet are eminently suited. In general, they resembled *Cranioleuca erypthrops rufigenis* of the mountain forests on the Volcán de Chiriquí.

The species is one that has not been found previously outside South America, where its more northern representatives range north only to the Orinoco Valley in southern Venezuela and southeastern Colombia, so that it is remarkable to find this colony on Coiba Island, where its presence has been wholly unsuspected. The Coiba birds represent a distinct race, which is described herewith.

CRANIOLEUCA VULPINA DISSITA subsp. nov.

Characters.—Similar to *Cranioleuca vulpina alopecias* (Pelzeln)[16] but bill slightly heavier; no indistinct streaking on chest and foreneck; much brighter brown on lower surface.

Description.—U.S.N.M. No. 460809, male, Isla Coiba, Panamá, collected Jan. 21, 1956, by A. Wetmore (orig. No. 20353): A few tiny feathers on forehead, immediately behind nostril, dull white on external webs, dark neutral gray on inner webs, producing a barely distinguishable mottling; pileum russet; hindneck, back, scapulars and wings, including coverts, between tawny and russet; rump snuff brown; tail russet; lores dull white; a very narrow superciliary pinkish buff; sides of head dull cream-buff, with faint edgings of dusky neutral gray, producing slightly indicated streaks; throat white; sides of neck light chamois with a band of tawny along lower edge; breast and abdomen dull chamois; sides dull isabella color; flanks isabella color; under tail coverts tawny; edge of wing and under wing coverts cinnamon-buff, with edgings of tawny; inner webs of primaries and secondaries dark mouse gray, edged widely toward the base with dull

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[16] *Synallaxis alopecias* Pelzeln, Sitzungsb. Kon. Akad. Wiss. Wien, math.-nat. Cl., vol. 34, 1859, p. 101. (Forte do São Joaquim, Rio Branco, Brasil.)

tawny. Maxilla fuscous; mandible deep olive-buff; tarsus and toes Chaetura black; claws drab (from dried skin).

Measurements.—Males (3 specimens), wing 62.8-65.8 (64.1), tail 59.6-61.4 (60.3), culmen from base 14.0-15.4 (14.8), tarsus 17.2-18.0 (17.7) mm. Females (3 specimens), wing 61.6-62.4 (61.9), tail 58.2-60.3 (59.5), culmen from base 14.6-15.3 (15.1), tarsus 17.0-17.8 (17.4) mm.

Type, male, wing 65.8, tail 61.4, culmen from base 14.9, tarsus 17.2 mm.

Range.—Isla Coiba, off the Pacific coast of Veraguas, Panamá.

Remarks.—The general appearance of this bird, a remarkable addition to the Panamanian avifauna, is that of the group of forms allocated under the species name *Cranioleuca vulpina* (Pelzeln), though the decidedly brighter brown of the lower surface separates it from them so definitely as almost to warrant species status. The distribution of *C. vulpina* is mainly in Brasil, the most northern of its races previously known, *C. v. alopecias* (Pelzeln) and *C. v. apurensis* Zimmer and Phelps, extending only into the Orinoco Valley. In southern Venezuela, it is recorded from San Fernando de Atabapo and the Apure and Arauco Rivers to the lower Orinoco, coming barely within the limits of eastern Colombia at Maipures, near the mouth of the Río Vichada. The population resident on Isla Coiba thus is separated from its nearest relatives by the entire width of Colombia and the greater part of Panamá.

The name given to the bird found on Coiba is taken from the Latin *dissitus,* lying apart, or remote.

The allocation of the race described above has entailed a survey of *Cranioleuca vulpina* as a species. In the course of this I have noted especially the bird described originally as *Synallaxis vulpecula* by Sclater and Salvin from the Río Ucayali, Perú, now recognized as a member of the genus *Cranioleuca* and currently allocated as a subspecies of *C. vulpina.* Compared with the other geographic races, *vulpecula* differs widely in the decidedly heavier bill, and in the much more distinct pattern of spotting and streaking on the under surface. As a character of lesser value, the rump is nearly concolor with the back, instead of being quite different in color. On the whole it appears that the sum of these differences warrants recognition of *vulpecula* as a separate species, distinct from any others of the genus.

Family FORMICARIIDAE: Antbirds

THAMNOPHILUS DOLIATUS (Linnaeus): Barred Antshrike, Pavita Rayada

Lanius doliatus LINNAEUS, Museum Adolphi Friderici Regis, vol. 2, 1764, p. 2. (Surinam.)

It was no surprise to find the barred antshrike on Coiba, since the species is one that I had seen earlier on the islands in the Archipiélago de las Perlas, distant from the mainland. They were encountered immediately on my first day afield, usually in pairs, and remained as one of the birds that I heard and saw daily during the entire period of my work on the island. I found them in the beginning in tangled growths bordering the vegetable gardens, and in thickets back of the beaches, as well as in the swampy woodland near the river mouths, these being the usual mainland habitats. As I became more familiar with Coiba I learned, to my surprise, that they ranged also in tangles of vines in the crowns of the tallest trees throughout the high upland forest, often so far above the earth that they were beyond gunshot with the heaviest shotgun loads. I came therefore to believe that, like the common woodpecker of Coiba, this may have been a normal home for them on the mainland, from which they were able to descend, when the forests were cut, to live in second-

FIG. 6.—Barred Antshrike, Pavita Rayada.

growth thickets (rastrojo) and other similar ground cover. At the end of January there was such a decided increase in their singing that I believed that their main nesting season was at hand.

They were secretive, but at the same time alert, so that by quietly waiting it was usually possible to draw them out from the denser coverts to places where they could be seen. Usually the pair came together, peering about with neck outstretched and erected crest, presenting a highly attractive appearance. In the higher trees I found them at times somewhat of a bother, since, against the brighter light above, birds were seen only in silhouette so that I was continually deceived by the antshrikes while searching for pepper-shrikes and other wilder game.

This antshrike was another of the birds apparently long resident in Coiba that had darkened so in color in comparison with those of the mainland that this was easily seen as soon as the first examples came to hand. They represent a hitherto unrecognized race which I now describe.

THAMNOPHILUS DOLIATUS EREMNUS subsp. nov.

Characters.—Similar to *Thamnophilus doliatus nigricristatus* Lawrence,[17] but definitely darker in both sexes; male with black bars broader below, the throat heavily streaked with black, and the white markings reduced on the dorsal surface; female decidedly darker brown both above and below, the darker coloration being especially prominent on the lower surface, where it spreads to the throat and under wing coverts.

Description.—Type, U.S.N.M. No. 460815, female, from Isla Coiba, Panamá, collected Jan. 22, 1956, by A. Wetmore (orig. No. 20389): Crown auburn, merging to Mars brown on the tips of the feathers; hindneck russet with indistinct shaft streaks of dark to dusky neutral gray; lower hindneck, back, and scapulars auburn; lower rump cinnamon-buff; inner webs of remiges and of wing coverts dusky neutral gray; outer webs, and a narrow edging on inner webs, russett; upper surface of rectrices russet, lower surface verona brown, with a faintly indicated subterminal central wash of neutral gray forming an indefinite spot; frontal feathers immediately behind nostril light buff, with whitish bases; the rather bristly loral feathers likewise whitish basally, but with dull black tips; somewhat indefinite superciliary and side of head behind eye warm buff, with

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[17] *Thamnophilus nigricristatus* Lawrence, Proc. Acad. Nat. Sci. Philadelphia, vol. 17, 1865, p. 107. (Lion Hill, Canal Zone.)

a line of dusky neutral gray along the feather shafts; circlet around edge of eyelids light buff, barred lightly with dusky neutral gray on upper lid; malar region and side of neck warm buff; throat and foreneck warm buff, with the feathers light buff at base, a few with an indistinct shaft streak of dark neutral gray; chest, sides, and under tail coverts ochraceous-tawny; lower breast and abdomen slightly darker than ochraceous-buff; edge of wing russet; under wing coverts ochraceous-buff, the distal ones slightly paler. Maxilla dull black; mandible fuscous, grayer at tip, with the cutting edge drab-gray; tarsus and toes dusky neutral gray (from dried skin).

Measurements.—Males (7 specimens), wing 69.9-72.3 (71.0), tail 54.2-57.7 (56.0), culmen from base 20.3-22.7 (21.1), tarsus 26.4-27.8 (27.1) mm. Females (8 specimens), wing 66.9-71.0 (68.9), tail 53.0-58.5 (54.7), culmen from base 20.9-22.4 (21.5), tarsus 25.7-27.8 (26.7) mm.

Type, female, wing 69.8, tail 55.6, culmen from base 22.4, tarsus 26.7 mm.

Range.—Isla Coiba, off the Pacific coast of Veraguas, Panamá.

Remarks.—The definitely darker coloration that marks this race when compared with *Thamnophilus doliatus nigricristatus,* though readily evident in both sexes, is particularly outstanding in the female. For this reason it has seemed desirable to select a female specimen as type. The male has the black bars of the lower surface wider than in *nigricristatus,* and also has the markings extended across the abdomen with little diminution in amount, so that this area is only slightly, if at all, less heavily barred than the rest of the lower surface. The throat also is more heavily marked with streakings of black. The birds agree with *nigricristatus,* and differ from *T. d. pacificus* in having only a relatively small amount of white concealed in the bases of the black crown feathers.

While comparison in the diagnosis has been made with *T. d. nigricristatus* of the adjacent mainland, the darker coloration is rather more similar to the condition found in the distantly located *T. d. intermedius,* which ranges from eastern Costa Rica and eastern Nicaragua north to Tamaulipas and San Luis Potosí. The male *intermedius,* however, has extensive white markings concealed in the crown, and also averages larger, except in the bill, which is slightly heavier in the birds from Coiba. The female of *eremnus* differs from *intermedius,* as it does from *nigricristatus,* in much darker color.

The subspecific name of the form here described is taken from the Latin adjective *eremnus,* swarthy, or dark.

Family Cotingidae: Cotingas

ATTILA SPADICEUS CITREOPYGUS (Bonaparte): Yellow-rumped Attila, Pájaro Gritón

Dasycephala citreopyga Bonaparte, Compt. Rend. Acad. Sci. (Paris), vol. 38, 1854 (not earlier than April 3), p. 657. (Nicaragua.)

Judging from their calls, attilas were fairly common, both in the swampy areas at the mouth of the Río Catival, and in the high forest inland, but as usual the birds remained hidden. They were less vociferous than is common, and after calling once or twice ordinarily they became quiet so that some time lapsed before I was able to collect one. On January 22 Vicente and I located one somewhere among fairly low branches and after half an hour of intensive scrutiny of the tree, leaf by leaf and twig by twig, Vicente's keen eye detected a slight movement, and with binoculars I could make out the side of the head and part of the bill of the bird through an opening in the screen of leaves. This was a male nearly in breeding condition, and the only one taken. Though we spent much time in looking we saw no others. Some of the men who worked in the edge of the forest were familiar with the excited calls of these birds, but were uncertain as to their source.

The one taken is in greenish phase, with only slight indication of brown on the lower back and tertials, and the fore crown quite gray. The measurements are as follows: Wing 92.2, tail 71.0, culmen from base 28.1, tarsus 24.1 mm. In wing length it agrees with the form of Central America, being larger than *A. s. sclateri* of the eastern half of the Republic of Panamá.

TITYRA SEMIFASCIATA COSTARICENSIS Ridgway: Masked Tityra, Borreguito

Tityra semifasciata costaricensis Ridgway, Proc. Biol. Soc. Washington, vol. 19, Sept. 6, 1906, p. 119. (Bonilla, Atlantic slope of Costa Rica.)

These cotingas were found in the higher branches of the forest trees, especially those with dead limbs, where they rested in the sun, or peered into cavities of various sizes. It is probable that they are more common than the few records that I made of their occurrence indicate, since they range regularly on or above the higher tree crowns, where they are hidden from below by the screen of leaves. Most of them were noted along the trails where the forest growth was more open. The two males and one female taken for specimens agree in color with skins from the western half of Panamá. As they are birds of strong flight it is possible that they cross back and forth to the mainland.

The name "borreguito" is given to them from the light-colored plumage of the male. They are also called puerquito or pájaro chancho, from their curious grunting calls.

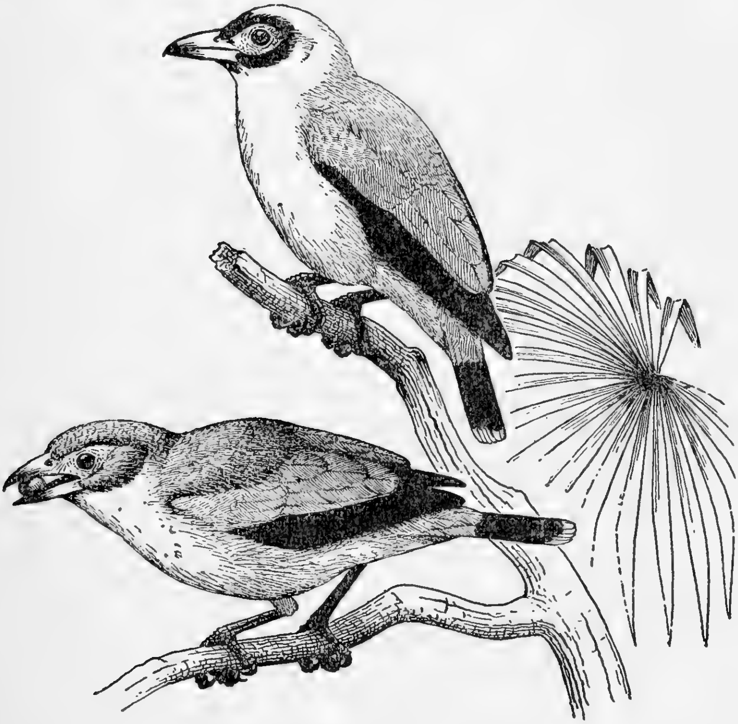

FIG. 7.—Masked Tityra, Borreguito.

Family PIPRIDAE: Manakins

CHIROXIPHIA LANCEOLATA (Wagler): Lance-tailed Manakin, Toledo

Pipra lanceolata J. WAGLER, Isis (of Oken), 1830, col. 931. (Cerro Turumiquire, Sucre, Venezuela.)

The attractive lance-tailed manakin, the only one of its family that I found on Coiba, was common in undergrowth everywhere on the island, ranging through the shadows of the high forest, in brush in the swampy woods near the mouths of the rivers, and in the low rastrojo of abandoned fields. Their musical, whistled calls came to us daily in our work afield, though it was necessary to watch closely to observe the musicians, as they remained behind cover. When not alarmed they came into open branches where the males postured, called, and drove at one another in harmless threats of combat. In these displays the full skin of the back of the neck is distended by an air sac that fills the space between the shoulders and the base of the skull, so that this region appears greatly enlarged. The musical note *to-le-do,* which gives them their common name, somewhat shortened in utterance, is easily imitated, and often serves to decoy the birds into view. They are known also as soldado. The series collected is similar in size and color to birds of the mainland.

Family TYRANNIDAE: Tyrant Flycatchers

MUSCIVORA TYRANNUS MONACHUS (Hartlaub): Fork-tailed Flycatcher, Tijereta Sabanera

Tyrannus (*Milvulus*) *monachus* HARTLAUB, Rev. Zool., vol. 7, June 1844, p. 214. (Guatemala.)

One seen at the San Juan work camp is attributed to subspecies on the basis of probability. The record has definite significance, as the casual presence of this flycatcher on an island so far from the mainland is indicative of some migratory movement, a matter that has been questioned. The species must be regarded as of irregular occurrence, since it is only in recent years that clearings have made a suitable habitat for it on Coiba.

They are called Tijereta de Palo also. Country people usually shorten the name to Tijereta, though it must be added that this same name is sometimes used for the frigate-bird. When there may be confusion the latter is called Tijereta del Mar. Golondrina is another country name often wrongly applied to this flycatcher.

TYRANNUS MELANCHOLICUS CHLORONOTUS Berlepsch: Tropical Kingbird, Pechi-amarillo Grande

Tyrannus chloronotus BERLEPSCH, Ornis, vol. 14, 1907, p. 474. (Temax, Yucatán.)

The tropical kingbird was found commonly on dead limbs and other perches in the lower brush, among the growths bordering the beaches, resting always when it had a clear view from which to watch for the insects that form an important part of its food. The extensive pastures back of the convict camps were favorite haunts, and it is one of the two species of birds seen regularly in this comparatively new open habitat. Undoubtedly it is more abundant, now that such areas have been opened, than it was formerly when the forests restricted it mainly to fringing areas near the beaches and around the river mouths. On January 17 I recorded a mated pair in evident search for a nest site.

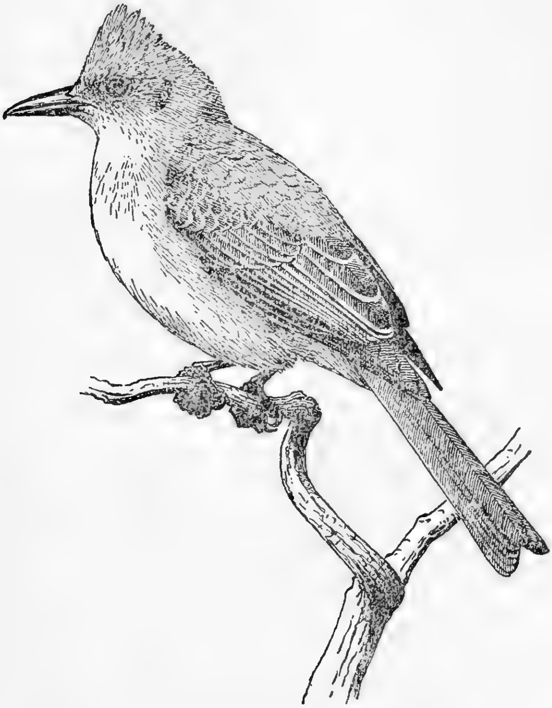

FIG. 8.—Tropical Kingbird, Pechi-amarillo Grande.

MYIODYNASTES MACULATUS DIFFICILIS Zimmer: Streaked Flycatcher, Piquigordo Rayado

Myiodynastes maculatus difficilis ZIMMER, Amer. Mus. Nov., No. 963, Nov. 18, 1937, p. 9. (Bebedero, Costa Rica.)

The streaked flycatcher was found on few occasions, usually in the trees along the forest trails, or occasionally in the border of mangrove swamps at the river mouths. As they called seldom at this season they may have been more common than the five specimens collected may indicate, since it was not easy to see them in the leafy branches amid which they usually rested.

MEGARYNCHUS PITANGUA MEXICANUM (Lafresnaye): Boat-billed Flycatcher, Pico Canoa

Scaphorhynchus mexicanus Lafresnaye, Rev. Mag. Zool. (Paris), ser. 2, vol. 3, October 1851, p. 473. (México.)

One was observed on Isla Ranchería on February 4. Countrymen usually include this species under the all-inclusive name of pechi-amarillo.

MYIARCHUS CRINITUS BOREUS Bangs: Great Crested Flycatcher, Pechi-amarillo de Paso

Myiarchus crinitus boreus Bangs, Auk, vol. 15, No. 2, April 1898, p. 179. (Scituate, Mass.)

A male taken on the Punta Damas trail January 19 was the only one recorded. In Panamá, attention is drawn to this bird by its clear call note, and when seen it is readily distinguished from its close relatives by the cinnamon-brown tail.

MYIARCHUS FEROX PANAMENSIS Lawrence: Short-crested Flycatcher, Pechi-amarillo Común

Myiarchus Panamensis Lawrence, Ann. Lyc. Nat. Hist. New York, vol. 7, May 1860, p. 284. (Atlantic slope of Canal Zone on the Panama Railroad.)

This was the most common species of the flycatcher family, found in the crown of the high forest, in brush back of the beaches, and in the wooded swamps near the river mouths. The birds move about deliberately, watching for insects, and also come to berry-bearing trees. Though they are active in seizing prey in the air, they regularly search for food, rather than rest in one spot waiting for insects to pass. I saw one fly out at a butterfly which, however, it missed. The call note is a high-pitched *whee-ee-ee,* a sound with little carrying power. Two were taken on Isla Ranchería February 4.

The specimens obtained on Coiba Island resemble those from Veraguas and Chiriquí in being slightly darker, more grayish above, than typical specimens from the Province of Panamá eastward into Colombia, and thus show some approach to the grayish *Myiarchus ferox actiosus* Ridgway of southwestern Costa Rica. All the Panamanian birds, including those of Coiba, are much brighter yellow on the lower breast and abdomen and darker gray on chest and foreneck than *actiosus.*

CONTOPUS CINEREUS (Spix): Tropical Pewee, Cazamoscas Tropical

Platyrhynchus cinereus Spix, Avium species novae . . . Brasiliam, vol. 2, 1825, p. 11, pl. 13, fig. 2. (Rio de Janeiro, Brasil.)

This friendly little flycatcher rests on low perches in forest areas relatively free of undergrowth, where it can see clearly in order to watch for its food of small flying insects. When its keen eye sights such prey it darts out quickly and seizes it, often with an audible snap of the bill. It then wheels gracefully to return to a perch, frequently the same twig from which it had made its sally. Often it is encountered in shaded areas of subdued light where its dull colors blended closely with the dark background. It is especially common along semi-open forest trails, and at times I found it in the brush back of the beaches. More rarely I sighted one in the high treetops, though it may have ranged regularly in the forest crown, where the leaves concealed it.

Those familiar with the wood pewees of the north will recognize it without difficulty, and will also note its smaller size and darker colors. The birds were entirely silent.

The specimens from Coiba are distinctly darker than those of the mainland, and are to be distinguished by the following name:

CONTOPUS CINEREUS AITHALODES subsp. nov.

Characters.—Similar to *Contopus cinereus brachytarsus* (Sclater)[18] but decidedly darker, more olive above and below; edge of wing washed with cinnamon.

Description.—Type, U.S.N.M. No. 460992, male, Isla Coiba, Panamá, collected Jan. 19, 1956, by A. Wetmore (orig. No. 20326): Pileum fuscous-black; back, rump and upper tail coverts hair brown; wings, including the coverts, Chaetura drab, with middle and greater coverts tipped indistinctly with hair brown, and greater coverts, in addition, edged lightly on ends of outer webs with dull white, the anterior wing bar being indistinct, the posterior one definite; tertials and secondaries edged lightly with dull white, which extends around the distal end; outermost primary also edged with dull white; rectrices Chaetura drab, the outer webs edged with hair brown basally; lores and feathers on margin of lower eyelid white; side of head hair brown; upper foreneck white, with the feathers on chin and throat basally, and on sides, mouse gray, producing indistinct streaks; chest light mouse gray, with a wash of deep olive-buff, shading on lower

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[18] *Empidonax brachytarsus* P. L. Sclater, Ibis, vol. 1, October 1859, p. 441. (Córdoba, Veracruz.)

breast to dull cream buff, and in turn to ivory yellow on the abdomen; under tail coverts hair brown, margined with olive-buff; sides hair brown, becoming light grayish olive on the flanks; edge of wing and tips of outermost under wing coverts dull cinnamon; innermost under wing coverts edged with dull cream-buff. Maxilla black; mandible olive-buff, the sides of the rami colonial buff; tarsus, toes, and claws black (from dried skin).

Measurements.—Males (11 specimens), wing 65.2-71.5 (68.7), tail 54.0-61.1 (57.0), culmen from base 14.8-15.9 (15.4), tarsus 11.5-12.9 (11.9) mm. Females (6 specimens), wing 63.2-68.4 (66.4), tail 52.8-57.9 (55.4), culmen from base 14.8-16.1 (15.4, average of 5), tarsus 11.5-12.7 (11.9) mm.

Type, male, wing 71.5, tail 58.6, culmen from base 15.4, tarsus 11.9 mm.

Range.—Isla Coiba, off the Pacific coast of Veraguas, Panamá.

Remarks.—While there is some individual variation, the paler specimens in the series are separable at a glance by definitely deeper olive color from the darker ones in the numerous skins available from the mainland range of *C. c. brachytarsus.* In average size *C. c. aithalodes* is slightly smaller, but there is overlap in the larger measurements with those of *brachytarsus.*

The subspecific name is taken from the Greek αιθαλωδης, sooty, black.

TODIROSTRUM CINEREUM FINITIMUM Bangs: Common Tody-flycatcher, Piqui-ancho Común

Todirostrum cinereum finitimum Bangs, Proc. Biol. Soc. Washington, vol. 17, May 18, 1904, p. 114. (San Juan Bautista, Tabasco, México.)

This tiny tody-flycatcher, marked by its yellow breast and broad, elongated bill, ranged in shrubs, the lower woods, and the trees back of the shoreline. Usually they are found in pairs, male and female hopping about near one another, moving through the branches with the narrow-feathered tail cocked over the back like little wrens. They are active in pursuit of insects and adept at snapping up the prey that they encounter among the twigs and leaves. Occasionally I found them among mangroves. One that I shot in such a location was seized and carried off by a large black lizard the instant it touched the ground.

The six prepared for specimens in series are very faintly deeper yellow on the lower surface than skins from the mainland, but individually they may not be separated.

CAPSIEMPIS FLAVEOLA SEMIFLAVA (Lawrence): Yellow Tyrannulet, Moscareta Amarilla

Elainea semiflava LAWRENCE, Ann. Lyc. Nat. Hist. New York, vol. 8, November 1865, p. 177. (David, Chiriquí.)

In the edge of the forest I found a few coming to low berry-bearing trees in company with other small birds, and also noted them in thickets at the border of mangroves and in old fields that were covered with brush, this being a common habitat with them on the mainland. They move about actively, usually in the lower branches or near the ground, often twitching the long tail like a gnatcatcher. The four taken resemble specimens from the mainland.

ELAENIA CHIRIQUENSIS CHIRIQUENSIS Lawrence: Lesser Elaenia, Moñoncita

Elainea chiriquensis LAWRENCE, Ann. Lyc. Nat. Hist. New York, vol. 8, November 1865, p. 176. (David, Chiriquí.)

I found this small elaenia visiting berry-bearing trees in company with manakins and other small birds, feeding in guarumo trees in the forest, and also ranging in low second growth bordering the cultivated fields, these being usual haunts of the species. In addition, they ranged over the forest crown in the summits of the tallest trees, where it was only occasionally that I could secure one for a specimen because of the great distance above the ground.

The nine specimens obtained agree in color with skins from Veraguas and Chiriquí. Two taken have the merest trace of white in the crown. In more or less worn plumage in the nesting season they become much darker above than when freshly molted.

ELAENIA FLAVOGASTER SILVICULTRIX Wetmore: Yellow-bellied Elaenia, Moñona Pechi-amarilla

Elaenia flavogaster silvicultrix WETMORE, Proc. Biol. Soc. Washington, vol. 59, Mar. 11, 1946, p. 51. (Isla San José, Archipiélago de las Perlas, Panamá.)

These elaenias were more common than the smaller species, and also were more prominent because of their louder calls. I found them regularly at trees bearing small ripening drupes, also in the thickets around the cultivated fields, and in the swampy forests along the lower courses of the rivers. Inland they were seen in the forest crown high above the ground, descending lower at times to feed in the guarumo trees. They are easily distinguished from the smaller moñona of the same genus by yellower abdomen and more prominent crest. The larger size also is evident on many occasions.

The excellent series of 16 skins from Coiba agrees so closely with the race that I have named earlier from the Pearl Islands in the Gulf of Panamá that they must be identified under that name. The Coiba birds, when compared in series with birds from Isla San José, Isla Pedro González, and Isla El Rey in the Archipiélago de las Perlas, average slightly darker but not sufficiently so to warrant their separation. It is interesting, however, to observe that this heavier pigmentation, when compared with the race of the adjacent mainland *Elaenia flavogaster pallididorsalis,* follows the pattern of darker coloration that marks other resident forms found on Coiba.

MYIOPAGIS VIRIDICATA ACCOLA Bangs: Orange-crested Elaenia, Moñona Copete-anaranjada

Myiopagis placens accola BANGS, Proc. New England Zoöl. Club, vol. 3, Jan. 30, 1902, p. 35. (Boquete, Chiriquí.)

This is primarily a forest species, found from the lower undergrowth to the intermediate branches of the higher trees, though I saw it occasionally in the platano plantations, in more open localities along the forest trails, and in fruiting trees with other small birds. It moves methodically among the smaller twigs, usually alone, and is often overlooked because its greenish and yellowish colors are not at all conspicuous in the subdued light of its forest haunts. There is seldom any hint of the brilliant orange of the crest until the bird is in the hand. It was fairly common.

The 12 skins taken on Coiba agree in color with birds from Chiriquí.

SUBLEGATUS ARENARUM ARENARUM (Salvin): Scrub Flycatcher, Moñona Ceniza

Elainea arenarum SALVIN, Proc. Zool. Soc. London, August 1863, p. 190. (Puntarenas, Costa Rica.)

These flycatchers were found in scrub growth back of the beaches, and in the border of mangroves, never in the densely shaded high forest. They were encountered alone, resting on leafy twigs, or occasionally feeding in fruiting trees with other birds. They moved quietly among the thickets, flying across small openings with undulating flight, and were silent. Though not timid it was difficult to see them because of their subdued colors.

The over-all similarity in color in this species throughout its extensive range makes careful study necessary to determine the geographic races. Twelve years ago, when I was studying collections from San José and Pedro González Islands in the Perlas group, the comparative material available from the mainland and from Colombia was so meager that my identification of skins from the island localities as *arenarum* was purely tentative. In the interim a fair series has been assembled through my own work in Panamá and through the collections made by M. A. Carriker, Jr., across northern Colombia, so that now it is possible to deal with these birds with some certainty.

In brief, the 19 skins from Panamá now at hand are quite uniformly gray on the dorsal surface, clear, light gray on the chest and foreneck, and paler yellow on the sides, with the axillars somewhat more yellow, being similar in these colors to typical *S. a. arenarum* from southwestern Costa Rica. The six obtained from Coiba Island agree with *arenarum,* as do also two from Taboguilla Island. The mainland series, which is uniform, includes skins from the eastern side of the Azuero Peninsula (Paris, Parita, Monagrillo, Los Santos), Canal Zone (Farfan, Corozal) and the eastern half of the Province of Panamá (Chico, Chepo, Majé).

The race *S. a. atrirostris* (Lawrence), with type locality Cartagena, northern Bolívar, Colombia, compared with *arenarum,* has the dorsal surface darker, slightly olive-gray, the crown cap slightly darker, and the sides darker, more grayish yellow. The fresh material now at hand in the National Museum collections includes a pair of topotypes from Cartagena, and a series of 12 others from Bolívar and northern Magdalena. The 10 adults that I took on San José and Pedro González Islands, Archipiélago de las Perlas, in 1944 agree with *atrirostris* and are so identified. They would seem therefore to represent an ancient establishment of the species, perhaps from the time when the formicariid *Formicivora grisea,* common across northern Colombia but found nowhere on the mainland of Panamá, also reached the same islands.

CAMPTOSTOMA OBSOLETUM (Temminck): Southern Beardless Flycatcher, Moñona Lampiña

Muscicapa obsoleta Temminck, Nouveau recueil de planches coloriées d'oiseaux, livr. 46, 1824, pl. 275, fig. 1. (Curytiba, Paraná, Brasil.)

The moñona lampiña is so small that it is probably more common on Coiba than is indicated by the four specimens obtained. One of these was secured in high virgin forest, the others in or near the mangroves along the beaches. Apparently they range across the high forest crown, as well as in the lower growth. They move rather quietly among the leaves, and when they fly usually disappear behind cover. The Coiba specimens are so much darker than those of the adjacent mainland that they require a name.

CAMPTOSTOMA OBSOLETUM ORPHNUM subsp. nov.

Characters.—Similar to *Camptostoma obsoletum flaviventre* Sclater and Salvin,[19] but darker, more olive, above, particularly on the crown.

Description.—Type, male, Isla Coiba, Panamá, collected Jan. 29, 1956, by A. Wetmore (orig. No. 20521): Pileum and upper hindneck Chaetura black, the tips of the longer feathers edged lightly with deep olive; lower hindneck, back, and scapulars deep olive; rump and upper tail coverts grayish olive; wing coverts and remiges blackish mouse gray; lesser wing coverts edged lightly with deep olive; middle and greater wing coverts tipped with white, forming two well-marked wing bars; tertials edged narrowly with white; secondaries edged lightly with Marguerite yellow; rectrices dark mouse gray, edged faintly with deep olive toward the base, and tipped narrowly with dull white; throat and upper foreneck dull white; lower foreneck and chest primrose yellow, changing to dull naphthalene yellow on lower breast and abdomen; sides of breast grayish olive; under tail coverts, edge of wing, and under wing coverts Marguerite yellow, the outer series of the last-mentioned being mouse gray centrally; inner webs of primaries and secondaries edged narrowly with dull white. Bill fuscous, except for the base of the mandible, which is wood brown, and the gape, which is honey yellow; tarsus and toes dull black (from dried skin).

Measurements.—Males (2 specimens), wing 52.0-52.1 (52.0), tail 39.2-39.3 (39.2), culmen from base 9.9-10.1 (10.0), tarsus 13.2-13.9 (13.5) mm. Females (2 specimens), wing 47.1-47.2 (47.1), tail 35.0-35.2 (35.1), culmen from base 9.7-10.4 (10.0), tarsus 13.6-14.0 (13.8) mm.

Type, male, wing 52.0, tail 39.3, culmen from base 9.9, tarsus 13.9 mm.

Range.—Isla Coiba, off the Pacific coast of Veraguas, Panamá.

Remarks.—Darker coloration sets the four specimens of this race off definitely from the series of 37 *Camptostoma o. flaviventre* that I have had available for comparison. In addition the bill appears very faintly larger, a minor difference that perhaps would disappear in a larger series of measurements, since it is equaled by the larger specimens of *flaviventre.*

The subspecific name is taken from the Latin *orphnus,* dark, dusky.

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[19] *Camptostoma flaviventre* P. L. Sclater and O. Salvin, Proc. Zool. Soc. London, 1864 (February 1865), p. 358. (Panamá.)

LEPTOPOGON AMAUROCEPHALUS Tschudi: Brown-capped Leptopogon, Moñona Coronimorena

Leptopogon amaurocephalus Tschudi, Fauna Peruana, Aves, 1846, p. 162. (São Paulo, Brasil.)

These birds were found on only two occasions, on January 31 and February 3, inland in high forest, on a broad ridge at about 500 feet elevation. On the first day two moved rather slowly through the middle branches, where it was difficult to see them in the dim light filtering through the leaves high overhead. One, that in the hand proved to be a male in breeding condition, called at intervals, a low trilling *pree-ee-ee,* while it trembled its partly open wings. On the second occasion another breeding male was taken in the same general area as it moved quietly among the branches above the higher undergrowth. In life, from this limited observation, there was little to distinguish these birds from the orange-crested elaenia (*Myiopagis viridicata*) that also ranged in this dimly lighted zone in the forest, as the two are quite similar in form and movement. In the hand, the relatively small feet of the leptopogon immediately attract attention.

Following is a description of bill, feet, and eyes taken from the adult male shot January 31: Iris light brownish yellow; maxilla and tip of mandible dusky neutral gray; base of mandible dull Marguerite yellow; tarsus and toes neutral gray; claws fuscous. I was interested to note that the elongated median apterion, characteristic of birds of this and related groups, found down the center of the expanded dorsal feather tract, was so narrow that close scrutiny was required to distinguish it.

The two specimens differ so definitely from the race of this species found on the mainland of Panamá that I have no hesitance in describing the Coiba Island bird as a race new to science.

LEPTOPOGON AMAUROCEPHALUS IDIUS subsp. nov.

Characters.—Generally similar to *Leptopogon amaurocephalus faustus* Bangs[20] but decidedly grayer throughout; much paler yellow below, and more grayish green above; no prominent dark area on the auriculars; wing bars paler; under wing coverts lighter.

Description.—Type, U.S.N.M. No. 460975, male, Isla Coiba, Panamá, collected Feb. 3, 1956, by A. Wetmore (orig. No. 20587): Small feathers immediately behind nostrils dull white; pileum clove brown, the feathers margined indistinctly with sepia; hindneck, back, scapulars, and rump grayish grape green; upper tail coverts light

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[20] *Leptopogon amaurocephalus faustus* Bangs, Auk, vol. 24, no. 3, July 1907, p. 300. (Boruca, Costa Rica.)

brownish olive; lesser wing coverts grape green; middle and greater coverts varying from hair brown to Chaetura drab, tipped with dull cream-buff to form two prominent wing bars; outer web of the large alula buffy brown; primaries and secondaries Chaetura drab, with the outer web edged with light yellowish olive; innermost tertial light brownish olive at tip and in a narrow line along shaft, varying through cream-buff to cartridge buff on the outer margins of the webs; rectrices dull light brownish olive, with the outer webs margined lightly with buffy olive; anterior lores deep olive-buff, with the bristly feather tips dark neutral gray; loral area immediately in front of the eye indistinctly hair brown, with shaft lines of dull Marguerite yellow; anterior segment of eye ring dull chamois, posterior segment dull Marguerite yellow, produced slightly as an indistinct line behind the eye; side of head grayish olive, the tips of the feathers very faintly darker, and the shafts faintly paler, not, however, producing a distinct patch or spot; throat and upper foreneck light olive-gray, with the sides of the feathers spotted indefinitely with dull Marguerite yellow, producing an appearance of irregular streaks: lower foreneck and chest light grayish olive, washed with light yellowish olive; lower breast, abdomen, and under tail coverts primrose yellow, becoming Marguerite yellow at sides of abdomen; sides dull vetiver green merging gradually into the lighter color of lower breast and abdomen; edge of wing dull colonial buff; under wing coverts between cartridge buff and cream-buff; inner webs of secondaries cream-buff, becoming light vinaceous-buff in the inner webs of the secondaries. Bill dusky neutral gray, becoming dull olive-buff on the mandibular rami; tarsus and toes fuscous (from dried skin).

Measurements.—Males (2 specimens), wing 64.3-65.3, tail 57.4-57.5, culmen from base 13.7-13.8, tarsus 14.4-14.5 mm. (The first measurement in each case is that of the type.)

Range.—Isla Coiba, off the Pacific coast of Veraguas, Panamá.

Remarks.—Endemism found in the birds of Coiba Island, where these differ subspecifically from their respective mainland populations, is expressed in the main in definitely darker coloration, or in greater extension of the more heavily pigmented part of the plumage pattern. It is therefore of especial interest to note in the present bird a paler, grayer appearance when it is compared with its nearest mainland congener. Actually the two skins from Coiba are more similar in appearance to *L. a. orenocensis* Zimmer and Phelps from the Río Orinoco in southern Venezuela, from which however they are easily separated by lighter color.

The specific name is taken from the Greek, ἴδιος, peculiar, distinct.

PIPROMORPHA OLEAGINEA LUTESCENS Griscom: Ochre-bellied Flycatcher, Moscareta Vientre Canelo

Pipromorpha oleaginea lutescens GRISCOM, Amer. Mus. Nov., No. 280, Sept. 10, 1927, p. 9. (Santa Fé, Veraguas.)

These small birds rest on open perches in the tops of the undergrowth, or in the lower branches of trees. As they are found in shaded forest, their subdued colors make them inconspicuous in their shadowed haunts, particularly since they tend to rest quietly for minutes at a time. On Coiba I saw them in heavy forest, and in more open woodland behind the mangroves.

The four specimens from Coiba are very faintly duller green above than mainland examples. The three males also have very slightly longer wings and tails than those from Veraguas and eastern Chiriquí. The differences however are too tenuous to warrant a name.

Family HIRUNDINIDAE: Swallows

PROGNE CHALYBEA CHALYBEA (Gmelin): Gray-breasted Martin, Golondrina de Iglesia

Hirundo chalybea GMELIN, Systema naturae, vol. 1, pt. 2, 1789, p. 1026. (French Guiana.)

The gray-breasted martin was seen regularly in and around dead trees standing in the clearings behind the convict camps, or flying about the plantations of coconut palms. On February 4, while in a cayuco a mile offshore and to the south of Isla Ranchería, one flew past in a line that led back to distant Isla Canal de Afuera, indicating that these birds of strong flight cross easily between the widely separated islands of these waters. Three males in nonbreeding stage were prepared as specimens.

HIRUNDO RUSTICA ERYTHROGASTER Boddaert: Barn Swallow, Golondrina de Paso

Hirundo erythrogaster BODDAERT, Table des planches enluminéez, 1783, p. 45. (French Guiana.)

The barn swallow, an abundant migrant and visitor from the north on the mainland of Panamá, appears to wander over the adjacent waters. On Coiba Island I collected a female bird from the telephone wire near Bajo España January 12. Another appeared January 25 at the Colonia Central during a rain, and January 27 I saw two near the mouth of the Río Catival. Since I had these areas under regular observation and saw no others, it appears that these swallows are of only casual occurrence.

IRIDOPROCNE ALBILINEA (Lawrence): Mangrove Swallow, Golondrina Manglatera

Petrochelidon albilinea Lawrence, Ann. Lyc. Nat. Hist. New York, vol. 8, May 1863, p. 2. (Atlantic slope near the Panama Railroad, Canal Zone, Panamá.)

These small swallows, of pleasing color in their contrast of white lower surface and rump and steely blue-green head, wings, tail, and back, are found always near or over water. On Coiba I recorded two January 27 on the flats laid bare by the tide at the mouth of the Río Catival, and February 2 I collected a pair flying over a wet meadow at Bajo España.

A race of the mangrove swallow has been described by van Rossem [21] from southern Sonora with range south to Nayarit. I am not able to recognize this from the fair series in the National Museum and the American Museum of Natural History. The material that should represent *rhizophorae* includes seven specimens from southern Sinaloa (Mazatlán, Los Lates near Rosario, Escuinapa) and seven from near the coast of Nayarit (Tuxpan, San Blas). From Panamá, the type locality of *albilinea,* there is a good series, including birds collected personally that I know to be breeding, so that with these the possibility of migrants from northwestern México is eliminated. Three birds from Los Lates near Rosario, Sinaloa, in freshly molted dress, are very distinctly greenish above, being equaled in this only by a skin in similar stage from Aguadulce, Province of Coclé, Panamá. As the season advances the dorsal color, through wear, becomes steadily bluer. A pair from the Río San Pablo, near Soná, Veraguas, Panamá, that represent the breeding stock of that area, are slightly bluer than any I have seen from Sinaloa, so that the difference in darker blue of the northern birds, listed by van Rossem, does not hold.

The distinction of greater amount of frontal and loral white proposed as one of the prominent characters of the northwest Mexican race varies decidedly in the Panamanian series, several from the latter group being as white as the northern birds, others less so. In some the frontal feathers are pure white at the base, this color becoming exposed by wear. Specimens with this character include birds shot in Panamá December 16, February 2 and 23, May 29, and June 2, so all of them could not be considered migrants from the north. There is similar individual variation in the rump color, and in size of the bill. I am forced to conclude that the population of northwestern México may not be separated by name.

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[21] *Iridoprocne albilinea rhizophorae* van Rossem, Proc. Biol. Soc. Washington, vol. 52, Oct. 11, 1939, p. 155. (Tóbari Bay, Sonora.)

The status of the little-known *Iridoprocne stolzmanni* (Philippi), described from the coast of Perú, also requires further study, since the characters ascribed to it appear to represent such a considerable difference from *albilinea*, that it should be treated as a separate species. I have therefore listed the Panamanian birds under the specific name, since no subspecies are apparent.

Family Troglodytidae: Wrens

TROGLODYTES AEDON Vieillot: House Wren, Ruiseñor

Troglodytes aedon Vieillot, Histoire naturelle des oiseaux de l'Amérique septentrionale, vol. 2, 1807 (1808?), p. 52, pl. 107. (New York, N. Y.)

The house wren was widely distributed since on Coiba it is a forest inhabitant, as it is on the islands in the Archipiélago de las Perlas.

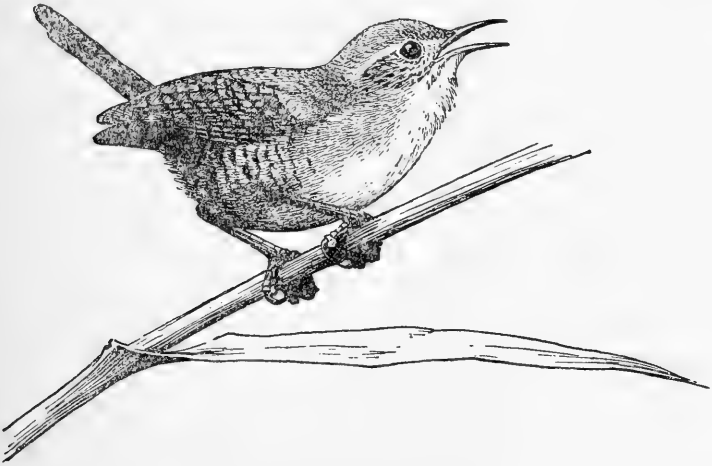

Fig. 9.—House Wren, Ruiseñor.

It was common in the brush near the beach line, also in the swampy woods back of the mangroves, and was encountered regularly throughout the high interior forest. Normally, I found the birds around fallen trees or in masses of vines in the undergrowth. When they ranged occasionally in the higher branches this seemed to be unusual. In the forest areas they were shy and often difficult to find, though they might call near at hand; but they had learned to come about the buildings of the headquarters and the penal camps to search around the roofs and walls and the crowns of the coconut palms, and then were more confiding.

It has long been my opinion that the southern house wrens are better songsters than their representatives in the United States, as their songs include fewer harsh, rattling sounds, and the bird on Coiba definitely excells its mainland relatives. Their rolling, trilling notes were pleasing to the highest degree, and as they sang regularly their music was a constant delight to me, both in my morning excursions afield, and in the afternoons when I was occupied in our quarters. The birds truly merited their name of ruiseñor, borrowed from the nightingale, famous for its song in Spain. The wrens were nesting at this season, and well-grown fledglings were brought to me on January 26.

With the considerable increase in information in recent years on house wrens as a group there is no longer reason or value for the separation of the southern races under the specific name *musculus,* since there is no clear-cut character that distinguishes these birds from those of farther north. The darker coloration of the Coiba population was noticeable at once when I first encountered the birds in life. The description of this race follows.

TROGLODYTES AEDON CARYCHROUS subsp. nov.

Characters.—Similar to *Troglodytes aedon intermedius* Cabanis,[22] but darker, brighter brown; bill much larger and heavier.

Description.—Type, U.S.N.M. No. 461091, male, Isla Coiba, Panamá, collected Jan. 21, 1956, by A. Wetmore (orig. No. 20373): Crown Prout's brown, the centers of the feathers dusky neutral gray, forming irregular dark spots; hindneck and back bister, the feathers with faint concealed bars of dark neutral gray; rump and upper tail coverts russet; lesser and middle wing coverts Prout's brown, with partly concealed bases dark neutral gray; greater wing coverts and outer webs of secondaries russet, barred with dusky neutral gray; primaries dull black, barred narrowly on outer webs with clay color; tail Mars brown, becoming Verona brown on the outer rectrices, barred narrowly and irregularly with dull black; lores pinkish buff, the feathers with very faint tippings of Saccardo's umber; circlet of feathers around edges of eyelids pinkish buff; an indistinct superciliary, more plainly indicated behind the eye, dull cinnamon-buff, bordered below, behind the eye, by a line of bister; rest of side of head dull pinkish buff, with the feathers tipped and edged narrowly with bister; throat, upper foreneck, and abdomen

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[22] *Troglodytes intermedius* Cabanis, Journ. für Orn., vol. 8, 1860 (May 30, 1861), p. 407. (San José, Costa Rica.)

white, washed with pinkish buff; sides of neck and breast pinkish buff; sides tawny-olive; flanks sayal brown bordering abdomen, changing to snuff brown toward the rump, barred faintly and sparingly with neutral gray; under tail coverts clay color, barred broadly with dusky neutral gray; under surface of tail olive-brown, with indistinct bars of dark neutral gray; edge of wing and under wing coverts pinkish buff, the latter white distally. Maxilla fuscous-black; tip of mandible hair brown, base pale olive-buff; tarsus and toes dark hair brown (from dried skin).

Measurements.—Males (11 specimens), wing 51.5-53.5 (52.2), tail 34.0-37.1 (35.5), culmen from base 16.9-19.1 (17.8), tarsus 18.6-20.5 (19.4) mm. Females (2 specimens), wing 49.0-50.1 (49.5), tail 31.5-33.2 (32.3), culmen from base 17.3-17.4 (17.3), tarsus 19.4-19.9 (19.6) mm.

Type, male, wing 52.4, tail 35.2, culmen from base 17.8, tarsus 19.1 mm.

Range.—Isla Coiba, off the Pacific coast of Veraguas, Panamá.

Remarks.—The decidedly darker coloration of this race as compared to the house wren of the Panamanian mainland was evident immediately when I first saw the birds about the buildings at the Colonia Penal. In fact, it is so different from the other house wrens of Central America not only in color but in larger bill that it might be considered a distinct species, if it were not for the marked diversity of form found in the related subspecies in South America and the Lesser Antilles. Three juvenal birds from Coiba, secured as they were about to leave the nest, compared with young of equivalent age of *T. m. inquietus* from the provinces of Veraguas and Panamá, are decidedly more brown on the lower surface, especially on the sides, flanks, and under tail coverts. The brown of the upper surface is slightly warmer, particularly on the rump, while the crown is slightly darker than the back instead of equivalent in color. Compared with juvenals of *T. m. intermedius* from Costa Rica the Coiba birds are more similar but differ in somewhat warmer brown on the sides, flanks, and under tail coverts, lighter, brighter color on the rump, and darker crown color.

The new form in color, as indicated in the diagnosis, appears somewhat similar to *T. m. intermedius,* but has the bill very much larger and heavier.

The subspecific name *carychrous* is taken from the Greek καρύχροος, nut brown.

Family Turdidae: Thrushes

TURDUS ALBICOLLIS COIBENSIS Eisenmann: White-throated Robin, Zorzal Gargantiblanco

Turdus assimilis coibensis Eisenmann, Auk, vol. 67, No. 3, July 1950, p. 365. (Coiba Island, Panamá.)

The white-throated robin is the most common bird in the forest undergrowth, ranging into the intermediate branches of the trees, but seldom going higher. They were encountered from the borders of the mangroves inland, but always in forest cover. One was taken on Isla Ranchería February 4. Sometimes, when I called with the usual "squeaking" technique, as many as a dozen came flying into the branches about me, where they remained motionless until they detected some movement, when they flew to some denser cover. Their flight is direct and rapid. When at all alarmed they remain closely hidden among leaves, more often in the lower undergrowth than in higher cover. It was interesting to find them common in these

Fig. 10.—White-throated Robin, Zorzal Gargantiblanco.

tropical lowlands, since elsewhere in Panamá the species inhabits the mountain areas in the high tropical or subtropical zone, though there are exceptions, as for example at San Félix in eastern Chiriquí, where I found them at an elevation of a little over 100 meters.

On Coiba, as elsewhere, these robins came to feed in berry-bearing trees, and at such times might range much higher above the ground than is their normal custom. Occasionally I noted them searching for food among dry, fallen leaves on the forest floor. Often I heard their complaining notes from the undergrowth, a low whining *pree-ee-er* or a slightly harsher *chur-r-r.* In the latter part of January they began to sing, the song suggesting that of the mainland clay-colored robin (*Turdus grayi casius*), but with notes higher and delivery slower.

As Dr. Eisenmann remarked in his original description, this race, peculiar to Coiba, is most similar in color and size to *Turdus a. daguae,* found from the highlands of eastern Darién through western Colombia to northwestern Ecuador. *T. a. coibensis* is larger, more olive above and grayer below, with the unmarked white area on the foreneck less in extent. The Coiba form is completely different from *T. a. cnephosus* of western Panamá, which is its near neighbor geographically, that bird being decidedly grayer above and on the sides, whiter on the abdomen, and decidedly larger. In life the bare edge of the eyelid in *coibensis* is dull yellow, as it is in the mainland race.

Since *coibensis* was described from only two specimens it is useful to give measurements from the series that I collected:

Males (8 specimens), wing 107.5-117.5 (111.7), tail 76.8-89.1 (84.0), culmen from base 20.5-22.9 (21.6), tarsus 29.7-31.8 (30.4) mm. Females (6 specimens), 108.0-113.4 (112.1), tail 79.5-86.8 (82.6), culmen from base 21.0-23.3 (22.2), tarsus 29.0-31.0 (30.3) mm.

As material of these white-throated robins has accumulated in museums, supposed distinct species have been found to merge, until now it is evident that there is no clear-cut line on which to divide them in the vast area between México and northern Argentina, though variation geographically is extensive. All are to be included under the specific name *Turdus albicollis.*

Family Sylviidae: Old World Warblers, Gnatcatchers

POLIOPTILA PLUMBEA (Gmelin): Tropical Gnatcatcher, Cazajején

Todus plumbeus Gmelin, Systema naturae, vol. 1, pt. 1, 1788, p. 444. (Surinam.)

This was another common species found in leafy cover that ranged indifferently from low second-growth thickets near the shore to the summits of the tallest forest trees in the interior of the island. Invariably they were moving about among the twigs and leaves in unceasing activity in pursuit of tiny insects, often so high above the ground that I could barely detect their tiny forms. The slender body, with long, narrow tail held at an angle above the back, and their quick, nervous movements, mark them even when the gray and white plumage is not clearly seen. I found them in pairs, and near breeding at this season. January 21 one male was much excited by my squeaking, and came to perch within a dozen feet of me while it sang repeatedly a series of high-pitched notes of the usual gnatcatcher quality, barely audible to my aging ears, mingled with beautifully clear, warbling phrases of much louder sound that would have graced the gifted song of a mockingbird.

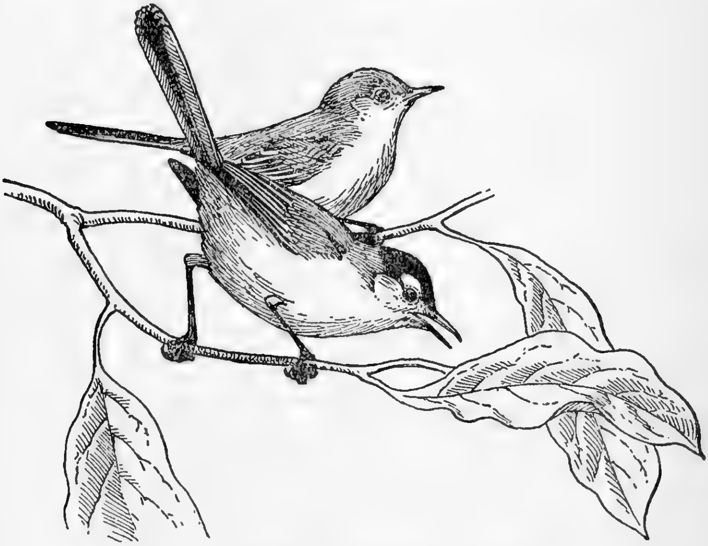

FIG. 11.—Tropical Gnatcatcher, Cazajején.

Darker coloration separates the birds of Coiba definitely from their mainland neighbors, as shown by the following description.

POLIOPTILA PLUMBEA CINERICIA subsp. nov.

Characters.—Similar to *Polioptila plumbea bilineata* (Bonaparte)[23] but dorsal surface, including the wings, decidedly darker gray; lower

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[23] *Polioptila bilineata* Bonaparte, Conspectus generum avium, vol. 1, 1850, p. 316. (Cartagena, Colombia.)

foreneck and breast gray (instead of white as in *bilineata*); sides darker gray; bill averaging broader.

Description.—Type U.S.N.M. No. 461129, male, Isla Coiba, Panamá, collected Feb. 1, 1956, by A. Wetmore (orig. No. 20558): Pileum, hindneck, and upper parts of sides of neck black, with a tiny white feather or two behind the nostril; back, scapulars, rump, and wing coverts somewhat darker than slate-gray; tips of the gray upper tail coverts faintly white; primaries and secondaries dusky neutral gray, with outer webs edged with slate-gray, except for the two outer primaries; tertials edged broadly with white on outer webs, the edging becoming pale neutral gray toward the tip; tail black centrally, the two outermost rectrices white, except for the base, the next ones tipped broadly, and the fourth narrowly, with white; lores and a broad superciliary white; eye ring black on lower eyelid, white on upper; a conspicuous black line extending from the eye to the back of the nape; rest of side of head, throat, ventral area of sides of neck, abdomen, and under tail coverts white; lower foreneck, breast, and sides pale neutral gray; edge of wing white, mixed with dusky neutral gray; under wing coverts, and inner webs of primaries and secondaries, toward the base, white. Maxilla and tip of mandible dusky neutral gray; base of mandible neutral gray, becoming pallid neutral gray from the anterior part of the gonys back along the lower margins of the rami; tarsus and toes black (from dried skin).

Measurements.—Males (9 specimens), wing 46.2-49.7 (48.5), tail 41.8-46.3 (44.1), culmen from base 13.0-14.9 (14.0), tarsus 16.6-17.8 (17.2) mm. Females (6 specimens), wing 45.1-47.4 (46.6), tail 41.9-45.3 (44.0), culmen from base 13.8-14.8 (14.4), tarsus 16.2-17.5 (17.0) mm.

Type, male, wing 49.7, tail 44.9, culmen from base 14.7, tarsus 16.9 mm.

Range.—Isla Coiba, off the Pacific Coast of Veraguas, Panamá.

Remarks.—Females, like the males, differ from the same sex of *bilineata* in darker color above. Below, the distinction is less striking, but still is evident.

In citing these birds as races of *Polioptila plumbea* I have followed current usage, though not entirely satisfied that this is the proper treatment. The birds of this section of the genus are in need of detailed study.

The subspecific name of the race described above is from the Latin *cinericius,* ash colored.

Family CYCLARHIDAE: Pepper-Shrikes

CYCLARHIS GUJANENSIS COIBAE Hartert: Yellow-breasted Pepper-shrike, Pájaro Perico

Cyclorhis coibae HARTERT, Bull. Brit. Orn. Club, vol. 12, Dec. 30, 1901, p. 33. (Coiba Island, Panamá.)

The pepper-shrike was fairly common but on my arrival at the beginning of the dry season their songs had become infrequent, and without these notes as a guide they are difficult to find. While they are robust in body, they move about behind leafy cover in such leisurely manner, resting for minutes with only slight movements of the head, that it is only casually that one is seen. They are birds of the high forest crown, but come also about clearings, even into the low second growth called rastrojo, or to the borders of mangrove swamps. At the María work camp I found one feeding in mango trees and cocoanut palms standing isolated in the extensive clearing.

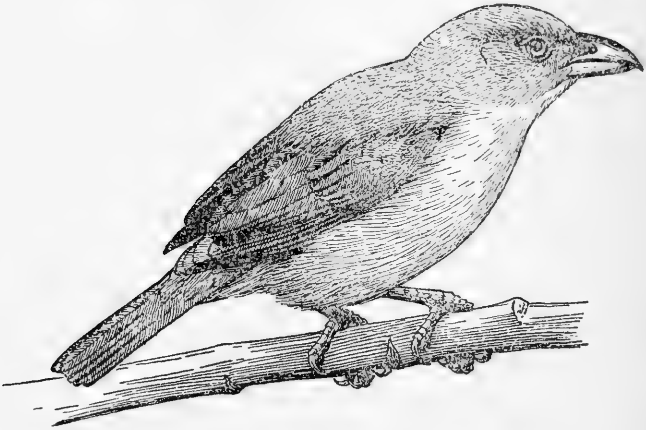

FIG. 12.—Yellow-breasted Pepper-shrike, Pájaro Perico.

The song is loud with strongly accented notes, and ends abruptly, when there is a pause of varying length, often of several minutes, before it is repeated. The first two or three syllables are uttered rather slowly, followed by a rapidly given louder phrase. The notes carry for several hundred yards, and, if the song is continued, eventually the bird may be located, though the process of finding one may require half an hour. The three males that I collected represent many hours of search, since, as already stated, during January the birds were not singing steadily.

In the original description, written 55 years ago, when relatively few specimens were available, Hartert compared the Coiba bird with the race of Cozumel Island, off the coast of Quintano Roo, México, which was suggested by the duller colors of *coibae*. Actually, the subspecies of Coiba Island is more closely similar to the forms of the Panamanian mainland from which it differs in very decidedly darker, duller colors, the breast and sides being distinctly greenish instead of bright yellow, the dorsal surface duller green, and the crown browner.

A male taken February 3 had the soft parts colored as follows: Iris wax yellow; maxilla mouse brown; mandible neutral gray; tarsus and toes avellaneous. Following is a summary of measurements based on males, including the two in the type series, now in the American Museum of Natural History. No females have been collected.

Males (5 specimens), wing 70.4-73.0 (71.8), tail 51.7-53.4 (52.5), culmen from base 17.5-18.6 (18.1), tarsus 20.7-23.1 (21.8) mm.

The type specimen, taken by Batty April 20, 1901, an immature bird as is shown by the dark, almost black, bill, is browner on the crown than adult specimens. The Batty collection contains another skin (Amer. Mus. Nat. Hist. No. 505408) labeled "Hicaron Island, ♂, Jan. 14, 1902." As this is an unmistakable specimen of *Cyclarhis gujanensis subflavescens,* found in the lower mountains of Chiriquí, the locality given certainly is erroneous. Isla Jicarón lies immediately to the south of Coiba, distant about 4 miles, with Coiba between it and the mainland, so that if *Cyclarhis* occurs there it would be expected to find it the same as, or at least closely allied to, *C. g. coibae.*

Family VIREONIDAE: Vireos

VIREO FLAVOVIRIDIS (Cassin): Yellow-green Vireo, Julián Chiví

The yellow-green vireo reached Coiba on its return from "winter" quarters in northern South America on January 19, when a small flight arrived, so that singing males were scattered at sunrise through the woods along the Punta Damas trail. Two days later several were found in the low forest back of the beach near the mouth of the Río Catival, and from that time they were recorded almost daily throughout the forest, ranging in the high tree-crown area of the taller trees as well as in the lower woodland near the river mouths. They were common on Isla Rancheriá February 4. Two races are represented in the eight specimens taken.

VIREO FLAVOVIRIDIS FLAVOVIRIDIS (Cassin)

Vireosylva flavoviridis CASSIN, Proc. Acad. Nat. Sci. Philadelphia, vol. 5, June 30, 1851, p. 152, pl. 11. (San Juan, Nicaragua.)

Four from Isla Coiba were shot January 20, 29, 30, and 31. One secured January 29 in high forest was evidently on its breeding ground as it was displaying and pursuing another.

The problem of the identity of the yellow-green vireos that breed in western Panamá still is not clear. The birds available that appear to have been on their nesting grounds, including those from Coiba, seem brighter colored than *V. f. insulanus* from the islands in the Gulf of Panamá, the Canal Zone, and the area to the eastward. They thus seem closer to typical *flavoviridis,* and are so identified.

VIREO FLAVOVIRIDIS HYPOLEUCUS van Rossem and Hachisuka

Vireo olivaceus hypoleucus VAN ROSSEM and HACHISUKA, Proc. Biol. Soc. Washington, vol. 50, Sept. 30, 1937, p. 159. (1,200 feet elevation in San Francisco Canyon, lat. 27° N., eastern Sonora, México.)

The two birds taken on January 19, on the first day of the return of this vireo from the south, have the characters of this race, particularly in the lighter, brighter yellowish green of the sides and flanks. They thus resemble the breeding bird of northwestern México, and are so identified.

VIREO PHILADELPHICUS (Cassin): Philadelphia Vireo, Virio de Filadelfia

Vireosylvia philadelphica CASSIN, Proc. Acad. Nat. Sci. Philadelphia, vol. 5, June 30, 1851, p. 153, pl. 10, fig. 2. (Philadelphia, Pa.)

A female of this migrant from the north was shot January 23 at the border of a mangrove swamp.

HYLOPHILUS FLAVIPES Lafresnaye: Scrub Greenlet, Verdecillo Común

Hylophilus flavipes LAFRESNAYE, Rev. Zool., vol. 8, September 1845, p. 342. (Bogotá, Colombia.)

These were among the more common of the small birds, though seen infrequently because they ranged among screening leaves and creepers. They were found in the scrub growths back of the beaches and at the borders of mangroves, and came also into the brushy rastrojo of old fields, habitats similar to those inhabited by other forms of the species in mainland localities. On Coiba I found that they lived also in the high crown of the inland forests, though it was near the end of my stay before I verified this, owing to the difficulty of detecting small birds in such situations. They move actively among the leaves and twigs, almost as quickly as wood warblers, and when seen often appear very close at hand. Occasionally I found them feeding on small drupes of fruiting trees. The yellowish-white iris of the adult birds is often apparent as they climb and hop among the smaller branches. The darker colored immature birds have dark eyes. The song, given in low tones, usually has three similar notes, *swee, swee, swee,* which are easily imitated by whistling.

The birds of Coiba described below are so much darker than the nearby mainland race that they might almost be treated as a distinct species.

HYLOPHILUS FLAVIPES XUTHUS subsp. nov.

Characters.—Similar to *Hylophilus flavipes viridiflavus* Lawrence [24] but bill heavier; much darker below, being definitely buffy instead of yellow; sides decidedly darker; darker green above.

Description.—Type, U.S.N.M. No. 461170, male, Isla Coiba, Panamá, collected Jan. 11, 1956, by A. Wetmore (orig. No. 20155): Pileum, hindneck, back, and scapulars dark citrine; rump citrine; wing coverts dull citrine; primaries and secondaries Chaetura black, the outer webs edged with serpentine green; tail olive-citrine; lores faintly olive-buff; sides of head citrine-drab; chin dull white; throat and upper foreneck light yellowish olive, merging with the light olive lake of the chest; lower breast, abdomen, and under tail coverts between primuline yellow and wax yellow; flanks between strontian yellow and yellowish citrine; edge of wing, under wing coverts, and margins of inner webs of remiges barium yellow. Maxilla buffy brown; mandible deep olive-buff; tarsus and toes wood brown (from dried skin).

Measurements.—Males (7 specimens), wing 55.8-58.3 (57.5), tail 47.0-50.9 (48.4), culmen from base 14.3-15.0 (14.7), tarsus 17.4-19.0 (18.6) mm. Females (6 specimens), wing 54.4-56.7 (55.9), tail 45.2-49.3 (47.8), culmen from base 14.6-16.1 (15.1), tarsus 18.2-19.4 (18.6) mm.

Type, male, wing 57.9, tail 48.1, culmen from base 14.3, tarsus 17.4 mm.

Range.—Isla Coiba, off the Pacific coast of Veraguas, Panamá.

Remarks.—A juvenile female with wings and tail not quite fully grown is more highly pigmented than the adults, being darker above and below, with a wash of ochraceous-orange on the abdomen and

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[24] *Hylophilus viridiflavus* Lawrence, Ann. Lyc. Nat. Hist. New York, vol. 7, 1861, p. 324. (Atlantic slope near Panama Railroad, Canal Zone, Panamá.)

under tail coverts, and a fainter indication of this color on the breast and back. The nearly grown bill in this bird is dark in color, and I noted that the iris was dark. Another female, fully grown, with light-colored bill, shows this same suffusion of ochraceous orange, and I believe that this also is immature. The bill is actually heavier at the base than in *viridiflavus* in addition to being slightly longer. In 15 males of *viridiflavus* the culmen from base varies from 13.1 to 14.2 mm., with an average of 13.6 mm. The iris in the adult *H. f. xuthus* is light colored, as in the other races of *flavipes*.

The subspecific name comes from the Greek ξουθός, brownish yellow, tawny.

Family COEREBIDAE: Honeycreepers

CYANERPES CYANEUS CARNEIPES (Sclater): Red-legged Honeycreeper, Azulito

Coereba carneipes P. L. SCLATER, Proc. Zool. Soc. London, 1859 (February 1860), p. 376. (Playa Vicente, Oaxaca, México.)

Conditions on Coiba seem especially favorable to the blue honeycreeper as it is one of the more common birds. Dozens were found at flowering trees in the mangrove swamps, dozens about fruiting trees in the forests, and other dozens crowded the guayabo trees in the pastures, when these came into bloom at the close of January. The birds fly about in small bands, probe actively in flowers for nectar and small insects, and then may rest quietly on dead twigs for a brief period. They are birds of strong flight seen often passing over or through tall trees. As they pass overhead the blue color of the males is lost against the sky, and they appear black except for a flash of lighter color from the yellow of the underside of the wings.

Commonly, they are called verdón, a name that may apply to the female but is hardly applicable to the brilliant blue of the male.

COEREBA FLAVEOLA MEXICANA (Sclater): Common Honeycreeper, Reinita Común

Certhiola mexicana P. L. SCLATER, Proc. Zool. Soc. London, pt. 24, 1856 (Jan. 26, 1857), p. 286. (Southern México.)

The active little yellow-breasted honeycreepers were common, though not so abundant as the blue species. They were distributed universally, ranging from the mangrove swamps and adjacent wet woodlands back into the high forest, and at times I saw them in shrubbery and palms around clearings. Males taken January 9 and

15 were in breeding condition, and the birds were observed building nests on January 27 and 30. One bird was taken and others seen on Isla Ranchería February 4.

The Coiba birds in series are very faintly darker when compared with skins from the Pacific slope of Panamá and Costa Rica, but are similar to specimens from Bocas del Toro. The heavier pigmentation common to Coiba residents thus is slightly indicated, but insufficiently to merit a name.

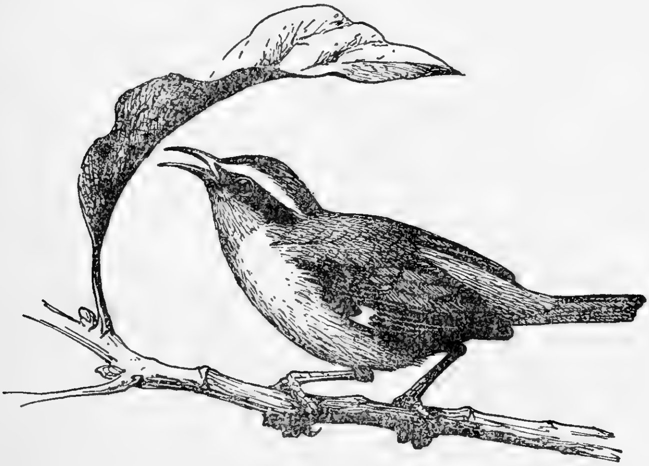

FIG. 13.—Common Honeycreeper, Reinita Común.

Family PARULIDAE: Wood Warblers

PROTONOTARIA CITREA (Boddaert): Prothonotary Warbler, Canario Protonotario

Motacilla citrea BODDAERT, Table des planches enluminéez, 1783, p. 44. (Louisiana.)

This handsome warbler, fairly common as a winter resident, was found near the sea, mainly in the mangroves and adjacent thickets, and also in the coconut palms. Specimens were collected January 8, 12, and 20.

VERMIVORA PEREGRINA (Wilson): Tennessee Warbler, Reinita Peregrina

Sylvia peregrina WILSON, American ornithology, vol. 3, 1811, p. 83, pl. 25, fig. 2. (Cumberland River, Tenn.)

This migrant warbler was seen January 12, 16 (specimen), and 28, in thickets near the sea.

PARULA PITIAYUMI (Vieillot): Tropical Parula Warbler, Mariquita

Sylvia pitiayumi Vieillot, Nouveau dictionnaire d'histoire naturelle, nouv. éd., vol. 11, June 21, 1817, p. 276. (Paraguay.)

On three occasions I saw pairs of these warblers moving quickly among leafy twigs in the high branches of tall forest trees, so high above the ground that they were barely within gunshot. Except for their restless movements they would never have been detected in the shaded light of these forest haunts. Only occasionally did they appear briefly in silhouette against some tiny opening that led to the open sky. Probably they were fairly common, as the forest cover of the entire great island was suited to their needs. The decidedly darker coloration of four taken for specimens requires their description as an insular form.

PARULA PITIAYUMI CIRRHA subsp. nov.

Characters.—Similar to *Parula pitiayuma speciosa* (Ridgway)[25] but more heavily pigmented; lower breast and abdomen orange, continuous with the chest color; sides darker; side of head darker, with the black of the lores and around the eye extended heavily beyond the posterior margin of the ear coverts; greenish area of back decidedly smaller; wing slightly longer.

Description.—Type, U.S.N.M. No. 461218, male, Isla Coiba, Panamá, collected Jan. 31, 1956, by A. Wetmore (orig. No. 20542): Line across forehead, lores, space about eye, and a narrow line on side of neck black; auricular area black, with an overwash of deep orient blue; forepart of crown Alice blue; back of crown and hindneck Columbia blue; back, scapulars, and upper tail coverts Tyrian blue to dark Tyrian blue; patch in center of back Roman green; rump cadet gray; lesser and middle wing coverts black basally, the tips Columbia blue; greater wing coverts black, edged with light Tyrian blue, except the central ones, which are edged and tipped with white to form a conspicuous spot; remiges black, edged with light Tyrian blue; rectrices also black, edged with light Tyrian blue, with a broad subterminal patch of white in the inner web of the two outermost; throat and upper foreneck lemon chrome; lower foreneck and chest light raw sienna, a light wash of this extending farther foreward toward the throat; lower breast and abdomen light cadmium, merging without a break into the darker color of the chest; feathers of sides bordering the chest black with the tips dark Tyrian blue; re-

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[25] *Compsothlypis pitiayumi speciosa* Ridgway, Auk, vol. 19, No. 1, January 1902, p. 69. (Boquete, Chiriquí.)

mainder of sides and flanks Delft blue, with a wash of yew green where this meets the yellow of the abdomen; under tail coverts white, this color spreading to the posterior part of the flanks; under wing coverts and a narrow margin on inner webs of remiges white. Maxilla black; mandible colonial buff; tarsus and toes olive brown (from dried skin).

Measurements.—Males (2 specimens), wing 56.9-58.5, tail 40.5-41.7, culmen from base 12.8-12.8, tarsus 16.9-16.9 mm. Females (2 specimens), wing 53.5-54.7, tail 39.2-39.8, culmen from base 11.7-12.6, tarsus 16.7-16.8 mm.

The measurements of the type, a male, are the larger ones in the male series, where a difference in dimension is present.

Range.—Isla Coiba, off the Pacific coast of Veraguas, Panamá.

Remarks.—The deeper coloration in both male and female separates this new form strikingly from the birds of the mainland. In the males, the pattern of the under surface merges from breast to abdomen with no distinct line of demarcation in the central area. According to Ridgway the wing in males of *C. p. speciosa* (11 specimens) measures 47.5-55.0 mm., and in females (2 specimens) 47.5 to 51.8 mm.

The subspecific name is taken from the Latin *cirrhus,* yellowish orange, with reference to the predominating color.

DENDROICA PETECHIA XANTHOTERA Todd: Golden Warbler, Canario Mangletero

Dendroica bryanti xanthotera Todd, Proc. Biol. Soc. Washington, vol. 37, July 8, 1924, p. 123. (Puntarenas, Costa Rica.)

I found these warblers fairly common in growths of red mangroves on the shores of Bahía Damas, from the mouth of the Río Catival to near Boca Grande, beyond Playa Blanca, this being the area in which mangrove swamps were extensive. They did not range inland in stands of other forest as the allied *Dendroica p. aequatorialis* does on some of the smaller islands, e.g., on Taboguilla, and on San José and Pedro González in the Perlas group. On Coiba, during January these birds were in resting stage, some in molt, and were not singing. I found also that they would not decoy, though in the display and nesting period they come quickly to a squeak, so that my series of nine males and six females was obtained only by close and careful watching. Rarely I found one or two in low trees or shrubs immediately adjacent to the mangrove border, but most were obtained directly in the swamps.

While the Coiba series is listed under the subspecific name *xanthotera* this allotment for the present is tentative. For several years I have obtained specimens of this warbler wherever practicable. On the Pacific coast of Panamá birds that represent *D. p. aequatorialis* are available from the mouth of Río Majé, near the western boundary of Darién, west to the swamps of the Río Chame below Bejuco, at the western border of the Province of Panamá. Beyond this point, to the west, there is a different population. Specimens from the eastern side of the Azuero Peninsula, from the mouth of the Río Vidal, near the eastern boundary of Chiriquí, and from Isla Coiba, are intermediate between *aequatorialis* and *xanthotera*. Males resemble the latter in the darker brown of the head cap and the ventral streaking, and the former in the heavier streaking of the breast and sides, and the greater extension of the brown on the foreneck. They differ thus from *xanthotera* in the decidedly greater extent of the brown streaks and brown foreneck. It may be desirable to separate this intermediate population by name, but judgment on this is held until it has been possible to secure specimens from farther west, along the coasts of Chiriquí.

DENDROICA PETECHIA AESTIVA (Gmelin): Yellow Warbler, Canario de Paso

Motacilla aestiva Gmelin, Systema naturae, vol. 1, pt. 2, 1789, p. 996. (City of Quebec, Canada.)

While the yellow warblers of the United States and Canada are placed currently in the same species as the golden warblers of the American Tropics it is convenient to list them separately, and to recognize them as "yellow warblers" in the Republic of Panamá, where they are common during the period of northern winter, in order to distinguish them from the quite different resident canarios mangleteros. They were found in small numbers during my stay on Coiba, mainly in low growth back of the beaches, and bordering mangrove swamps, and also in abandoned fields grown to brush. The English name expresses the yellow color that marks them from others of like size as they appear momentarily among the leaves. When encountered in the swamps they may usually be distinguished from the golden warbler by smaller size and more active movements.

The seven taken include two geographic races, which ranged together. Specimens of the present subspecies were taken January 8, 11, 21, and 26.

DENDROICA PETECHIA AMNICOLA Batchelder

Dendroica aestiva amnicola Batchelder, Proc. New England Zoöl. Club, vol. 6, Feb. 6, 1918, p. 82. (Curslet, Newfoundland.)

The two secured were shot January 16 and 27. The present form is distinguished by darker color, particularly on the back.

DENDROICA PENSYLVANICA (Linnaeus): Chestnut-sided Warbler, Reinita de Lados Castaños

Motacilla pensylvanica Linnaeus, Systema naturae, ed. 12, vol. 1, 1766, p. 333. (Philadelphia, Pa.)

Specimens of this warbler were taken January 12 and 29. No others were identified.

SEIURUS NOVEBORACENSIS NOTABILIS Ridgway: Northern Waterthrush, Pizpita Mangletera

Seiurus naevius notabilis Ridgway, Proc. U. S. Nat. Mus., vol. 3, 1880, p. 12. (Como Lake, Carbon County, Wyo.)

Waterthrushes ranged singly among the mangroves near the river mouths, and in the low shrubbery in the swampy areas adjacent at high tide when much of their usual range was covered with water. Their habit is to walk quickly along the ground with rapidly vibrating tail. When alarmed they call with a sharp note, and when flushed often light on logs or low branches, still continuing the nervous tail movement. It is this motion that brings them to attention as the dark dorsal surface matches the background over which they range.

The seven specimens taken from January 8 to 28 are all of this northern and western race.

OPORORNIS FORMOSUS (Wilson): Kentucky Warbler, Reinita Hermosa

Sylvia formosa Wilson, American ornithology, vol. 3, 1811, p. 85, pl. 25, fig. 3. (Kentucky.)

On January 19 I shot a female in low undergrowth along the Punta Damas trail.

SETOPHAGA RUTICILLA RUTICILLA (Linnaeus): American Redstart, Candelita

Motacilla Ruticilla Linnaeus, Systema naturae, ed. 10, vol. 1, 1758, p. 186. (Virginia.)

Occasional individuals of this migrant were seen in high forest, moving about as actively as when in their northern nesting grounds. The bright patches of color in the tail and wings, yellow in females, orange in males, that flash as they dart out or drop through the branches after flying insects, is attractive, and is the basis for the name in Spanish. Females collected January 19 and 21 have the lighter color that marks the typical race. Two adult males were secured January 13 and 15.

BASILEUTERUS DELATTRII Bonaparte: Chestnut-capped Warbler, Reinita Cabecicastaña

Basileuterus delattrii Bonaparte, Compt. Rend. Acad. Sci. Paris, vol. 38, 1854, p. 383. (Nicaragua.)

These warblers are inhabitants of undergrowth, where they feed in low branches, or occasionally on the ground. On Coiba I encountered them from near the shoreline back through high forest in the interior of the island. They also came into thickets in abandoned fields near the work camps. They were common, but of secretive habit, keeping behind cover. As they frequently carry the tail at an angle over the back they often suggest wrens as they move about behind the screening twigs and leaves. At this season they were silent except for an occasional chipping call. Usually they are found in pairs, and during January most of those that I killed for specimens were nearly ready to breed. The Coiba population is so different from that of the mainland that it requires the following name:

BASILEUTERUS DELATTRII ACTUOSUS subsp. nov.

Characters.—Similar to *Basileuterus delattrii mesochrysus* Sclater,[26] but bill larger, and coloration darker; back duller green; gray of hindneck slightly darker; under surface duller yellow; sides and flanks darker green.

Description.—Type, U.S.N.M. No. 461248, male, Isla Coiba, Panamá, collected Jan. 23, 1956, by A. Wetmore (orig. No. 20409): Forehead black, with the feathers tipped lightly with deep neutral gray; crown dark russet; hindneck between deep and dark olive-gray; back and scapulars Roman green; lower rump, upper tail coverts and wing coverts serpentine green; remiges and primary coverts between deep and dark mouse gray, edged with serpentine green; rectrices deep mouse gray, edged with light serpentine green; lores black; a broad superciliary, extending to the nape, white; chin and malar region, extending back beneath eye, white; feathers on edge of eyelids, and a line extending posteriorly to above the ear coverts, black; ear

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[26] *Basileuterus mesochrysus* P. L. Sclater, Proc. Zool. Soc. London, vol. 28, 1860, p. 251. (Bogotá, Colombia.)

coverts and remainder of side of head dark russet; foreneck lemon chrome; center of breast and abdomen strontian yellow; sides of neck olive-gray, continuous with the hindneck; sides dull citrine; flanks olive lake; under tail coverts yellowish citrine, tipped lightly with citron yellow; edge of wing mixed serpentine green and strontian yellow; outermost under wing coverts olive-citrine, innermost and axillars yellowish citrine; inner margins of primaries and secondaries edged lightly with tilleul buff. Bill black; tarsus and toes buffy brown (from dried skin).

Measurements.—Males (11 specimens), wing 57.6-62.5 (60.1), tail 51.1-55.8 (53.3), culmen from base 13.3-14.4 (13.8), tarsus 20.5-22.5 (21.3) mm. Females (5 specimens), wing 56.1-60.2 (57.5), tail 50.0-53.5 (51.8), culmen from base 13.5-13.9 (13.6), tarsus 20.0-21.6 (21.0) mm.

Type, male, wing 60.0, tail 51.6, culmen from base 13.7, tarsus 20.8 mm.

Range.—Isla Coiba, off the Pacific coast of Veraguas, Panamá.

Remarks.—While the total length of the bill in the Coiba Island birds is only slightly greater than in mainland individuals, breadth and general bulk are appreciably more. The generally darker color of the new race is in line with the general tendency of the resident races on Coiba.

The subspecific name *actuosus,* lively, active, has been chosen to indicate the sprightly actions of these attractive birds.

Family ICTERIDAE: Blackbirds and Orioles

CASSIDIX MEXICANUS PERUVIANUS (Swainson): Boat-tailed Grackle, Changamé

Quiscalus Peruvianus SWAINSON, Animals in Menageries, pt. 3, Dec. 31, 1837, p. 354. (Perú.)

There appear to be few of these grackles present, and those few during January ranged only in the southern section of the Bahía Damas. We saw the species first on January 18 in the outer mangroves at the mouth of Río Catival, when we encountered a pair and secured the female. Two days later we shot a male at this same point, presumably the one seen on the first occasion. The guards stationed at the María work camp told me that there was a morning and evening flight of a few small flocks from a roost somewhere near Playa Blanca to feeding grounds around the swamps at the mouth of the Río San Juan.

ICTERUS GALBULA (Linnaeus): Baltimore Oriole, Calandria Grande Pasajera

Coracias Galbula Linnaeus, Systema naturae, ed. 10, vol. 1, 1758, p. 108. (Virginia.)

Specimens were taken January 8 and 16, and two others were seen on January 19 and 20. This is a common migrant on the mainland.

Family Thraupidae, Tanagers

THRAUPIS VIRENS (Linnaeus): Blue-gray Tanager, Azulejo

Loxia virens Linnaeus, Systema naturae, ed. 12, vol. 1, 1766, p. 303. (Surinam.)

This well-known tanager was not abundant on Coiba, being common only along the southern side of Bahía Damas near Salinas and María, and seen only casually elsewhere. In accordance with their usual habits, they often were noted flying for considerable distances across the high forest crown, or over the clearings. One was seen on Isla Ranchería February 4. They are birds of such strong flight that it did not occur to me in the field that they would not cross regularly to the distant mainland, so it has been a great surprise to determine that they represent a distinct subspecies, as is indicated in the following paragraphs.

THRAUPIS VIRENS CUMATILIS subsp. nov.

Characters.—Similar to *Thraupis virens quaesita* Bangs and Noble,[27] but with sides and flanks darker blue; under wing coverts, especially the outer ones, darker.

Description.—Type, U.S.N.M. No. 416334, male, Isla Coiba, Panamá, collected January 23, 1956, by A. Wetmore (orig. No. 20419): Top and sides of head and hindneck light glaucous-blue; lores pale glaucous-blue, distinctly outlined from the darker color of the adjacent forehead; upper back neutral gray basally, with the barbs tipped and edged with Alice blue, this area appearing blue but with the darker basal color showing through irregularly; lower back, rump, and upper tail coverts Venetian blue; lesser wing coverts diva blue, the feathers having a distinct sheen; middle coverts basally Delft blue, becoming diva blue at the tips; greater coverts Payne's gray basally, edged with King's blue; primaries and secondaries dull black, edged widely with Vanderpoel's blue; primary coverts edged with cadet blue; rectrices blackish along the shaft, merging gradually

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[27] *Thraupis cana quaesita* Bangs and Noble, Auk, vol. 35, No. 4, Oct. 16, 1918, p. 460. (Sullana, Depto. Piura, Perú.)

on the webs to Venetian blue; abdomen and under tail coverts pale glaucous-blue; rest of under surface of body Alice blue, except the posterior parts of the sides and the flanks, which are orient blue; under wing coverts gray No. 9 (light gull gray), somewhat paler internally. Bill, tarsi, and feet dull black (from dried skin).

Measurements.—Males (2 specimens), wing 87.4-89.0 (88.2), tail 63.0-63.4 (63.2), culmen from base 14.4-14.7 (14.5), tarsus 19.0 mm. Females (3 specimens), wing 82.6-86.8 (84.1), tail 59.6-60.4 (59.9), culmen from base 13.7-14.8 (14.2), tarsus 18.8-19.5 (19.2) mm.

Remarks.—The six specimens of this race taken include one immature male with wings and tail so worn that it is not included in the measurements listed above. The darker coloration of the Coiba birds when compared with our long series of *Thraupis virens diaconus,* found from southern México to Panamá, is evident on the most casual inspection, and it is only with *quaesita,* which ranges from Nariño in southwestern Colombia to northwestern Perú, that the form here described shows any similarity. *T. v. cana,* distributed through northern Colombia and northern Venezuela, differs from *cumatilis* more than does *diaconus.* The subspecific name *cumatilis* signifies the dark blue of the sea.

PIRANGA OLIVACEA (Gmelin): Scarlet Tanager, Cardenal Alinegro Pasajero

Tanagra olivacea GMELIN, Systema naturae, vol. 1, pt. 2, 1789, p. 889. (New York.)

A male taken at the edge of the high forest on January 7 is an individual less than a year old, as shown by the dull grayish-brown tail feathers, edged extensively with green. It was about to start the molt to adult dress, as is indicated by a single, tiny, new feather only partly grown, in one eye-ring. The main migration route of this tanager crosses the Caribbean Sea from Yucatán and Cuba to Colombia, with only occasional individuals wandering to the westward. The few previous records from Panamá have been of migrants bound northward in spring between March 25 and April 9, except for one sight record on March 16, 1911. The bird from Coiba is the first one for the wintering season, a period when the species regularly is found from Colombia to Bolivia.

PIRANGA RUBRA RUBRA (Linnaeus): Summer Tanager, Come-Abejas

Fringilla rubra LINNAEUS, Systema naturae, ed. 10, vol. 1, 1758, p. 181. (South Carolina.)

This winter resident from the north, fairly common in Panamá, was taken twice on Coiba, a female January 20, and a male in highly colored female dress on February 1. One came each evening to sleep in a mango tree below my living quarters, calling briefly as it moved through the adjacent trees. While the nonobservant often confuse the brightly colored males with the crimson-backed tanager, and call it "Sangretoro," those more familiar with the summer tanager recognize the male and female as being of the same species, and know it as the come-abejas from the constant habit of feeding at the nests of small wild bees.

RAMPHOCELUS DIMIDIATUS Lafresnaye: Crimson-backed Tanager, Sangretoro Común

Ramphocelus dimidiatus Lafresnaye, Mag. Zool., vol. 7, cl. 2, 1837, pl. 81 and text. (Cartagena, Colombia.)

This is another of the common birds on the island that came frequently into the trees and shrubbery around the habitations but was seen more usually in the lower woodlands back of the beaches and near the river mouths. I was interested to find them equally common in the high crown of the tall virgin forest inland. They may come out in the open to feed but at any alarm retreat to cover behind leaves and creepers. At the same time they have considerable curiosity and are easily called by squeaking.

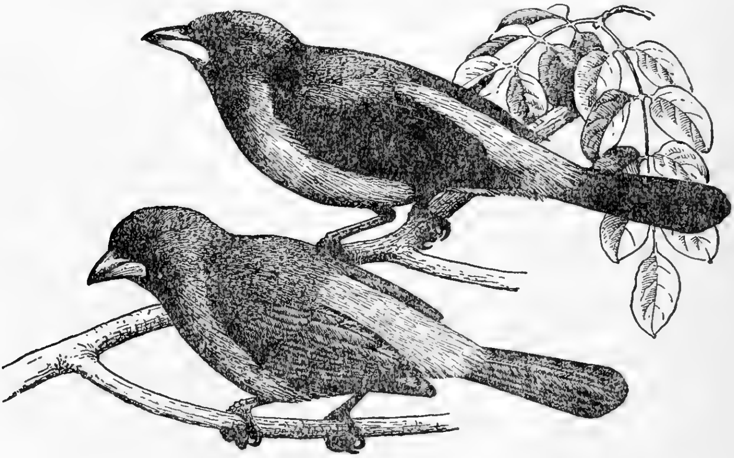

Fig. 14.—Crimson-backed Tanager, Sangretoro Común.

The differences that distinguish the birds of Coiba from those of other parts of the range of the species are outlined in the following description.

RAMPHOCELUS DIMIDIATUS ARESTUS subsp. nov.

Characters.—Darkest of the races of *Ramphocelus dimidiatus;* male similar to *Ramphocelus dimidiatus limatus* Bangs,[28] but red deeper throughout, especially on the abdomen; female decidedly darker.

Description.—Type, U.S.N.M. No. 461317, male, Isla Coiba, Panamá, collected Jan. 8, 1956, by A. Wetmore (orig. No. 20095): Crown, side of head, hindneck, and foreneck maroon; upper back garnet brown; lower back, rump, and upper tail coverts slightly darker than spectrum red; wing black, with the outer webs of the wing coverts and the tertials maroon; tail black; chest carmine; lower breast, sides, abdomen, and under tail coverts between nopal red and garnet brown; tibia and a lightly marked band down center of lower breast and abdomen black; under wing coverts black. Maxilla and tip of mandible black; base of mandible plumbeous centrally, margined with gray; tarsus and toes black (from dried skin).

Measurements.—Males (8 specimens), wing 74.3-78.9 (77.3), tail 65.5-70.0 (67.9), culmen from base 16.6-19.6 (17.4), tarsus 19.3-21.3 (20.6) mm. Females (7 specimens), wing 73.3-75.2 (74.3), tail 65.6-69.7 (67.5), culmen from base 17.6-18.5 (18.2), tarsus 20.2-21.8 (21.0).

Type, male, wing 77.5, tail 70.0, culmen from base 17.2, tarsus 17.0 mm.

Range.—Isla Coiba, off the Pacific coast of Veraguas, Panamá.

Remarks.—The notably darker coloration that marks this geographic race is more readily apparent in the female than in the male, as is especially noticeable when comparison of *arestus* is made with the female of *R. d. limatus* of the Pearl Islands, this being the darkest of the other forms. The under surface of *arestus* is duller than that of the female of *R. d. dimidiatus,* while the crown is darker, and the back duller.

The male of the new form agrees with that of *limatus* in the restricted black area on the center of the lower breast and abdomen, this being decidedly less than in the mainland races.

The subspecific name is from the Greek ἀρεστός, pleasing, in allusion to the attractive coloration of these tanagers.

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[28] *Rhamphocelus limatus* Bangs, Auk, vol. 18, No. 1, January 1901, p. 31. (San Miguel Island, Bay of Panamá = Isla El Rey, Archipiélago de las Perlas.)

Family FRINGILLIDAE: Finches, Grosbeaks, and Buntings

SALTATOR ALBICOLLIS Vieillot: Streaked Saltator, Lechosero Pechirrayado

Saltator albicollis VIEILLOT, Nouveau dictionnaire d'histoire naturelle, nouv. éd., vol. 14, Sept. 13, 1817, p. 107. (Martinique.)

Streaked saltators were found in undergrowth throughout the high forest, where they lived in such subdued light that often it was difficult to see them. Sometimes they were in pairs, but at this season they were not breeding, so the males were not in song. They remained under cover, moving about quietly even when feeding, but could be called into sight readily. While not abundant, they were widely distributed, so the total number of individuals found on the island is considerable. The Coiba birds are so heavily pigmented in comparison with those of the mainland that they require separation as a distinct form.

SALTATOR ALBICOLLIS SCOTINUS subsp. nov.

Characters.—Darkest of the subspecies of *Saltator albicollis;* similar to *Saltator albicollis isthmicus* Sclater [20] but darker, grayer green above; sides of head and streaks on lower surface definitely darker; sides of breast darker; edge of wing brighter yellow; under tail coverts slightly deeper buff.

Description.—Type, U.S.N.M. No. 461415, male, from Isla Coiba, Panamá, collected Jan. 26, 1956, by A. Wetmore (orig. No. 20457): Crown and hindneck dark greenish olive; back and scapulars yellowish olive; rump deep olive; upper tail coverts deep mouse gray; wing coverts yellowish olive; primaries, secondaries, and alula Chaetura drab, with outer webs of innermost secondaries yellowish olive, and of outermost secondaries and primaries yellowish citrine; outer web of alula dark greenish olive; rectrices Chaetura drab, with the exposed webs dull storm gray; edge of upper eyelid and a narrow line on edge of lower eyelid at its center Marguerite yellow, with traces of this color extending to the base of the nostril, forming an indistinct light line; loral area, extending to below center of eye, deep mouse gray; an indefinite whitish malar streak; rest of side of head dark greenish olive; center of throat and foreneck white, bordered by a broad line of dark greenish olive that broadens behind to merge with the same color on the side of neck and the chest; breast Marguerite yellow, becoming white on the abdomen; chest streaked

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[29] *Saltator isthmicus* P. L. Sclater, Proc. Zool. Soc. London, August 1861, p. 130. (Isthmus of Panamá.)

heavily with dark greenish olive, the streaks becoming narrower on lower breast until they are reduced to lines on the upper abdomen and on its sides; center of abdomen white; sides dark greenish olive; flanks and under tail coverts between cartridge buff and cream-buff, streaked indefinitely with Chaetura drab; edge of wing citron yellow; outer under wing coverts primrose yellow; inner series and axillars cream-buff. Bill black; tarsus and toes fuscous-black (from dried skin).

Measurements.—Males (6 specimens), wing 84.6-90.5 (87.8), tail 76.4-78.7 (77.6), culmen from base 17.3-18.8 (18.3), tarsus 23.4-24.0 (23.6) mm. Females (7 specimens), wing 84.3-88.8 (86.8), tail 74.5-79.8 (77.3), culmen from base 17.7-19.0 (18.4), tarsus 22.0-24.2 (23.0) mm.

Type, male, wing 90.1, tail 87.6, culmen from base 17.5, tarsus 23.4 mm.

Range.—Isla Coiba and Isla Ranchería, off the Pacific coast of Veraguas, Panamá.

Remarks.—The darker coloration sets this form apart as conspicuously distinct from the other known subspecies. The green hues have a definitely dark-gray cast, and the streaking on the under surface is heavy, even more so than in *S. a. furax* of western Chiriquí and southwestern Costa Rica.

The name is taken from the Greek σκοτινος, dark, obscure, referring to the color.

TIARIS OLIVACEA (Linnaeus): Yellow-faced Grassquit, Yerbero

Emberiza olivacea Linnaeus, Systema naturae, ed. 12, vol. 1, 1766, p. 309. (Hispaniola.)

The grassquit was common along the borders of the pastures and at the edge of the forest, congregating especially where tall grasses bore ripening seeds. They feed by balancing on the grass heads as these sway and bend beneath their slight weight. At headquarters dozens came to feed about the mill that hulled the rice, and in the remote work camps, where rice was pounded by hand, the grassquits gleaned the fallen grain about the kitchens. They were completely tame, and often came hopping about the feet of men sitting on the benches at guard headquarters. Fully grown young were common, and on January 14 adults were mating.

The dark color of these birds was noticeable even in life, the differences from the mainland group being detailed in the following description.

TIARIS OLIVACEA RAVIDA subsp. nov.

Characters.—Similar to *Tiaris olivacea pusilla* Swainson,[30] but darker; fully adult male with black of upper surface of head deeper and extended down entirely over the hindneck; green of dorsal surfact duller, grayer; sides, flanks, and under tail coverts darker, grayer green; black of under surface, on average, more extensive, particularly on the upper abdomen and sides; female grayer green throughout.

Description.—Type, U.S.N.M. No. 461411, male, Isla Coiba, Panamá, collected Jan. 31, 1956, by A. Wetmore (orig. No. 20557): Crown and hindneck black, feathers of hindneck edged very lightly with yellowish olive; back, scapulars, and upper tail coverts yellowish olive; rump light yellowish olive, with shaft lines of dusky neutral gray on the middle coverts; inner webs of greater wing coverts Chaetura black, with outer webs and tips yellowish olive; alula and remiges Chaetura black, edged with yellowish olive; central pair of rectrices yellowish olive, with shafts Chaetura drab; remainder of rectrices dark hair brown, edged with yellowish olive; lores and line extending back over eye cadmium yellow to above center of eye, then becoming apricot yellow, and continuing posteriorly as a narrow superciliary to above the anterior margin of the ear coverts; remainder of side of head black, edged faintly on ear coverts and sides of neck with yellowish olive; throat and upper edge of foreneck somewhat dull cadmium yellow, forming a squarely outlined patch; rest of foreneck, breast, anterior part of sides, and center of abdomen black, the latter tipped very lightly with pale olive-buff; posterior edge of sides, flanks, and sides of abdomen dull light yellowish olive; under tail coverts reed yellow; edge of wing narrowly reed yellow; under wing coverts dark neutral gray, edged with reed yellow; axillars yellowish olive; inner webs of inner remiges pale smoke gray. Bill black; tarsus and toes fuscous-black (from dried skin).

Measurements.—Males (7 specimens), wing 50.2-53.9 (52.6), tail 38.7-40.9 (39.8), culmen from base 10.2-11.3 (10.6, average of 6), tarsus 15.9-18.0 (17.1) mm. Females (5 specimens), wing 50.7-52.0 (51.6), tail 37.0-38.1 (38.2), culmen from base 10.4-11.2 (10.7), tarsus 16.2-17.7 (17.0) mm.

Type, male, wing 53.9, tail 40.9, culmen from base 11.3, tarsus 16.8 mm.

Range.—Isla Coiba, off the Pacific coast of Veraguas, Panamá.

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[30] *Tiaris pusillus* Swainson, Phil. Mag., n.s., vol. 1, No. 6, June 1827, p. 438. (Temascáltepec and Real del Monte, México.)

Remarks.—The resemblance of these birds from Coiba is nearest to the populations of *T. o. pusilla* found from Costa Rica to México, from which, however, the new form is decidedly different. Birds from the mainland of Panamá average paler than those from farther north in Central America, with less black on the crown. It seems probable from preliminary study that the latter may warrant recognition as *Tiaris olivacea dissita,* a name proposed by Thayer and Bangs in 1906.

The subspecific name of the Coiba form is from the Latin *ravidus,* grayish.

SPIZA AMERICANA (Gmelin): Dickcissel, Arrocero Americano

Emberiza americana GMELIN, Systema naturae, vol. 1, p. 2, 1789, p. 872. (New York.)

On January 8 I flushed two from litter scattered over a wet pasture. Country people often call these birds "veinticuatro," from their habit of ranging in little flocks that popularly are believed always to number 24 individuals.

SPOROPHILA AURITA AURITA (Bonaparte): Variable Seedeater, Arrocero Común

Spermophila aurita BONAPARTE, Conspectus generum avium, vol. 1, pt. 2, (late in) 1850, p. 497. (Panamá.)

A few of these seedeaters were found in the open edge of mangrove swamps, particularly near the beaches, which must have been their original range as they do not penetrate heavy stands of woodland. They are locally common now at the borders of pastures and cultivated areas, which give them a considerable increase in the habitat suited to their needs. They were seen especially where there were stands of ripened grass heads on which they fed in company with the yellow-faced seedeaters. On January 18 I observed them mating.

Recently de Schauinsee[31] has treated *Sporophila aurita* as conspecific with *Sporophila americana* (Gmelin), considering that the two are united through a subspecies *murallae* described by Chapman from three specimens from Caquetá in southeastern Colombia. This proposal I prefer to leave for further study, since little is known of Chapman's race. The eight males and four females secured on Coiba do not differ from specimens from Veraguas east to the Canal Zone.

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[31] Proc. Acad. Nat. Sci. Philadelphia, vol. 104, Dec. 23, 1952, pp. 169, 172.

VOLATINIA JACARINA SPLENDENS (Vieillot): Blue-black Grassquit, Arrocero Negrito

Fringilla splendens Vieillot, Nouveau dictionnaire d'histoire naturelle, nouv. ed., vol. 12, June 1817, p. 173. (Cayenne.)

Wherever tall grass and weeds grew at the borders of the cultivated fields and pastures this grassquit was found, living as usual in little bands that fed in the open in early morning, and remained under cover for the remainder of the day. The two skins preserved were taken January 11 and 23, a male secured on the date last named being in brown-tipped plumage. I recorded one male seen January 27 as being in the glossy black breeding dress.

ORYZOBORUS FUNEREUS Sclater: Lesser Rice Grosbeak, Arrocero Prieto

Oryzoborus funereus P. L. Sclater, Proc. Zool. Soc. London, pt. 27, 1859 (February 1860), p. 378. (Suchapam, Oaxaca, México.)

The arrocero prieto was found in small numbers in the borders of the swampy woodlands along the lower courses of the Catival and San Juan Rivers, not far from the sea. On January 27 I recorded two birds in song, so that the nesting season appeared to be near. They are shy inhabitants of thickets, though coming at times to open perches to sing.

The two adult males and one female that I collected on Coiba, and another female labeled "Coiba" in the Batty collection in the American Museum of Natural History, differ from the average mainland birds in having definitely larger bills. In a series of 129 skins, male and female, covering the entire range from Veracruz to western Ecuador, there are only two individuals that vary from normal bill size. A male from Gatun (U.S.N.M. No. 207550) equals the two males from Coiba. A female from Arenosas, Antioquia, Colombia (A.M.N.H. No. 388791) has the bill decidedly more massive than the Coiba series, though in most of the Colombian birds it is very slightly smaller than the average of the population of Central America. I attribute the larger dimension in these two to gigantism, in other words to an abnormality. The uniform difference evident in the four birds from Coiba is so striking that it seems probable that they represent an island group that should be recognized as distinct. This is a matter, however, that is left for decision whenever more material may become available. Size in both sexes, and the shade of color in the females, in the four skins from Coiba agree with what is found in the mainland group.

De Schauinsee [32] has remarked on the occasional specimens of male

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[32] Caldasia, vol. 5, No. 25, Aug. 5, 1951, p. 1094.

Oryzoborus funereus that show traces of chestnut on the abdomen, recording such skins from Guatemala, Honduras, Canal Zone, and the Santa Marta region, Colombia. Traces of this color are found in skins in the U.S. National Museum from Veraguas, Panamá, and Bolívar, Magdalena, and Santander, Colombia, as additional localities to those mentioned. Because of this the author cited places *funereus* as a race of *Oryzoborus angolensis* in which the male has the lower breast, abdomen, and sides solid chestnut. It seems to me preferable to interpret the occasional occurrence of this chestnut marking in *funereus* as a deep-seated character that indicates ancient relationship to *angolensis* through some common ancestral stem, since it occurs at random and is not restricted to the area where the two styles of color pattern are in contact. It must be remembered also that males of *funereus* in first plumage vary from clay color to tawny olive and sayal brown on the lower surface, pigmentation which might affect the normal black of the adult dress in occasional instances.

ARREMONOPS CONIROSTRIS (Bonaparte): Green-backed Sparrow, Chen-chen

Arremon conirostris BONAPARTE, Conspectus generum avium, vol. 1, pt. 2, (late in) 1850, p. 488. (Colombia.)

While this common sparrow lived in thickets near the beaches and at the borders of the swampy lowland forests, it ranged also inland

FIG. 15.—Green-backed Sparrow, Chen-chen.

in the undergrowth of the high gallery woodland across the central part of the island. It was found low down near the ground, in pairs or small groups, often in the same localities as the streaked saltator. Probably it was some supply of berries or other food that brought the two together, though their choice of haunt was identical. In the dim light of the forest areas it was often difficult to see the chen-chen because of its dark coloration, and its lack of any conspicuous color pattern. At this season they were not singing their labored songs.

The bird of Coiba is described in the following paragraphs.

ARREMONOPS CONIROSTRIS VIRIDICATA subsp. nov.

Characters—Similar to *Arremonops conirostris striaticeps* (Lafresnaye)[33] but decidedly darker; white on lower surface less in extent, with corresponding increase in gray on breast and sides, which are darker; under tail coverts darker buff; dorsal surface darker throughout, both in the gray on the head, and in the green of the rest of the dorsal plumage; wings and tail decidedly darker.

Description.—Type, U.S.N.M. No. 461362, male, from Isla Coiba, Panamá, collected January 13, 1956, by A. Wetmore (orig. No. 20209): Broad lateral crown stripes, extending posteriorly onto the upper hindneck, black; center of crown and of upper hindneck neutral gray; back, scapulars, rump, and upper tail coverts Saccardo's olive; lesser and middle wing coverts buffy citrine, with the outer webs washed with old gold; greater coverts buffy citrine, edged with old gold; remiges Chaetura drab; tertials, secondaries, and inner primaries edged with Dresden brown; outer secondaries and alula edged with mignonette green; rectrices between Dresden brown and mummy brown; space behind nostril dull white, extended posteriorly as a neutral gray superciliary that broadens behind the eye and extends onto the side of the neck; feather circlet on edge of upper lid and on center of lower lid dull white; loral area and a narrow line extending from the posterior margin of the eye, including the feathers on the edge of the lower eyelid except those in the center, black; rest of side of head, including the ramal area, neutral gray; throat and upper foreneck white; lower foreneck, breast, and anterior area of sides light neutral gray; center of abdomen white; flanks light brownish olive, merging anteriorly with light neutral gray of sides; under tail coverts Isabella color; edge of wing and outer under wing coverts cadmium yellow, mixed with light orange-yellow; inner under

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[33] *Embernagra striaticeps* Lafresnaye, Rev. Mag. Zool., ser. 2, vol. 5, February 1853, p. 61. (Panamá.)

wing coverts dull white; axillars Naples yellow. Maxilla and tip of mandible black; rest of bill dull neutral gray; tarsus and toes light fuscous (from dried skin).

Measurements.—Males (6 specimens), wing 75.5-80.3 (78.0), tail 64.6-69.3 (66.7), culmen from base 16.7-18.3 (17.6), tarsus 27.0-29.0 (27.8) mm. Females (6 specimens), wing 69.9-74.6 (72.3), tail 60.0-64.9 (62.6), culmen from base 16.2-17.9 (16.9), tarsus 26.2-28.5 (27.4) mm.

Type, male, wing 77.5, tail 67.3, culmen from base 17.6, tarsus 27.6 mm.

Range.—Isla Coiba, off the Pacific coast of Veraguas, Panamá.

Remarks.—The dull orange tint found as a faint wash on the tertials and inner secondaries of some specimens from the mainland is much intensified in the Coiba Island birds, especially on the tail. In several this color becomes a strong hue of Dresden brown, present extensively on the outer webs of the back feathers, indicated lightly over the gray of the central crown stripe, and found even on the white of the abdomen, where it is modified to ochraceous-tawny.

In the darker coloration the Coiba race actually resembles rather closely *Arremonops conirostris centrata* Bangs of eastern Honduras, differing from this in duller cast of the green dorsal surface, decidedly darker tail, more buffy under tail coverts, and in the dull orange cast just described. The Honduras race, represented in the National Museum collections by a male from La Ceiba, the type locality, and a female from Trujillo, appears decidedly better marked than Todd in his review[34] of this genus has indicated.

The name of the Coiba Island bird, from the Latin *viridicatus,* deep green, is given in recognition of its predominant dorsal color. It may be remarked that the generic name *Arremonops,* though treated by some writers as masculine, is of feminine gender.

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[34] Proc. Biol. Soc. Washington, vol. 36, Mar. 28, 1923, p. 41.

Cockroaches migrating out of a trickling filter at the University of Florida sewage treatment plant during the process of flooding. (See p. 12 for details. Courtesy of Division of Public Relations, University of Florida, Gainesville.)

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THE MEDICAL AND VETERINARY IMPORTANCE OF COCKROACHES

(WITH SEVEN PLATES)

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FOREWORD

It is rare indeed that a reviewer finds that a publication completely changes his orientation to the matter discussed. In all honesty that was the end result of reading this detailed, comprehensive, and fascinating review of the relationships, both probable and possible, of cockroaches and disease.

Although the cockroach has long been the target of intensive control efforts in both the civilian and the military communities, my personal grudge against the insect has been based more on suspicion than fact. I would surmise that most physicians, like myself, have been influenced by the lack of emphasis on the disease transmission potential of the cockroach in most medical curricula. This review has corrected that deficiency. It has replaced a complacent acceptance of the insect as an unpleasant nuisance in areas of poor sanitation with a firm belief that greater attention must be placed on increased attempts to demonstrate, both in the laboratory and in the field, possible relationships between the prevalence of cockroaches and the incidences of certain diseases. Perhaps these insects have received less attention in this country than they have deserved. One could say the same for typhoid fever, smallpox, yellow fever, dengue, and malaria. The pronounced and sustained increase in the level of sanitation in the United States over the past one hundred years has relegated many diseases and disease vectors to a very low level of attention. It is only appropriate that the general medical population in this country should turn greatest attention toward problems of current domestic importance. On the other hand, the Medical Officer and related medical scientists of the Armed Forces must of necessity consider such problems in the light of conditions existing today in areas in which they may be required to serve. With complete candor I recommend this review to all who, in uniform or out, practice the art and skill of disease prevention the world over.

LT. COL. HERBERT L. LEY, JR., MC
Research and Development Division, Office of The Surgeon General
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CONTENTS

THE MEDICAL AND VETERINARY IMPORTANCE OF COCKROACHES[1]

By

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(With Seven Plates)

> As concerns the field of insect microbiology, we seem to have got ahead of ourselves in many respects. There has been very little effort to group our forces, so to speak, and for the most part the available knowledge and information is not properly known, organized, or appreciated.
>
> Steinhaus (1946).

I. INTRODUCTION

Since World War II there has been a resurgence of interest in the infectious agents transmitted by cockroaches, in the pathogens that survive experimental introduction into cockroaches, and in the dispersal of cockroaches from sewers. We realize that it is rarely practicable for investigators to scan all the pertinent literature or to bolster reports of experimental research with detailed accounts of related observations. Yet a thorough knowledge of all relevant material will always be needed in planning and evaluating future investigations. No previous publication has adequately summarized the background literature relating cockroaches and disease; in fact, some of the earlier literature and some contemporary foreign publications seem to have escaped notice. For these reasons, it has seemed desirable to survey the known relations of cockroaches to disease and to make the integrated results of the survey available for general use.

Because there is a voluminous literature on the transmission of disease agents by cockroaches, one might expect to find this subject well covered in current textbooks and reference books. Such is not the case. We surveyed about a dozen prominent books in the fields of

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[1] Part of the cost of publication of this paper was borne by the Office of the Surgeon General and the Quartermaster Research and Engineering Center, Department of the Army.

medical entomology, parasitology, and preventive medicine to determine the extent to which this subject was covered. All the authors agreed that cockroaches are sanitarily undesirable because they are potential health hazards. Yet, generally, the subject was handled briefly and was based on only a few references.

Pierce (1921) devoted a chapter to disease agents transmitted by cockroaches, in which he summarized about a dozen papers published between 1900 and 1916. Riley and Johannsen (1938) indicated that cockroaches have long been under suspicion as carriers of disease organisms; they discussed the problem in about two pages with a dozen references. Neveu-Lemaire (1938) covered the subject in about three pages with a few incomplete references (only authors' names were cited). Rosenau (1940) summed up his half-page discussion of five references: "Roaches must therefore be regarded as a sanitary menace." Dunham (1940) flatly stated, "Roaches do not transmit any disease to man." Nevertheless, he admitted in the next sentence that they might mechanically contaminate food with pathogenic organisms. Herms (1939) devoted three and a half pages to cockroaches as carriers of infectious agents but stated no definite conclusions (six references and original data). Chandler (1949) cited cockroaches at least eight times, as prominent transmitters of disease agents. Matheson (1950) devoted a half page to cockroaches and human disease but concluded, ". . . nothing has been established of the importance of roaches in disease dissemination." Busvine (1951), in a half page, discussed the hygienic importance of cockroaches and concluded that ". . . the cockroach is less likely to carry infection than the common housefly, because, though its habits are equally unpleasant, its mobility is less." Martini (1952) devoted about three pages to cockroaches but very little to their relation to disease. Faust (1955) cited cockroaches as intermediate hosts of human helminths and mechanical vectors of several pathogenic organisms. The one current text most likely to counteract this almost universal lack of emphasis is "Insect Microbiology" by E. A. Steinhaus. Although he did not discuss cockroaches and disease as an entity, Steinhaus (1946) cited numerous instances of biologic relationships between cockroaches and micro-organisms.

In addition to the textbook authors cited above, several of the authors of experimental reports have concluded that cockroaches are vectors of disease agents; these are cited in section XV.

This review is a documented summary of the tangled relations between cockroaches and the organisms that cause disease in man and other animals. It directs attention to the impressive body of literature that incriminates cockroaches as actual or potential vectors of disease agents. Undoubtedly we have overlooked some of the literature; we have eliminated some reports that were too fragmentary to form a basis for conclusions. But we have attempted to cite the significant publications.

We hope that the information assembled herein will provide epidemiologists, sanitarians, and medical entomologists with both basic knowledge and a keener appreciation of the potentialities of common cockroaches as transmitters of the agents of disease.

To make the review easier to read, we have grouped the annotated lists of pathogenic organisms, naturally or experimentally associated with cockroaches, in appendices. The appendices contain the meat of our argument; they should not be overlooked.

> One of my native patients in S. Rhodesia always slept in the open, as he preferred to give up his hut to the cockroaches! He placed food there for them and slept outside undisturbed.
>
> MOISER (1947).

II. THE VECTOR COCKROACHES: THEIR HABITS, HABITATS, AND DISPERSAL

There are more than 3,500 known species of cockroaches (Rehn, J. W. H., 1951). J. A. G. Rehn (1945) estimated that less than 1 percent of the known species are domiciliary pests. However, we should point out that most species of cockroaches have never been implicated in the transmission of disease agents. The pest cockroaches, which are all more or less closely associated with man, are the only ones of proven medical or veterinary importance. The vast majority of cockroaches are presumed to be medically harmless; but it is well to keep in mind that, should any of these change their habits and become followers of man, they too may become as potentially dangerous as the known domiciliary species.

The following cockroaches have been incriminated, naturally or experimentally, in the transmission of pathogenic agents or have been claimed to bite man. The cited common names were taken from Rehn (1945) or Sailer (1955).

Scientific Name	Common Name
1. *Blaberus atropos* (Stoll)	....
2. *Blaberus craniifer* Burmeister	....
3. *Blaberus discoidalis* Serville	....
4. *Blaberus fuscus* Brunner	....
5. *Blatta orientalis* Linnaeus	Oriental cockroach

Scientific Name	Common Name
6. *Blattella germanica* (Linnaeus)	German cockroach
7. *Eurycotis floridana* (Walker)	....
8. *Leucophaea maderae* (Fabricius)	Madeira roach
9. *Nauphoeta cinerea* (Olivier)	Cinereous cockroach
10. *Neostylopyga rhombifolia* (Stoll)	Harlequin cockroach
11. *Periplaneta americana* (Linnaeus)	American cockroach
12. *Periplaneta australasiae* (Fabricius)	Australian cockroach
13. *Periplaneta brunnea* Burmeister	....
14. *Periplaneta ignota* Shaw	....
15. *Polyphaga saussurei* (Dohrn)	....
16. *Pycnoscelus surinamensis* (Linnaeus)	Surinam roach
17. *Shelfordella tartara* (Saussure)	....
18. *Supella supellectilium* (Serville)	Brown-banded roach

The habits of common, cosmopolitan species such as the American, oriental, German, and brown-banded cockroaches are so well known that we shall not expound them here, except to emphasize their relation to the dissemination of infectious agents. General information on the habits of cockroaches can be found in any current entomological textbook, in Mallis (1954), in Gould and Deay (1940), and in U.S.D.A. leaflet No. 144 (1950). Rehn (1945) gives an excellent account of the mechanism and extent of the world-wide dispersal of 11 domiciliary cockroaches, "man's uninvited fellow travelers."

Very little biological information has been recorded for most of the species listed above or for unlisted domiciliary species that are much less well known and which have not yet been implicated in transmission of disease agents. With the exception of *Blaberus atropos* and *Blaberus fuscus,* whose habits are unknown to us, the species listed are all domiciliary to some degree; evidence for this statement is given below.

Blaberus craniifer. This species is a household pest in Cuba (Deschapelles, 1939).

Blaberus discoidalis. This species is found in Ecuador in eating places as well as in patios and gardens (Campos, 1926). In Puerto Rico it may be found with *Leucophaea maderae* in fruit debris in stores (Wolcott, 1950) or in homes where, however, it is never abundant (Seín, 1923). Occasionally this species is introduced with tropical plants and it may become temporarily established in greenhouses in the United States (Hebard, 1917).

Eurycotis floridana. This species has been recorded from Georgia, Florida, and Mississippi, where it is found outdoors in sheltered areas such as stumps, under signs, and bark of dead trees (Hebard, 1917). Occasionally it enters houses (Creighton, 1954; Roth and Willis, 1954).

Leucophaea maderae. This is a widely distributed tropical and subtropical species (Rehn and Hebard, 1927). It frequents habitations, warehouses, and other structures, and at times is a very abundant and serious pest (Rehn, 1945). It is apparently of African origin (Rehn, 1937). Heer (1864) found that in Funchal, Madeira, this species is found mainly in houses, primarily in kitchens. During the day the insects group together in dark places and at night roam throughout the house and feed on material of plant origin. Wolcott (1950) considered *L. maderae* to be semidomesticated in Puerto Rico, where it is found most often in fruit stores and markets. Seín (1923) stated that it is not often found in homes but abounds in small inns and other places where fruit, particularly bananas, and vegetables are kept. This species has been reported as a household pest in the Windward Islands (Marshall, 1878) and the Philippines (Uichanco, 1953); it is definitely a domiciliary species in tropical regions where it is established, although it is capable of living apart from man in a purely wild state (Gurney, 1953). In New York City an infestation of this species was reported to be localized in apartment buildings occupied by migrant families from Puerto Rico; it is highly probable that the species was introduced from Puerto Rico (Gurney, 1953).

Nauphoeta cinerea. This is considered to be at least a semidomestic species. Rehn (1937) stated his impression that the species originated in East Africa and has spread throughout much of the Tropics along trade routes. He considered it to be a domiciliary species and stated that it occurs in the huts of the Shilluk natives in the Sudan (Rehn, 1945). It is found in feed rooms of poultry plants in Hawaii (Illingworth, 1942) and in grain stores and fowl-feeding pens in Australia where adults have also been found in dwellings (Pope, 1953). Mackerras and Mackerras (1948) captured this species in hospital wards in Australia (see p. 67). *N. cinerea* has become established in feed mills around Tampa, Fla. (Gresham, 1952; Ratcliffe, 1952; Gurney, 1953).

Neostylopyga rhombifolia. Hebard (1917) stated that this species is probably domiciliary with habits similar to those of *Periplaneta americana.* According to Rehn (1945), it is a domiciliary species of Indo-Malayan origin that has spread to Africa and the New World (Mexico, Venezuela, Argentina) through the inadvertent agency of man. It has been reported as a household pest in the Philippines (Uichanco, 1953).

Periplaneta australasiae. This circumtropical species (Hebard, 1917) is a household pest in the Philippines (Uichanco, 1953). Pope (1953) stated that in Brisbane, Australia, it is commoner in dwellings than *P. americana.* In Puerto Rico its habits are similar to those of

P. americana and *P. brunnea* (Seín, 1923). *P. australasiae* is generally domiciliary, but it also occurs in various outdoor hiding places in the West Indies (Rehn and Hebard, 1927) ; its habits are similar in Florida (Hebard, 1917). It is very abundant in tropical Africa and tropical America under domiciliary conditions (Rehn, 1945). In Ecuador it is one of the commonest cockroaches in kitchens and pantries of houses (Campos, 1926).

Periplaneta brunnea. This species is a circumtropical domiciliary pest that in this country is established in Florida, Georgia, and Texas (Hebard, 1917). "It is widely distributed in the American tropics and also those of the Old World, often occurring with *americana.*" (J. A. G. Rehn *in* Mallis, 1954.) According to Seín (1923), the habits of this species are identical to those of *P. americana* in Puerto Rico.

Periplaneta ignota. In Brisbane, Australia, this species is occasionally found in dwellings (Pope, 1953).

Polyphaga saussurei. This species appears to be one of the commonest domiciliary cockroaches in south-central Asia (Bei-Bienko, 1950). It apparently feeds on human feces, because human cestode eggs have been found in its intestine (Zmeev, 1936).

Pycnoscelus surinamensis. This is a circumtropical species whose range extends into subtropical regions (Rehn, 1945). In the United States it is established in parts of Florida, Louisiana, and Texas, and occasionally becomes established farther north in greenhouses or other structures that are heated during the winter months (Hebard, 1917). In Tanganyika it is sometimes found in enormous numbers in huts, infesting baskets of stored millet, African beer, or the remains of a meal (Smith, 1955). Uichanco (1953) cited it as a household pest in the Philippines. *P. surinamensis* is less likely to occur withindoors than under stones, boards, and other loose trash (Rehn, 1945). This species also burrows into the soil.

Shelfordella tartara. This common species of Central Asia is often found in houses having clay floors; it may be of epidemiological importance because of its domiciliary habit (Bei-Bienko, 1950).

In temperate climates domiciliary cockroaches tend to establish themselves in heated buildings, but during summer months they may breed prolifically out-of-doors. In tropical and subtropical climates breeding may occur outdoors or in unheated structures the year around. Cockroaches generally congregate in dark, sheltered areas that afford them suitable microclimates and easy access to food. Presumably it is the search for these amenities that results in the dispersal of cockroaches into new areas.

Being omnivorous, cockroaches eat practically every food used by man and his animals, as well as biological waste products such as garbage and sewage. Cockroaches are found wherever man stores or prepares food for himself or for his domestic, experimental, and exhibition animals. So from market to kitchen, laboratory, or zoo, cockroaches have ample opportunity to contaminate food that is not adequately protected. This contamination may be feces and vomitus, dead cockroaches, or disease organisms. Except for parasites for which cockroaches are intermediate hosts, the disease organisms are transmitted mechanically in the insect's feces, in its vomitus, and on its legs and body.

People living in civilized, highly sanitized areas rarely are aware of the truly tremendous cockroach infestations that may exist under poor hygienic conditions. Gal'kov (1926) cited conditions in mineworkers' living quarters in the Nizhne-Tagil district of the Ural region: "The cockroaches and bedbug population of the barracks was terrifying. Every crack in the doors and beams of the walls and ceilings, in the floor, the boards of the cots, benches, and tables were positively crammed with them. In the corners near the stove, the cockroaches covered the walls in a dense carpet." Lamborn (1940) emphasized similar conditions in Africa. Moiser (1947) reported that more than 2,500 cockroaches were trapped in one night in a wide-mouthed bottle, baited with cooked meal, that had been placed in an African native's hut.

Wolcott (1950) cited an infestation of *Leucophaea maderae* in a small fruit store in Puerto Rico where the owner cleaned out over a bushel of these cockroaches. Seín (1923) stated that in their hiding places, "hills" of Madeira cockroaches can be seen composed of individuals clinging to one another.

DeLong (1948) described the types of heavy cockroach infestations that may be encountered in supermarkets (i.e., grocery department stores). He had seen 100-pound bags of onions and potatoes in which the number of German cockroaches surpassed the number of vegetables. Hundreds of German cockroaches were found in balances and cash registers; behind the sloping mirrors used in back of the produce racks, German cockroaches ". . . may be massed several inches deep on the back of the mirror for the full length of the fluorescent tube." DeLong reported that the oriental cockroach is also common and numerous in supermarkets, where it hides during the day in cracks in the foundations, inside walls, under furniture, or behind cartons. At night this species is conspicuous on the floor where it feeds on available food. The American cockroach occasionally becomes a pest in supermarkets, but is of minor importance when compared with the other two species.

Mallis (1954) described conditions in a four-room apartment in Austin, Tex., in 1947. The cockroach population was estimated to be 50,000 to 100,000, mostly *Blattella germanica.* These insects were killed with an insecticidal spray, but within six months it was estimated that 15,000 to 25,000 German cockroaches had again established themselves in the apartment. Mallis (1954) also reported finding approximately 280,000 cockroaches in 177 apartments examined in four cities in Texas in 1947. Over 99 percent of these were German cockroaches.

Current literature on insect control indicates that, in spite of modern insecticides, cockroaches are a continuing problem in food-handling establishments: dairies (Adams, 1947; Gerlach, 1947; Gould, 1946); bakeries (Vincent, 1949); food and meat packing plants (Burke, 1944; Parker, 1948; Somers, 1951); mess halls and restaurants (Carpenter, 1944; U.S.P.H.S., 1952). Even food plants with an adequate sanitation program report new invasions of cockroaches from time to time (Clark, 1954).

Although there are specific differences in their behavior, many cockroaches show relatively little discrimination in their choice of food and habitat. This does not imply that all species are found in exactly similar locations, but only that all domesticated species may be found in both clean and dirty habitats, the latter being those in which disease organisms may be acquired. For example, cockroaches indiscriminately eat both the food and the feces of man and domestic and other animals. By feeding first on infected feces and later on food, cockroaches may readily effect the transfer of enteric parasites from animal to animal by the fecal-oral route.

Although Jennings and King (1913) reported that cockroaches will not readily feed on fecal material, other observers have found otherwise. Barber (1914) stated that in his experiments, *Periplaneta americana* ate human feces readily. Porter (1930) stated that fecal matter is highly attractive to cockroaches. Human feces were apparently the sole food of *P. americana* in mines in western Bengal (Chandler, 1926). Jung and Shaffer (1952) found experimentally that *P. americana* ingested about 0.1 gram of human feces at a single feeding. A photograph showing *Periplaneta americana* apparently feeding on human feces in a sewer manhole is shown in plate 4. These examples could be multiplied, but there is no doubt that cockroaches will eat feces on occasion and become carriers of pathogenic viruses, bacteria, and protozoa (see appendices). In fact, in nature it is only by coming in contact with or by eating feces that the insect can acquire intestinal parasites.

Mallis (1954) reported that a dairy in San Antonio, Tex., found its bottled milk contaminated with coliform bacilli. The contamination was traced to the bottle caps, and it was only after the bottle caps were stored where cockroaches could not enter that the contamination disappeared.

Cockroaches become contaminated with feces in sewers, latrines, privies, animal cages, chicken houses, etc. Monkeys, other zoo or laboratory animals, birds, and possibly man, may become infected by eating captured cockroaches. More probably, however, man would be infected by disease organisms carried onto his food or his person by cockroaches that have fed on or crawled over feces or some other source of infection.

Jettmar (1935) concluded from observations in Manchuria and Transbaikalia (Buriat Mongol Republic) that cockroaches were well suited to carry infectious material. He saw great numbers of *Blattella germanica* feeding on secretions flowing from the nostrils and mouths of corpses of persons that had died of lung diseases. These secretions were recognized as containing masses of infectious bacteria in almost pure culture.

Morrell (1911) cited sputum, pus, and decaying refuse as supplementary foods of cockroaches. In his experiments, he fed German cockroaches tuberculous sputum which they "devoured voraciously."

Antonelli (1930), while investigating two outbreaks of typhoid fever in Italy, found that *Blatta orientalis* frequented sewers and open latrines and migrated into the houses. Dow (1955) trapped *Blattella germanica* (or possibly *B. vaga* [R. P. Dow, p. c.[2]]), *Periplaneta americana,* and *Periplaneta brunnea* in outdoor privies in Texas in 1948. Paired traps were placed in both house and privy in the same yard. Greater numbers of *P. americana* were found in the privies than in the houses, but the opposite was true for the other species. *P. americana* was found in great numbers in latrines in Iran (Bei-Bienko, 1950). Cockroaches greatly favor latrine pits in Venezuela, also (Tejera, 1926). In Malaya the favorite breeding places for cockroaches are improperly sealed septic tanks and covered drains (Anonymous, 1939). Large populations of cockroaches are also found in septic tanks and cesspools in Java (Jan H. Vanderbie, p. c.). Bonnet (1948) stated that in Hawaii, *Periplaneta americana* and *P. australasiae* are frequently found in restaurants and homes, but can always

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[2] p. c. = personal communication.

be collected just inside the tops of cesspools and sewer manholes. In Queensland, Australia, *P. australasiae* is usually found in homes, while *P. americana* is more prevalent in sewers and manholes (Pope, 1953).

In southwestern Georgia, *Blattella germanica* outnumbered all other species of cockroaches inside homes, but *Periplaneta americana* was most prevalent (99 percent) in sewer manholes (Haines and Palmer, 1955). Population pressure, it was concluded, may be a factor inducing movement from sewerage systems into homes. Haines and Palmer found that *Periplaneta fuliginosa* (Serville) was the most common cockroach in and around privies, but during the summer months the numbers of *P. americana* trapped in privies approached those of *P. fuliginosa.* What their data also show, but which these workers did not comment on, was that *P. fuliginosa* was, next to *B. germanica,* the most common cockroach inside homes. So far as we know, *P. fuliginosa* has not been examined for pathogens, yet its habit of frequenting both privies and homes suggests that such an investigation would be desirable. *Periplaneta brunnea* apparently was also trapped in significant numbers in both privies and homes during the warmer months of the year.

Gould and Deay (1940) stated that *Blatta orientalis* frequently migrates into homes through sewerage and drain pipes, but they cited no specific observations. Fair (*in* Rosenau, 1940) stated that for sanitary reasons the plumbing should be tight to prevent egress of cockroaches and other vermin that may find their way into the drainage system.

Eads et al. (1954) experimentally tested the ability of *Periplaneta americana* to pass through two common types of plumbing traps. American cockroaches were placed in a cage attached to one end of a P-type trap having the usual water baffle, similar to those used under sinks and wash basins (see photograph in Anonymous, 1953). Another cage was placed over the other end of the trap. In the first test, 1 of 16 cockroaches passed the barrier within 6 days. In a second test, 3 of 16 cockroaches passed the barrier within a few days. In another test, 49 cockroaches were caged at the lower end of a drum-type trap, of the kind used under bathtubs, that contained water as a deterrent. Within a week, 4 cockroaches had passed through the trap. This same information is given by Von Zuben (1955).

Gary (1950) noted that in Houma, La., the sewage lift stations had always been heavily infested with cockroaches; when the walls of the wet well were sprayed with insecticide, the men were almost driven out by the fleeing cockroaches. Gary instituted odor and cockroach control in the city's sewers by dosing the sewage at the heads of the lateral sewers with orthodichlorobenzene. The first day that the treatment was applied, the influent sewage carried a mass of dead cockroaches. Workmen also reported that when the dosing stations were put into operation, cockroaches were quickly driven out of cracks in the manholes. From the photograph accompanying Gary's article (see pl. 2), the cockroach was apparently *Periplaneta americana* or another species of *Periplaneta.*

In a recent personal communication, Dr. Theodore Olson has described a very heavy infestation of *Periplaneta americana* (pl. 3) which was found in the sewer system approximately 90 feet from the surface of the ground, under the University of Minnesota campus; this sewer receives wastes from a group of hospital buildings. Dr. Olson wrote us as follows: "When I first entered the area, roaches scurried away in all directions and in their haste many lost their grip on the ceiling. As a result we were unpleasantly pelted by a shower of scrambling half-flying insects picked up by the gust of air which was produced when we opened the steel doors between the tunnel and the sewer. By the time we returned to take these pictures not all of the roaches had yet returned to the area and the photo shows only a part of the total aggregation. The warmth from the heating tunnel undoubtedly attracted the insects to this area where humidity was right and food and water could be obtained readily. To us it is an interesting example of the heavy roach population which may develop even in the northern tier of states." An examination of plate 3 shows clearly that these insects were well established in the sewer; nymphs, recently molted individuals, adult males and females, and females forming oöthecae are visible.

Although most reports have implicated the American cockroach in sewer infestations, heavy infestations of the oriental cockroach have also been found in sewers in Bedford, Ind. (Anonymous, 1957): "People reported roaches invading homes and apartments from outlets in bathtubs, sinks and lavatories. Basements were heavily infested with 'water bugs' coming up through drains. Pest control operators were finding yards, walks and porches teeming with Oriental roaches at night." Heavy cockroach infestations were found in most sewer manholes. Inspections two weeks and a month after the manholes had been sprayed with 4-percent chlordane revealed a successful decrease in oriental cockroaches in premises.

Lohmeyer (1953) reported an extremely heavy infestation of cockroaches (identified as *Periplaneta americana* by Dr. L. A. Hetrick [p. c.]) in the standard-rate trickling filter of the sewage treatment plant at the University of Florida. This filter had been in operation for five years but had never been flooded during that time to control filter flies. The filter was finally flooded because cockroaches had been seen collecting on the outside walls at night. When the flooding water was within 4 inches of the top, the filter medium was covered with a mass of cockroaches so thick that the rocks were completely hidden (see frontispiece, pl. 1). When the insects were killed by insecticide, those removed occupied a minimum volume of over 2½ cubic yards; several times that quantity died in the adjacent woods. Contamination of cockroaches in trickling filters can probably be assumed. Fair (*in* Rosenau, 1940) stated that trickling filters remove 90 to 95 percent of the sewage bacteria. Obviously, more pathogenic bacteria are present in the influent sewage than are present in the effluent. Silverman and Griffiths (1955) state that the percolating filter is not a serious obstacle to the passage of helminth ova in sewage, and they cite experiments by others to prove this point. Hence, helminth eggs could also be a source of contamination to cockroaches residing within the filter bed.

Nelson (1952) reported that cockroaches were the most prevalent filth-carrying insects of San Tomé, Venezuela. They were present in practically every building under natural conditions of no control, and they were numerous in sewer lines as well: "Literally millions of roaches, crickets, and centipedes—not to mention rats—live in sewer lines and invade homes through connecting lines or overland. . . . Cockroaches overran the kitchen and dining hall; they hid under and in sugar bowls; they were sometimes found in soup and in food. The first treatment of the messhalls and other kitchen installations yielded an approximate half barrel of dead bodies, and it was impossible to walk across a floor without crushing hundreds of bodies."

Schoof and Siverly (1954) surveyed 22 sewer manholes in Phoenix, Ariz., for a 7-week period and found a weekly average of 92 to 143 specimens of *Periplaneta americana* per manhole. Jackson and Maier (1955) surveyed sewer manholes in the same city and found 300 to 400 *P. americana* in certain manholes.

Eads et al. (1954) reported that about 40 percent of 762 sewer manholes in Tyler, Tex., were found to be infested with *P. americana.* Four other species of cockroaches were also captured in the manholes: *Periplaneta fuliginosa* in 3 manholes, *Blatta orientalis* in 10 manholes, *Parcoblatta bolliana* (Saussure and Zehntner) in 1 manhole and *Parcoblatta pensylvanica* (DeGeer) in 1 manhole. Dr. R. B. Eads (p. c.) stated that *P. fuliginosa* has become a very common domiciliary cockroach over much of the State.

Of 67 sewer manholes examined in Austin, Tex., over 77 percent contained light to heavy infestations of *Periplaneta americana* (Eads et al., 1954). In Galveston, Houston, and Corpus Christi, Tex., Eads et al. (1954) found the American cockroach present in over 50 percent of the manholes inspected. They reported that similar conditions were found in other Texas cities.

Domestic cockroaches may live and breed in close association with their food, or they may move out of sheltered areas under cover of darkness and migrate to obtain food and water. Natural migrations of cockroaches have been observed only a few times. Probably migrations are common, but as they undoubtedly occur at night or other periods of low illumination, they have seldom been observed. Recent experimental studies, reported below, have been made in an attempt to determine the extent of cockroach dispersal from sewers. This field holds much promise and it is hoped that further studies will be made.

Dorsett (*in* Howard, 1895), on a dark, drizzly day, observed thousands of *Blattella germanica* issue from the rear of an old restaurant in Washington, D. C., and march directly across a muddy street to the building opposite. Several men with brooms were unable to stop the advance. Howard believed that this was a true migration brought about by overpopulation, as there was no evidence of insecticide being used in the restaurant.

Walden (1922) reported a heavy infestation of *Blattella germanica* in a dump in New Haven, Conn. At one edge of the dump this species was found in numbers under loose bark and in cavities in trees. Several specimens of *Periplaneta americana* were also found in the trees. The cockroaches were active at night and swarmed on nearby houses and street trees as far as a city block from the dump. Felt (1926, 1928) reported a similar occurrence in a city in the Hudson Valley, in which *B. germanica* multiplied in a dump to such an extent that it became a veritable nuisance to the neighborhood. Hansens (1949, 1950) stated that a dump in New Jersey was sprayed with fuel oil and set on fire in an attempt to control German cockroaches: "This treatment resulted in flights up to four blocks from the dump even though these insects do not usually fly. There are a number of other instances where fire has resulted in otherwise harmless and unnoticed cricket and roach infestations becoming municipal problems in a few hours." Many years ago in Austin, Minn., Dr. Theodore Olson (p. c.) witnessed a mass migration of *B. germanica* from a city dump to a relatively new sewage treatment plant approximately one-quarter of a mile away. "The insects completely overran the plant even penetrating the electrical conduit system. Later when certain electrical junction boxes were opened they were literally packed with dead roaches. The migration occurred just prior to the first snowfall, and shortly after the city council decided to discontinue the use of an open dump."

Gould and Deay (1940) reported that specimens of *Periplaneta americana* have been observed migrating from restaurants and city dumps on several occasions. In one instance these cockroaches migrated during the summer from store buildings three blocks away and established themselves in decaying trees from which they entered homes. Alfieri (1920) reported an extraordinary abundance of this species in depots and warehouses in Egypt from which both nymphs and adults migrated into habitations, especially during the night. Stenburg (1947) reported that inside treatment of houses with insecticide only partially reduced infestations of American cockroaches. But after an outside application of spray to incinerators, garbage disposals, garages, and outside lavatories, no further migrations into the treated buildings occurred. The Unionport section of the Bronx (New York City) has been "invaded" by hordes of flying cockroaches (Anonymous, 1952). According to Dr. Ralph Heal (p. c.), these cockroaches were *Periplaneta americana* which swarm out of the sewers each year and appear in the streets and basements of adjacent buildings.

Lederer (1952) for several years observed the *Periplaneta americana* that inhabited the zoo at Frankfurt am Main. The insects congregated in groups of 20 to 300 individuals in heated spaces. After dark they traveled extensively through the aquarium building in search of food, returning to their resting places by daybreak. During warm weather, the cockroaches spread to all parts of the building, but when cooler weather arrived they withdrew into heated areas. During warm, sunny days, individuals or small groups left the aquarium building and migrated to nearby animal houses which they colonized. Dispersion from aquarium to animal houses apparently occurred only with an increase in the cockroach population and in warm weather. However, dispersal within the aquarium building could occur with a limited population. On these migrations between buildings, *P. americana* occasionally flew distances up to 30 meters in fairly straight courses or in flat arcs about ½ meter to 1½ meters above ground.

Beebe (1951) observed a daytime migration of at least 30 individuals of *Blaberus giganteus* (Linnaeus) through the pass at Rancho Grande, Venezuela, at an elevation of 1,100 meters. The insects were flying in a compact group at 10 o'clock in full sunlight.

Kudo (1926) observed that at the University of Illinois, from March to November, *Blatta orientalis* crawled out of crevices at the bases of buildings in the evening and were found in large numbers on walls and lawns. Weinman et al. (*in* Shuyler, 1956) stated that this species is frequently found outdoors around homes during the summer months and can become exceptionally numerous in garbage and trash dumps. Spear et al. (*in* Shuyler, 1956) stated that in warm climates or during warm weather, the oriental cockroach may live outside buildings and feed inside the buildings. Shuyler (1956) reported a marked increase in the frequency of occurrence and duration of infestations outdoors in the temperate north-central area. He also stated that the yards of whole blocks of homes have been described as "alive" with oriental cockroaches on warm summer nights. Shuyler (1956) also observed that the German cockroach occurs, sometimes in large numbers, outside buildings.

Experimental studies of the dispersal of marked cockroaches have barely scratched the surface of this field. Porter (1930) released 10 marked *Blattella germanica* at Johannesburg, South Africa. Four were recaptured between 34 and 48 hours after release and at distances 105 to 360 feet from the release point. The remaining 6 insects were not seen again. According to Stenburg (1947), the sphere of activity of *B. germanica* in houses is quite limited; the insects seemed to move only short distances from their resting places and apparently always returned to approximately the same place.

Schoof and Siverly (1954) released 6,500 radioactive *Periplaneta americana* in four sewer manholes in Phoenix, Ariz., in October 1952. Marked cockroaches were recovered at three of the release sites for 8½ weeks. One marked specimen was trapped at a yard site 60 feet from a release point. There was no evidence that the cockroaches migrated either within the sewer system or into homes.

On the other hand, Jackson and Maier (1955), in a similar study in Phoenix in July 1953, obtained positive evidence of cockroach migration from sewers. When 1,200 radioactive *Periplaneta americana* were superimposed on a native manhole population of 300, 71 tagged individuals were recaptured during the next 15 days. One was caught in a kitchen 80 feet from the manhole. Five others were caught in yard traps at distances of 15 to 95 feet from the release site. In addition, 65 tagged cockroaches were captured in the sewer system adjacent to the release site at distances up to 350 feet from the release manhole. In another experiment, 500 cockroaches native to a manhole were made radioactive. Four tagged individuals were recaptured in 15 days of trapping, one in a yard trap 33 feet from the release point and three in a manhole 170 feet downstream. Similar results were reported earlier by these workers (Jackson and Maier, 1953, 1954).

Eads et al. (1954) observed the dispersal of marked *Periplaneta americana* from sewers in Tyler, Tex. Prior to the experiment, they had observed as many as 11 cockroaches per hour leave a manhole at night (pl. 5). In May 1953, 1,000 cockroaches were painted and returned to the manhole from which they were originally obtained. The first recovery of a marked cockroach was from an apartment house 6 days after the release. Within a 3-week period, 15 marked cockroaches were recovered from the same apartment house. So many other marked cockroaches were seen by the residents that they demanded that the manhole be sprayed to eliminate the insects. About 2 months after the release, one marked cockroach was taken in a grocery one block from the release site. After a second release of 1,000 marked cockroaches in another manhole, 5 were collected in a home adjacent to the release site. Four marked specimens were killed in a home 3 days after a third release of 1,000 painted cockroaches. A week after a fourth release, one marked insect was captured in a home.

It has been conclusively demonstrated that cockroaches do migrate from sewers into homes. Probably the extent of migration is much greater than recovery of marked insects would indicate. The marking technique is admittedly an insensitive method for measuring insect dispersal because so few marked insects are ever recovered. The problem is further complicated by the probable migration of unmarked cockroaches from the sewers between manholes. In the cited experiments, large numbers of unmarked cockroaches were trapped with the few marked individuals. If a means could be devised for marking all cockroaches within a sewer system, the extent of migration into adjacent dwellings would undoubtedly be much more readily apparent.

III. VIRUSES

Recent laboratory studies have shown conclusively that cockroaches may acquire, maintain, and excrete various viruses. Results of these experiments are described in Appendix A. Four unspecified strains of poliomyelitis virus have been found occurring naturally in wild-caught cockroaches. Four identified strains of poliomyelitis virus have been successfully inoculated into cockroaches with subsequent recovery of virus. In addition, cockroaches have also been experimentally infected with Coxsackie virus, mouse encephalomyelitis virus, and yellow-fever virus.

Natural transmission of viral diseases by cockroaches has not yet been proved, but the published data show that cockroaches are certainly potential vectors of viruses. The experimental transmission of poliomyelitis virus from *naturally infected* cockroaches to susceptible hosts has been a particularly significant finding (Syverton et al., 1952). These workers isolated four strains of poliomyelitis virus from four lots of cockroaches captured in two States on the premises of paralytic poliomyelitis patients. The cockroaches were the common domiciliary species: *Blattella germanica, Supella supellectilium,* and *Periplaneta americana.* This is apparently the first time cockroaches have been found contaminated with a virus in nature.

Insect vectors apparently are only accessory to the general mode of spread of poliomyelitis, which is still unknown (Howe *in* Rivers, 1948, 1952). The virus has frequently been recovered from house flies and filth flies during epidemics, but epidemics have built up and run their course during fly-control programs (Howe *in* Rivers, 1952). Epidemics continue into cold weather beyond the fly season, and people in clean suburbs with well-screened homes suffer to the same degree as those in slums (Howe *in* Rivers, 1948). Paffenbarger and Watt (1953) reported that fly-control measures which reduced the incidence of dysentery did not reduce the number of cases of poliomyelitis or affect the duration of an epidemic in Texas. They concluded that the major role in the spread of the epidemic was person-to-person contact between paralytic cases and susceptible hosts, directly or through an intermediary. Sabin (1951) concluded that the most important route in poliomyelitis infection is the spread from person to person by the fecal-oral route and that contaminated food or drink, whether by humans or flies, is an important mode of entry. Theoretically, transmittal of poliomyelitis virus by contaminated cockroaches could fit into all of these situations, perhaps better than house flies.

Cockroaches, being less obvious and less feared than flies, rarely are subjected to widespread eradication as have been flies. Cockroaches are no respecters of homes and may be brought into the cleanest with groceries, in cases of beer, or may enter by migration. Cockroaches, unlike flies, breed indoors the year around, a fact that makes them potential vectors in winter when flies are dormant. Obviously, much more work remains to be done before the role of cockroaches as possible vectors of poliomyelitis can be ascertained. Yet the finding of poliomyelitis virus in three species of wild-caught cockroaches (as opposed to laboratory-inoculated) suggests that a more concerted effort should be made to control cockroaches, as well as to determine their relation to this disease.

The Coxsackie virus may retain its virulence in the American cockroach for 15 days after being ingested (Fischer and Syverton, 1951a). The "C" viruses have been recovered in feces and from sewage in cities where Coxsackie infections had occurred, which suggests that cockroaches might be vectors as they have ample opportunity to acquire the virus in sewers.

Although Findlay and MacCallum (1939) reported that yellow-fever virus retained its activity when injected into the abdomen of *Blattella germanica,* they did not suggest that cockroaches necessarily play any part in the epidemiology of yellow fever. However, they point out that monkeys supplement their diets with insects and suggest that it would be of considerable interest to determine the natural animal foods of monkeys in yellow-fever areas. It would also be of interest to determine whether these monkeys could be infected with yellow fever by eating cockroaches that had been injected with the virus; this experiment apparently was not run.

We have found several records (e.g., see section on helminths, pp. 27, 95, 105) of monkeys feeding on cockroaches, but only the following reference indicates how cockroaches might acquire the yellow-fever virus in nature. Whitfield (1940) stated ". . . cockroaches are omnivorous, and no considerable employment of the imagination is necessary to see a possible connection between dead mosquitoes, excreta from other sick monkeys, and general detritus, etc., infected with the virus; scavenging cockroaches, and monkeys catching the cockroaches. The possibilities of such a cycle of infection are not confined to the laboratory, and it is reasonable to suppose that infection *via* the alimentary canal may possibly be a contributory cause of jungle or rural yellow fever."

Yellow fever is basically an infection of the hemapoietic system; during the first 3 days of fever, the virus is readily available to certain blood-sucking mosquitoes in which it must multiply for about 12 days before the mosquito can transmit it by bite. (Theiler *in* Rivers, 1948; Herms, 1939). Cockroaches have been known to bite man (see pp. 30-32), yet we do not know definitely whether they imbibe blood. Cockroaches have been known to gnaw on the extremities of dead and dying humans (Drury, 1782), but the virus has only once been isolated from a man dead of yellow fever (Theiler *in* Rivers, 1948). Cockroaches are known to feed on dejecta, but it has been conclusively shown that dejecta from yellow-fever patients are not factors in the epidemiology of yellow fever (Herms, 1939). There remains, of course, the unanswered question, can cockroaches be infected with yellow fever perorally? There would seem to be no other way in which they could become infected in nature. Findlay and MacCallum injected the virus into their cockroaches parenterally.

IV. BACTERIA

The evidence that implicates cockroaches in the transmission of bacterial disease agents is largely circumstantial. Yet much of the evidence is so persuasive that we find it impossible to accept cockroaches as only minor annoyances of little medical importance. Although papers that demonstrated natural and artificial contamination of cockroaches with bacteria began to appear in the last century (e.g., Cao, 1898), more papers on this subject have been published since 1940 than in all the years before. This gathering momentum can hardly be fortuitous.

The information relating cockroaches to transmission of pathogenic bacteria (Appendix B) includes isolation of bacteria from wild-caught cockroaches and experimental inoculation of cockroaches with bacteria in the laboratory. Both categories implicate cockroaches as potential vectors of infectious agents. The first class is particularly significant because it includes organisms that the cockroaches acquired naturally through their own activities. Certain bacteria that have been transmitted to cockroaches experimentally may be of lesser importance because under natural conditions these bacteria may be less accessible to the insects.

About 45 species of bacteria that are not pathogenic to vertebrates have been found in cockroaches. These are not discussed.

More species of pathogenic bacteria have been found associated with cockroaches than all other kinds of disease organisms together. Cockroaches have been found naturally contaminated with about 40 species of pathogenic bacteria; many of these have also been transmitted to cockroaches experimentally. In addition, over 20 other species of bacteria have been introduced into cockroaches experimentally. At least three species of bacteria did not survive in cockroaches; this latter figure does not include negative results with bacteria that were positive in other experiments.

The diseases caused by pathogenic bacteria that have been found occurring naturally in or on cockroaches include various generalized and specific infections, dysenteries, gastroenteritis, summer diarrhea, enteric fever, food poisoning, typhoid fever, plague, gas gangrene, leprosy, and nocardiosis.

Additional diseases caused by bacteria that have been transmitted to cockroaches experimentally include Asiatic cholera, cerebrospinal fever, pneumonia, diphtheria, undulant fever, glanders, chicken cholera, anthrax, black leg, tetanus, rat leprosy, and tuberculosis.

One of the most convincing examples of the transmission of a bacterial disease agent by cockroaches is the report by Graffar and

Mertens (1950) describing the role of *Blattella germanica* in the transmission of *Salmonella typhimurium.* These workers observed the following facts during an epidemic of food poisoning in the nursery at the Clinique Pédiatrique de l'Hôpital Universitaire de Bruxelles: 1. Persistence of an epidemic of intestinal infection of *Salmonella typhimurium* in spite of quick isolation of the patients, the absence of healthy carriers, and the suppression of infecting contact, direct or indirect, between the babies, with the exception of indirect contact through cockroaches. 2. Finding that cockroaches ran over the covers, clothing, and bodies of the babies at night. 3. Capture of a cockroach carrying numerous bacteria of the species *S. typhimurium,* in the vicinity of the babies. 4. Immediate check of the epidemic when the nursery was disinfected with DDT.

This epidemic prevailed for nearly 2 months in a nursery containing permanently 16 to 20 infants. Of the 50 children that passed through the nursery, 16 were contaminated with *S. typhimurium.* During most of the epidemic, cockroaches had not been suspected because they were not seen during the day. When the nursery was about to be closed, a night nurse called attention to the cockroaches. Thirty *Blattella germanica,* one of which was contaminated, were captured before the nursery was disinfected. It is highly significant that from the day the nursery was sprayed with DDT no more living cockroaches were seen, and no more cases of evident or hidden infections of *S. typhimurium* were detected.

Concerning salmonellosis, Watt (*in* Maxcy, 1951) stated that the case against arthropods as transmitters is circumstantial and the lack of direct evidence in itself indicates that insects probably play a minor part in the spread of human salmonellosis. However, the findings to date indicate that intensive control measures are warranted in any area where both cockroaches and *Salmonella* infections are prevalent and that strong efforts should be made to control these insects in hospitals and public eating places (Mackerras and Pope, 1948; Graffar and Mertens, 1950; Janssen and Wedberg, 1952).

In recent years, cockroaches as well as other insects have come under suspicion as possible vectors of the bacillus of Hansen's disease. Doull (*in* Maxcy, 1951) stated that the evidence for insect vectors in the transmission of leprosy is based on analogy and is largely presumptive. Simons (1952) strongly inclined to the view that the cockroach and the bedbug should be suspected, because leprosy is the pauper's disease and the vector should be an insect that is important in the lives of unhygienically living people.

Clinical evidence for the transmission of leprosy is conclusive

(Smith et al., 1948). Leprosy is not highly contagious and is probably acquired by infecting superficial abrasions of the skin (Freund and Middlebrook *in* Dubos, 1948). Although transmission is presumed to be from person to person, indirect transmission has not been disproved; in fact, Smith et al. (1948) cite three examples of indirect transmission of leprosy, one in which leprosy developed after an injection of leprous blood, and two cases in which leprosy began in tattooed areas about three years after the tattooing.

Moiser (1944, 1945, 1946, 1946a, 1947) observed that cockroaches in southern Africa bite savagely at night, leaving scars which in patients (Moiser, 1946a) at least, have repeatedly been found to contain Hansen's bacillus. This observation was anticipated by Lamborn (1940) who stated that cockroaches may on occasion feed directly on the leper. These findings, together with the data from field and laboratory studies of the relationship of several species of cockroaches with *Mycobacterium leprae,* warrant serious consideration (see pp. 75-77). Wilson (1946) points up the problem succinctly in his evaluation of Moiser's study: ". . . if the work of several observers, operating in widely separated districts, should establish the fact that micro-organisms resembling Hansen's bacillus are commonly found in cockroaches associated with human leprosy, and are not found in cockroaches generally, then the evidence of the association of leprosy with cockroaches would be strong enough to demand further investigation, and even to justify the instigation of preventive measures."

In 1954 Dubois reviewed the role of invertebrates in the transmission of leprosy. He cited only Arizumi and Moiser for evidence of cockroach transmission, although Macfie, Tejera, Lamborn, and Radna had all published supplementary observations prior to 1950. Dubois's main objections to accepting cockroaches as vectors are (1) that the exact nature of the acid-fast bacilli found in the cockroaches is not known (except by morphological appearance), and (2) the fact that cockroaches bite humans seems to be poorly established. These objections are sufficiently valid to deserve comment.

Man is highly resistant to experimental infection, and no other animal is susceptible to infection with human leprosy (Smith et al., 1948). Hence, it has not been possible to prove that the acid-fast organisms found in cockroaches are identical to *M. leprae.* Yet the isolation of bacilli that are morphologically similar to *M. leprae* from insects that have fed on leprous material is highly suggestive, especially when similar organisms are not found in control cockroaches (Lamborn, 1940). Moiser (1946) suggested that leprosy may be primary in the cockroach and secondary in man, and that the bacteria multiply in the cockroach.

Dubois (1954) cited the opinions of three individuals who stated that cockroaches do not bite man. One, an entomologist, was quoted as writing, "I have never heard nor read a statement to the effect that species of Blattidae bite human beings and if I did, would not believe anything so ridiculous." The biting of humans by cockroaches is discussed on pages 30 to 32. The biting habit is not characteristic of cockroaches, however, and is probably restricted to primitive areas with poor sanitation and heavy cockroach infestations.

Infection through cockroach bites alone need not be an essential mechanism in the transmission of leprosy. Moiser (1946, 1946a) contended that the bites or the feces of infected cockroaches are the real source of infection in leprosy. Wilson (1946) expounded this idea in suggesting a mode of infection analogous to the transmission of *Pasteurella pestis* by fleas: contaminated cockroach feces may be rubbed or scratched into the skin. Under primitive conditions, such contamination may be commonplace.

If cockroaches are entirely mechanical vectors of leprosy, they could conceivably transport *M. leprae* on their legs from leprous individuals to existing lesions in the skin of sleeping humans without either biting man or excreting the organism in the feces. There are many references to cockroaches climbing over the bodies and faces of sleeping children and adults, summarized on pages 28 to 30, in addition to the references on biting.

The Leprosy Research Department, School of Tropical Medicine, Calcutta (1948), has investigated the relationship of cockroaches to transmission of leprosy. The examination of cockroaches (species not identified) captured in a leprosy hospital and in other areas disclosed the presence of acid-fast bacilli in the gut contents of over 50 percent of 398 insects. These bacilli were morphologically unlike the leprosy bacillus and were not more numerous in cockroaches collected in the hospital than in those collected elsewhere. Cultures of acid-fast bacilli were prepared from the gut contents of six cockroaches. These workers, therefore, concluded that the acid-fast bacilli in captured cockroaches were not the leprosy bacillus. However, when leprous material was fed to a number of cockroaches showing no acid-fast bacilli in their feces on three consecutive days, acid-fast bacilli were found in the cockroach feces in decreasing number for two weeks thereafter. There was no indication that the ingested bacilli multiplied in the gut of the cockroaches. On this basis, these workers concluded that their work did not support Moiser's hypothesis that cockroaches may play an important role in the transmission of leprosy. Yet, in their conclusions, they ignore their successful experiments in contaminating cockroaches with leprous material which presumably was recovered as acid-fast bacilli for a period of two weeks following ingestion.

The possible transmission of leprosy bacilli by insects has not yet been exhaustively investigated, but until the epidemiology of leprosy is determined, cockroach control should certainly be encouraged in areas where leprosy is endemic.

Herms and Nelson (1913) found more *Micrococcus pyogenes* var. *albus* on the single pair of hind legs of the German cockroach than on the remaining two pairs of legs combined. They attempted to explain this heavy infestation as a result of the manner in which the cockroach uses its legs in walking; they stated, "The tibia and tarsi are in contact with the surface on which the insect walks, being parallel with the body. Very often the insect stands on the hind pair of legs, with the remaining legs barely touching the surface." Actually, during the normal walking process, the tibiae of the cockroach rarely touch the substrate and contact with the surface is made with the euplantulae, arolia, or claws, depending on whether the substratum is smooth or rough (Roth and Willis, 1952). Perhaps the difference in the size of the legs may be a factor in the greater number of micro-organisms found on the hind legs; the hind legs being larger than the others could harbor more bacteria. Jettmar (1935) found that, after *Blatta orientalis* had walked on a culture of hemolytic streptococcus, the cockroach transferred more of the pathogens mechanically from the hind end of its body than from its feet. This observation may be related to those of Herms. The cockroach cleans its abdomen with its hind legs, using them like a scraper or brush (Turner, 1913; Wille, 1920), and in this way could pick up more bacteria on its hind legs than on the others.

Cockroaches are naturally immune to many of the bacteria that are pathogenic to man. Most of the micro-organisms listed in Appendix B have no effect on the insects. In some instances, the numbers of micro-organisms decreased in the cockroaches and could not be recovered from the feces. McBurney and Davis (1930) concluded that *Salmonella typhosa* is either killed in the intestines of *Blatta orientalis* by some unknown agent, or its ability to ferment and to agglutinate is destroyed. On the other hand, Morischita and Tsuchimochi (1926) tested the sterilizing power of the intestinal contents of *Periplaneta americana*, as represented by a solution of feces. *S. typhosa* did not die even after 3 hours in this solution. Possibly this was too short an exposure. Wedberg et al. (1949) failed to recover *S. typhosa* from *Blaberus craniifer,* even though billions of the bacteria were fed repeatedly to these insects. Similar results were obtained by Janssen and Wedberg (1952) with *Blattella germanica* which failed to produce a single positive stool 24 hours after feeding on billions of *S. typhosa;* only 2 of 45 stools were found to be positive, and these were passed within the first 18 hours after the insects had fed on the pathogens. Jung and Shaffer (1952) concluded that, although *P. americana* appears to have some mechanism for eliminating many hundreds of ingested *Salmonella,* it may harbor certain strains for at least a week if it eats feces containing at least several thousand of these microorganisms.

Not all *Salmonella* decreased rapidly in the cockroach, however. Various species listed in Appendix B survived in the guts or feces of cockroaches for periods of 18 to 42 days, and on the pronotum 78 days (Olson and Rueger, 1950). Fecal pellets have remained infective for more than 4 years (Olson, p. c.; see p. 66).

The results of experiments with the vibrios of Asiatic cholera have been variable possibly because of differences in techniques of feeding the pathogens to the test insects (Akkerman, 1933). Some workers have reported a relatively rapid decrease in the number of microorganisms excreted (Toda, 1923). In *Periplaneta americana* most of the vibrios died in the foregut and Akkerman (1933) suggested that the degree of acidity that prevails in the gut may be harmful to the pathogens and have something to do with their depletion. Morischita and Tsuchimochi (1926) tested the sterilizing properties of a solution of feces from *P. americana.* The pH of the solution was about 6.7; it did not kill *Vibrio comma* within 3 hours. Jettmar (1935) claimed to have extracted a bacteriophage active against *V. comma* from the intestinal tract of *Blattella germanica.*

Periplaneta americana and *Leucophaea maderae* are relatively little susceptible to plague bacilli inoculated directly into the body cavity of these insects (Barber, 1912). Plague bacilli rapidly died or lost their virulence in the intestine of *Blattella germanica* (Jettmar, 1927).

Macfie (1922) failed to recover *Neisseria gonorrhoeae* Trevisan (cause of gonorrhea) from the feces of *P. americana* after the insects had fed on the pathogen. *Brucella abortus* (cause of undulant fever in man) does not remain alive in the intestinal tract of the American cockroach for more than 24 hours (Ruhland and Huddleson, 1941). Other negative results in feeding experiments are listed in Appendix B. The reader is referred to Steinhaus (1946, 1949) for a general discussion of immunity in insects.

The anthrax bacillus can multiply in the intestine of *Blatta orientalis* (Cao, 1898). Küster (1903) reported data suggestive of multiplication of anthrax bacilli in the gut of *B. orientalis.* There was an inverse relation between the number of days the anthrax bacillus remained in the cockroach's gut and the infection time in hours after injection into mice: 6 days/104 hours, 12 days/41 hours, 15 days/36 hours, and 16 days/24 hours. This is based on the assumption that an increase in the number of micro-organisms shortens the infection time. Cao (1898, 1906) found that certain bacteria (e.g., "Bacillo similcarbonchio" and "Bacillo proteisimile") isolated from the oriental cockroach were pathogenic for guinea pigs. Continued passage through the cockroaches and variation in diet increased the virulence of these and other originally nonpathogenic bacteria. Ekzempliarskaia (*in* Pavlovskii, 1948) also found that the virulence (to guinea pigs) of *Mycobacterium avium* and *Mycobacterium piscium* increased after the bacteria passed through the intestine of *Blatta orientalis.* Moiser (1946, 1946a) stated that *Mycobacterium leprae* is found in such numbers in cockroaches that have fed on leprous nodules as to suggest multiplication in the body of the insect.

V. FUNGI

Two fungi, *Aspergillus fumigatus* and *Aspergillus niger,* which are sometimes found associated with pathological conditions, have been found naturally in cockroaches. *Geotrichum candidum* was successfully inoculated into a cockroach, but *Histoplasma capsulatum* was not recovered in feces after feeding experiments. An annotated list of these organisms is given in Appendix C. These observations apparently cover the field. Yet a very large number of fungi are associated with insects (Steinhaus, 1946); for this reason, the dearth of information about pathogenic fungi that may possibly be associated with cockroaches is particularly surprising. This might be a fertile field for further study.

About 40 species (mostly Laboulbeniales) of nonpathogenic fungi and about 6 yeasts have been found on or in cockroaches. These are not discussed.

VI. PROTOZOA

Only four protozoa pathogenic to man have been reported to be associated naturally or experimentally with cockroaches (Appendix D), in contrast to many nonpathogenic forms. The pathogenicity of three of these, *Balantidium coli, Entamoeba histolytica,* and *Giardia intestinalis,* is unquestioned, but that of the fourth, *Trichomonas hominis,* is doubtful.

About 90 species of nonpathogenic protozoa have been found in cockroaches. Approximately half of these are found in the wood-feeding cockroaches, *Cryptocercus* and *Panesthia.* Although interesting, the nonpathogenic forms are beyond the scope of this review.

> It becomes more and more evident that eating roaches is a very bad habit for animals that habitually indulge in it.
>
> CHANDLER (1949).

VII. HELMINTHS

Cockroaches are known to harbor a fairly large number of helminths, some of which may occur as primary parasites of man and other vertebrates (Appendix E).

Next to the bacteria, the helminths form the largest group of pathogenic organisms transmitted by cockroaches. The eggs of seven species of helminths have been found naturally in cockroaches; eggs of five other species were passed unharmed through the guts of cockroaches and appeared in their feces. Cockroaches have been found to serve naturally as the intermediate hosts of 12 species of helminths and as the experimental intermediate hosts of 11 other species. Four doubtful records are listed and discussed. Attempts to infect cockroaches experimentally with three cestodes and five nematodes were completely negative. About 45 species of helminths that are primary parasites of cokroaches and not pathogenic to vertebrates are known. These are not discussed.

Some cockroaches have been found to serve as excellent experimental hosts in studies on the life histories of various parasitic worms (Hall, 1929). It is this ability to support the development of certain species of helminths, especially spirurids and acanthocephalids in nature, that makes cockroaches potentially dangerous. The development of species of *Gongylonema,* primary parasites of sheep, cattle, and horses, as accidental parasites in cockroaches is an example of cockroaches serving as hosts for worms that cannot depend on such hosts for transmission in nature (Hall, 1929).

The finding of *Protospirura columbiana* in rats killed in the National Zoological Park in Washington, D. C., but not in rats caught in other parts of the city suggested to Cram (1926) that the normal host of this spirurid may be a rodent other than the rat present in the park. Cram suggested that rats and cockroaches, commonly present in zoological gardens, may play a part in the dissemination of parasites not native to a country but brought into zoos with exhibition animals.

This belief of Cram's was vindicated by Brumpt and Urbain (1938, 1938a), who found that the acanthocephalids *Prosthenorchis elegans* and *Prosthenorchis spirula,* which in nature are found in monkeys, lemurs, and coati, were able to adapt easily to new hosts found in zoological parks. These worms developed there in the German cockroach which, though probably not a host in the forests where the normal primary hosts are found, was capable of maintaining and spreading infection in zoos.

The rat parasite *Gongylonema neoplasticum* occurs naturally in at least four species of cockroaches which serve as intermediate hosts. The work of Fibiger with *G. neoplasticum* in relation to rat cancer is of interest because for it he was awarded a Nobel prize in 1926. However, this work provoked a controversy of acclaim and criticism that has continued up to the present time. Fibiger (1913, 1913a) believed he had found a correlation between the presence of *G. neoplasticum* and the occurrence of stomach tumors in rats. The arguments about the importance of parasites in the production of cancer (see Anonymous, 1913; Sambon, 1924, 1926a; Simpson, 1924; Yokogawa, 1924, 1925a; Goyanes, 1926; Leiper, 1926; Oberling, 1944) have been resolved only recently. Hitchcock and Bell (1952), using *Gongylonema neoplasticum,* in carefully controlled experiments failed to produce acceptable malignant lesions in rats. They showed further that lack of vitamin A in the diet heightens the deleterious effect of the parasites; rats that were maintained on a diet deficient in vitamin A developed pathologic changes similar to those described by Fibiger. Hitchcock and Bell concluded that *G. neoplasticum* acts as a biologic, chronic irritant and produces only minimal effects on the forestomach epithelium in the absence of concurrent nutritional deficiency.

Sondak (1935) found cockroaches, captured in places where food was prepared in Leningrad, carrying normal eggs of *Enterobius vermicularis* and *Trichuris trichiura;* as a result, he concluded that the most radical measures must be undertaken to destroy cockroaches in places where food is prepared and served. He cited a 1930 report by Filipchenko and Dansker on conditions contributing to infection of communal eating places and children's institutions by eggs of parasitic worms of man. They had found eggs of *Taenia* sp., *Ascaris lumbricoides,* and *T. trichiura* on dining tables, chairs, benches, and even on dishes. Although admitting that fouling of these objects can be due to insufficient cleansing of the hands, Sondak pointed out that cockroaches, crawling through a dirty environment, can also be a mechanism for carrying eggs of these parasites.

> Tropical hygienists must be strongly recommended to pay attention to the connection between cockroaches and eventual inexplicable cases of illness.
>
> AKKERMAN (1933).

VIII. ALLERGY

Cockroaches have long been known to crawl over sleeping persons. As early as 1699, Lehmann (*in* Hennicke, 1761) reported cockroaches feeding on milk that had flowed around the neck of a newborn child. Vinson (*in* Hasselt, 1865) stated that it was not at all rare on Reunion (=Bourbon) Island for cockroaches to crawl over the faces of sleeping people, attracted there by the taste or odor of food or drink on the mouth or lips. Moseley (1892) observed that a large cockroach on board H.M.S. *Challenger* would sip moisture from his face and lips while he was dozing. In Brazil, H. H. Smith (*in* Marlatt, 1902) and his wife sometimes had to brush cockroaches from their faces at night. Rau (1940) noticed that, while he was sleeping in his laboratory, *Periplaneta americana* would crawl on his face and imbibe moisture from his nostrils. More recently, cockroaches have been seen in hospitals crawling on the faces of sleeping babies (Frings, 1948; Graffar and Mertens, 1950). In a personal communication about his original observation, Frings wrote as follows: "As to the matter of cockroaches crawling on infants—I saw this myself. . . . The incubators had a beautiful population of roaches which the pest control man I was accompanying was not allowed to go after. It was while watching the playful antics of these *Blattella germanica* that I noticed some of them walking around on the infant and actually feeding on a little bit of caked milk at the corners of its mouth." In addition to these observations, the numerous records, in the next section, of cockroaches biting man also imply that the insects crawl over sleeping persons.

The possibility of bodily contact with cockroaches is thus well established, particularly in tropical areas and even in temperate climates where control measures are not adequate. Small wonder, then, that certain skin diseases have been attributed to contact with cockroaches. Vinson (*in* Hasselt, 1865) noted that among the residents on Reunion there appeared a special blistery rash on the face about the mouth. This agreed with the condition known as herpes simplex (=labialis [Scott *in* Rivers, 1948]), but Vinson believed that the dermatitis should be called herpes blattae. He stated that, unlike herpes simplex, herpes blattae could be easily prevented by rinsing or washing the face before sleeping. He attributed the blister-raising properties to the cuticular grease or to a discharge from the mouths of the cockroaches.

Simons (1952) indicated that certain linear dermatoses in the Tropics are caused by secretions left on the skin by crawling insects and that cockroach dermatitis is one of these. An edema of the eyelids is also attributed to the cockroach. Simons (1952) also noted that in the Tropics, both East and West, a type of urticaria or edema is frequently attributed to the bite of the cockroach.

A recent personal communication from Mary F. Lerner, M.D., of Brooklyn, N. Y., is of interest. Dr. Lerner treated a patient who had severe generalized hives. The clinical history of this case follows: "In September, 1943, . . . I had occasion to move some cartons which had been there for over a year. An army of cockroaches appeared and I started to stamp on them. Two days later I started to itch all over and was covered with hives. Bathing in bicarbonate only exacerbated the condition. The doctor gave me adrenalin and that helped for four hours. No other medications seemed to help. This lasted four days. Then, when I started to get dressed it started all over again. When I removed my shoes and peds (which were the sames ones I had worn) the itch disappeared. The doctor told me to discard these shoes and peds and I never had a recurrence." Dr. Lerner stated that the hives and itching were controlled by the administration of adrenalin every four hours and a mixture of ephedrine and sedation repeatedly; the situation was not controlled until it was realized that putting on the shoes and peds, which the patient had worn while crushing the cockroaches, caused a recurrence of the hives and itching.

Certain species of cockroaches produce secretions which are stored in quantity in specialized glands and which may be irritating to man. For example, the adults of *Eurycotis floridana,* when disturbed, eject an aldehyde, 2-hexenal. This secretion is irritating to sensitive areas of the skin of some individuals (Roth et al., 1956). Recently, William and Anne Bunting of Yorkshire, England, experienced poisoning while cleaning out a culture container in which they kept *Eurycotis decipiens* (Kirby) from Trinidad. He (p. c.) wrote, "We both suffered from vertigo, running eyes, nausea; we were unable to face any food that day, and our tongues were yellow for twenty-four hours." He also observed that this cockroach is capable of ejecting the secretion a distance up to 3 feet.

Pavlovskii and Shtein (1931), in studying the effects of the bite of *Blatta orientalis* on human skin, noticed a degeneration of epithelial cells, necrosis, and inflammation which they attributed to a toxic effect of the insect's saliva. An emulsion of the salivary glands produced the same symptoms as the bite of the cockroach when rubbed into skin damaged with a sterile needle.

> A Kenya doctor was asked whether cockroaches bite. His reply was "Of course they bite! I can demonstrate half-a-dozen bites in my outpatients any morning."
>
> MOISER (1947).

IX. COCKROACH BITES

Whether cockroaches naturally bite man has been the subject of some controversy (see Dubois, 1954, and our discussion of leprosy, pp. 20-23). In areas where cockroaches are well controlled or where cockroach populations are not large, cockroach bites may be rare phenomena. In primitive areas that lack adequate insect control, and especially in tropical areas that support large cockroach populations, particularly in sleeping quarters, biting has been well documented.

Ligon (*in* Sloane, 1725) and Jeffereys (1760), describing conditions in the West Indies, stated that cockroaches entered beds and bit the sleepers. Catesby (1754) mentioned cockroaches scratching the faces of men and biting the greasy fingers of sleeping children. A similar occurrence was noted by de Azevedo Marques (1925); he also reported that in Brazil cockroaches gnaw on the fine flakes that collect on the skin covering the heads of sleeping people, on the substance that collects in the corners of the eyes, and on the feet. Drury (1782, 1837) stated that in the West Indies *Blaberus discoidalis* (=*giganteus* of Drury [Rehn and Hebard, 1927]) attacked people who were not sleeping under bed nets, that the sick and dying had their extremities attacked, and that the ends of the toes and fingers of the dead were frequently stripped of flesh. Hartnack (1939) reported that persons have been thought to be victims of crimes until it was found out, by accident, that skin defects had been caused by cockroaches feeding on the corpses. He also stated that the oriental cockroach may eat dead rats down to the skeleton.

Durie (1870) reported an instance of cockroaches nibbling off all of a toenail down to the quick. Nicols (1870) mentioned that sailors frequently complained of having their toenails and fingernails and the hard parts of the soles of their feet and hands nibbled by cockroaches. He also recounted a personal experience: "On returning from a shooting excursion in salt swamps in tropical Australia, with my feet blistered and sodden, I was put to sleep in a room swarming with cockroaches (the small species). The night was intensely hot, and my feet were exposed. I had slept soundly for some hours, when an intolerable itching and irritation about my feet awoke me. I felt these objectionable insects running over and gnawing at my feet. On striking a light, I found they had attacked the skin and entirely eaten it away from a large blister, leaving a raw place as large as a shilling. I slept again, and in the morning found they had completed the work, and established a painful sore. The whole of the hard skin of the heel was also eaten down to the pink flesh. The nails were not attacked. I have now, at a distance of four years' time, bluish scars on the skin." Kingsley (1870) confirmed Nicols's account, citing a similar experience of a friend who was "marked for life" by cockroaches on board a ship from Jamaica.

Webster (1834) also stated that cockroaches will attack the toenails of persons in their sleep. Smith (*in* Marlatt, 1902) observed that in Brazil the toenails were bitten off by cockroaches, and that in the house where he was staying cockroaches had bitten off the eyelashes of about a dozen children. Kellogg (1908) reported that ships came to San Francisco from voyages around the Horn with the sailors wearing gloves to protect their fingernails from being gnawed off by the hordes of cockroaches that infested the ships. Gates (1912) stated, "All of us who have been more than a short time in the naval service have had our troubles with roaches . . . and it is solemnly affirmed [that] even the toe nails of the personnel of the navy have long suffered from their ravages." Heiser (1936) mentioned that on board ship in the Orient, cockroaches gnawed off the passengers' corns. Bronson (1943) recounted the experience of a friend who was cook on a small West Indies schooner. This man awakened from a nap with his face sweating terribly. On looking into his mirror, he found that the cockroaches had eaten the galley grease from his face, taking off a layer of skin as well. Each night the cockroaches gnawed the calluses on the bare feet of the sleeping crew.

Gal'kov (1926), in workers' quarters at platinum mines in the Urals, saw a nursling child whose face, hands, and belly were covered with tiny wounds caused by cockroach bites. In another barracks a child's corpse which had lain exposed overnight had its face eaten away by cockroaches. According to the inhabitants of the barracks, cockroaches very often attacked sleeping persons, especially the women, biting the skin of their ears, face, and other places where the epidermis is thin. Moiser (1945, 1946) reported that cockroaches bite African natives savagely at night. Although he mentioned that

Blattella germanica and *Oxyhaloa buprestoides* (=*murrayi*) are common in Southern Rhodesia, Moiser did not specifically implicate these species as biting man. Moiser (1947) also reported that although he had never seen a cockroach in the act of biting, the African natives were well aware that cockroaches bite. Zimmerman (1948) reported that cockroaches gnawed on his feet while he slept on a copra schooner traveling in Fijian waters.

Rageau and Cohic (1956) stated that in heavy infestations, *Blattella* and *Periplaneta* would attack man (particularly nursing infants), nibbling the skin, especially at the ears, and gnawing at scabs, thus enlarging wounds. They observed exceptional cases of such attacks by *Periplaneta australasiae* and *P. americana* at Nouméa (New Caledonia) and received information from J. Guiart who reported a similar attack by *Blattella germanica* at Espiritu Santo (New Hebrides).

Lederer (1952) observed that *Periplaneta americana* fed readily on open wounds of animals in the zoo at Frankfurt am Main, Germany, but he did not imply that the wounds were cockroach bites.

According to Pospelow (1904; *in* Pavlovskii and Shtein, 1931), the bite of *Blatta orientalis* produces characteristic triangular patterns, particularly at the neck, chest, elbows, and feet, which are covered by dried blood crusts. Pavlovskii and Shtein (1931) experimentally determined the effect of the bite of *B. orientalis* on human skin. The insects were induced to bite skin moistened with sugar solution. The bite resulted in a slight pain and itching; 24 hours later, the bitten areas were covered with scabs. In these spots, the skin was destroyed almost to the corium. Damage to the epidermis was attributed to mechanical effects of the bite.

The positive act of cockroaches biting humans has been reported at least 18 times; there are undoubtedly other similar reports that we have not seen. Admittedly, many of the accounts lack the authenticity of direct personal observation, but even so, this body of evidence cannot be ignored. Most of the reports seem to be independent observations as there were no attempts to document the statements. Moiser (1947) even stated that he had found no references, other than his own, to the fact that cockroaches bite man. He also pointed out that African natives habitually live, cook, eat, store food, and sleep in huts that are heavily infested with cockroaches. We conclude that under such primitive, unsanitary living conditions, food-seeking cockroaches may incidentally bite man. (See also Sells, 1837, p. 132.)

X. ACCIDENTAL INVASION OF MAN

Kalm (1772), on his travels in North America, was told a firsthand account by a man whose ear had been entered by a cockroach while he was asleep. The experience was described as being extremely painful. The cockroach backed out of the ear canal after the man threw water into his ear. Baldwin (1906) described a similar occurrence in which a "kitchen" cockroach, a little over an inch long, had wedged itself tightly into the external auditory meatus. The patient complained of a "tremendous buzzing" in her head. The meatus was considerably reddened by the scratching cockroach. Stiles and Hassall (1928) reported two other cases of invasion of the ear. In the first case (attributed to Mader [1897]), a male patient who slept in a kitchen complained of ringing in his ear and headache. A dead *Blatta orientalis* was removed from the ear, in which it had been lodged for several days. In the other case, the invasion was attributed to *Blattella germanica.*

Sheard (1922) reported that while he was on shipboard in the Mediterranean his nasal passage was entered by a cockroach. He had experienced a slight fullness in the left nostril for about a day. After blowing his nose forcibly several times, he obtained sudden and complete relief by ejecting a full-grown cockroach from his nostril. The insect was quite dead and was enmeshed in a film of clear, tenacious mucus. Presumably the cockroach had crawled into the nostril while Sheard was asleep, possibly two or more days earlier.

Stiles (1918) received specimens of several nymphs and an oötheca of *Blattella germanica* purported to have come from an abscess of the jaw. A patient under observation in a hospital, with a large swelling under the angle of his left jaw, expectorated a bloody sputum. The oötheca and the cockroaches were apparently present in the sputum. However, it is extremely doubtful that the egg case was placed in the abscess by the female cockroach, or that the egg case and nymphs migrated through the abscess into the patient's mouth. A female cockroach may have dropped an egg case on the patient just before the eggs hatched or as they were hatching; the egg case and nymphs may even have been in the receptacle for the sputum before the patient spit.

Hennicke (1761) reported an invasion of a 1-year-old child, through the mouth, by cockroaches similar to *Blatta orientalis.* The infant coughed up one insect that was still alive and excreted another after being treated with a prescribed medicine.

Johnson (1899) reported that a nursling of 6 months, who showed symptoms of a toxic condition apparently of intestinal origin, had been invaded by cockroaches. About 2 hours after the child had taken a prescribed purgative by mouth, the father reported that the patient had passed 6 "cockroaches" and that the stools were of an extremely disagreeable odor. The floor of the room was overrun with cockroaches, and Johnson suggested that the insects had been attracted to the child's mouth by the sirupy cough mixture she had been taking.

> Cockroaches thrive in British Columbia. . . . On this trip I had them served to me in three different styles, alive in strawberries, a la carte with fried fish and baked in biscuit.
>
> CAUDELL (1904).

XI. COCKROACHES AS HUMAN FOOD

Inasmuch as cockroaches may harbor organisms pathogenic to man, it is significant that in some areas of the world these insects are eaten as food. The following summary includes only reports of cockroaches that were apparently consumed as food rather than as medicine; the medicinal uses of cockroaches are discussed in the next section.

According to Miall and Denny (1886), salted cockroaches were said to have an agreeable flavor which was apparent in certain popular sauces. This information was probably taken from Webster (1834) who noticed that ". . . common salt and water saturated with the juices of the cockroach had all the odour and some of the flavour and qualities of soy. . ." Dagen (*in* Melville-Davison, 1911) claimed that "shelled" cockroaches tasted like shrimp.

Bristowe (1932) saw a Lao at Hua Hin, Thailand, collect *Blatta orientalis* and *Neostylopyga* (=*Stylopyga*) *rhombifolia*. In that district and in Korat the Laos eat cockroaches, but in most districts they are not touched because they "stink." In all districts, children appeared to collect cockroach eggs [oöthecae] for frying.

The Australian aborigines eat cockroaches as well as other insects, and in some localities in China and Japan, *Periplaneta americana* and *Periplaneta australasiae* are eaten (Bodenheimer, 1951).

Brygoo (1946) reported that he had known a commandant of the colonial army who ate cockroaches raw with evident pleasure, joining the Kissi (a tribe in French Guinea) in this practice. He also stated that the more civilized Annamites (Annamese?) ate cockroaches only after they had been held in the fire. Coupin (1905) attributed the following recipe to Harris: A succulent dish is made from cockroaches simmered in vinegar all morning and then dried in the sun. The insects, freed of heads and intestines, are then boiled together with butter, farina, pepper, and salt to make a paste which is spread on buttered bread. He intimated that this concoction was appreciated by some Englishmen in London, and that cockroaches were eaten in Ireland also.

> Blatta (Grillon des fourniers) leurs entrailles broyees et cuites dans l'huile, sont bonnes aux douleurs d'oreille.
>
> MATTHIOLE, 16th-century Viennese physician, *in* Paillard (1942).

XII. COCKROACHES IN MEDICINE AND MEDICAL FOLKLORE

The folklore of medicine contains recipes for many strange concoctions that are reputed to cure divers ills. Hence, it is not surprising to find references in medical literature to the therapeutic uses of cockroaches. The effectiveness of most of these remedies is highly questionable and, as Caudell (1916) stated, their use may be based almost entirely on pristine beliefs and popular fallacies. Nevertheless, a summary of the relations of cockroaches to disease would be incomplete without a résumé of this pertinent literature.

Although not strictly a medical usage, it is interesting that in many European countries the cockroach was honored and respected and even considered to be a protector of life. It was therefore the custom to take some of these insects into new dwellings. In Finland cockroaches were allowed to live and multiply freely in many prosperous homes and they were not supposed to be killed, particularly by burning. (Rytkönen, 1945.)

Takahashi (1924) reported that the Formosans removed the head and digestive organs of *Periplaneta americana,* placed salt in the body, and then fried and ate the insect. This, they said, aided the digestive process. They also cooked the hard, dark feces of this cockroach as a medicine for their children. Ealand (1915) reported that this same species was used in homeopathy in Europe. Pliny (cited by Blanchard, 1837) advised mixing the entrails of "Blatta" with oil as a cure for various ailments. There seems to be some doubt, however, whether Pliny's "Blatta" was a cockroach; Blanchard (1837) cited the conviction of Latreille that it was a species of *Blaps,* a beetle. This identification is moot.

The diseases and disorders reputedly cured by cockroaches and the specific uses of these insects in medicine are listed below. We make no attempt to evaluate the medical worth of the recommended treatments. However, the use of cockroaches to treat certain diseases has received some clinical support. This usage will be discussed at the end of the following list.

Albuminuria.—See discussion.

Antihydropin.—The diuretic principle of the cockroach; see discussion below.

Antispasmodic.—Webster (1834), surgeon on H. M. Sloop *Chanticleer,* was told by Capt. William Owen, of the British Navy, that an infusion of cockroaches was a most powerful antispasmodic. "Marquart's Pharmaceutische Zoologie" also lists this use (Geiger, 1839), apparently using Webster as a source.

Arteriosclerosis.—See discussion.

Boils.—Pliny (*in* Blanchard, 1837) recommended crushed "Blatta" as a cure. "Merck's 1907 Index" lists an oily decoction of *Blatta orientalis* as an external treatment for boils. This and other uses taken from Merck (1907) are also cited by Illingworth (1915).

Bright's disease.—See discussion. The use of cockroaches as a cure is cited in "Merck's 1907 Index."

Cirrhosis of liver.—See discussion.

Constipation.—Sloane (1725) reported that the Indians in Jamaica drank ashes of cockroaches as a physic.

Diaphoresis.—Usage cited in "Merck's 1907 Index." See discussion also.

Diuresis.—See discussion. Usage listed in "Merck's 1907 Index." Recent publications still list the use of dried, powdered *Blatta orientalis* as a diuretic: (1) 16th revised edition of "Stedman's Practical Medical Dictionary" (Taylor and Taylor, 1946); (2) 22nd edition of "The American Illustrated Medical Dictionary" (Dorland, 1951).

Dropsy.—Usage listed in "Merck's 1907 Index."

Earache.—Dioscorides (*in* Blanchard, 1837) stated that the entrails of the Sylph (possibly a cockroach, according to Blanchard), when mixed with oil and put into the ear, cured earache. Pliny (*in* Blanchard, 1837) also stated that the fat of certain "Blatta," when ground with oil of roses, was very good for earaches. Paillard (1942) cited the use, by Matthiole, a 16th-century Viennese physician, of the entrails of *Blatta,* crushed and boiled in oil, for the treatment of sore ears.

Heart disease.—See discussion.

Indigestion.—Lafcadio Hearn, in the New York Tribune, January 3, 1886, reported that the Negroes in Louisiana used cockroaches fried in oil with garlic for indigestion (Weiss, 1925).

Influenza.—Clausen (1954) cited the following item from the New York Times, November 12, 1944. During an epidemic of influenza in Iquitos, Peru, one of the most commonly used remedies was an infusion of red Iquitos cockroaches steeped in pisco, a fiery Peruvian liquor.

Itching.—Pliny (*in* Blanchard, 1837) recommended crushed "Blatta" as a cure.

Nephritis.—See discussion.

Pericarditis.—See discussion. The powdered, medicinal form of *Blatta orientalis* was sold in Europe as Pulvis Tarakanae as a remedy for pericarditis (Ealand, 1915). Weiss (1947) cited similar information.

Peritonitis.—See discussion.

Pleurisy.—See discussion. Same cited information as for pericarditis (Ealand, 1915; Weiss, 1947).

Scabbing.—Pliny (*in* Blanchard, 1837) recommended crushed "Blatta" as a cure.

Scrofula.—Blanchard (1837) cited Pliny's statement that the "Blatta" with wings and feet cut off cured scrofula.

Sting-ray injuries.—Russell and Lewis (1956) list macerated cockroaches as one of the substances that have been used in the treatment of sting-ray injuries. They also state that "certain aborigines perfused the wounds produced by venomous fishes with the extracts of macerated cockroaches and fish livers." They suggest that the rather high concentrations of enzymes, coenzymes, and carriers related to the oxidative cycle within insect muscle might possibly influence changes provoked by a venom.

Tetanus.—Webster (1834) was told by Captain Owen that ". . . the infusion of cockroaches is useful in tetanus, and that his [Captain Owen's] surgeon in the Eden, Dr. Birnie, had used it with beneficial effect." Webster went on to state, however, that a Dr. Hall tried it at Maranham in a case of tetanus without beneficial results. This same usage is listed in "Marquart's Pharmaceutische Zoologie" (Geiger, 1839). Weiss (1925) cited the following item by Lafcadio Hearn in the New York Tribune, January 3, 1886: the Negroes in Louisiana used cockroach tea for tetanus, supplemented by a poultice of boiled cockroaches over the wound.

Tuberculosis.—See discussion.

Tumors.—Pliny (*in* Blanchard, 1837) recommended crushed "Blatta" as a cure.

Ulcers.—Pliny (*in* Blanchard, 1837) stated that "Blatta" is good for ulcers deemed incurable. Sloane (1725) stated that the Indians in Jamaica bruised cockroaches, mixed them with sugar, and applied the concoction to ulcers and cancers to cause them to suppurate. "Merck's 1907 Index" lists the external use of *Blatta orientalis* for ulcers.

Warts.—External use of *Blatta orientalis* is listed in "Merck's 1907 Index."

Whooping cough.—Webster (1834) stated that an infusion of cockroaches was used in Bermuda as an antispasmodic in whooping cough. "Marquart's Pharmaceutische Zoologie" also lists this use in Bermuda for choking coughs (Geiger, 1839). Radbill (1945) reported the following beliefs of the Nantikoke (Nanticoke?) Indians: As many cockroaches were secured as there were children affected with whooping cough. Each cockroach was named after a child who placed it in a bottle which was then tightly corked. The sickness was believed to pass with the death of the insect. During this period, it was necessary to keep the child's bowels open or the charm might react and kill him. Radbill also reported that a person in the city was advised to put a cockroach in a thimble, tie it in a cloth, and wear it around the neck, "You will never whoop after wearing it." The same information is given by Weiss (1946).

Worms.—Sloane (1725) reported that in Jamaica, cockroaches were given to children as a vermifuge.

Discussion.—The action of dried Tarakanen, *Blatta orientalis,* as a diuretic has the benefit of some clinical usage to support it. The remedy was tested extensively in St. Petersburg, by Dr. P. Bogomolow (1876). This was not the first use of cockroaches as a diuretic, however, because Bogomolow reported that a Dr. Kuprianow had submitted the following thesis as part of his doctoral dissertation: "Die blatta orientalis ist ein sicheres Diureticum in der Gabe von einem Gran" and also that cockroaches had been used successfully by peasants in Russia as a folk remedy for dropsy. Pavlovskii and Shtein (1931) mention that powder and decoctions of *B. orientalis* were introduced by S. P. Botkin as a diuretic in scientific medicine.

Bogomolow (1876) treated nine patients with dried cockroaches, in powder form, as a tincture, and as an infusion. The diseases included nephritis (4 cases), arteriosclerosis (4), Bright's disease (3), cirrhosis of the liver (1), and heart disease (1). In all cases, urine excretion increased; the amount of albumin in the urine decreased (5 cases); edema of hands and feet as well as ascites quickly disappeared; body weight decreased; in four cases there was increased sweating; digestion was not upset and the kidneys were not irritated. Bogomolow (1876) isolated, in crystalline form, what he considered to be the diuretic principle of cockroaches and designated it antihydropin.

Unterberger (1877) used *Blatta orientalis* to treat children with nephritis after scarlatina (4 cases) and measles (1 case). In all cases, after a few days there was a shrinkage of the edematous conditions; body weight decreased; excretion of urine increased; amount of albumin became moderate (4 cases); kidneys and intestine were not irritated.

Koehler (1878) prescribed Tarakanen for 13 patients with the following diseases: arteriosclerosis (1 case), atherosis and angina pectoris (1), nephritis (4), exudative pleurisy (1), pernicious anemia (1), heart disease (1), exudative pericarditis (1), and Bright's disease (3). In all cases there was increased excretion of sweat and urine; edema and ascites were reduced or completely disappeared; albumin was reduced (2 cases) or eliminated (5 cases); stomach and intestine were not irritated.

Fronmüller (1878) used powdered *Blatta orientalis* as a diuretic in treating patients with lung tuberculosis (3 cases), bronchitis (1), exudative pleurisy (1), and albuminuria (1). Five of the six patients showed increased urine output; there was no digestive disturbance; it was concluded that the stronger doses of *Blatta* were strikingly effective and were not bad to take.

Budde (1878) used powdered *Blatta* to treat patients with albuminuria (2 cases) and nephritis (3 cases). He was unable to conclude that the therapy was effective. There was not a distinct increase in urine excretion or sweating, and the excretion of albumin remained unchanged.

Wyschinski (1879) used *Blatta* in treating patients with dropsy (7 cases), cirrhosis of the liver (2), organic heart disease (4), and Bright's disease (1). Excretion of urine increased in the patients with cirrhosis of the liver. The results with the other patients were negative, and Wyschinski questioned whether antihydropin from *Blatta* had produced the effects claimed by Bogomolow and Unterberger.

Kurz (1879) reported that he used *Blatta* in treating a man with nephritis and a girl with chronic peritonitis and ascites. The urine output increased in both patients; the amount of albumin in the man's urine was reduced relatively but the absolute amount remained unchanged; the circumference of the girl's abdomen was reduced 3 cm.

Steinbrück (1881) in his dissertation reported exhaustively on the use of *Blatta* as a diuretic. He examined the earlier literature thoroughly and included detailed case histories of 15 of his own patients to whom he had administered *Blatta.* The diseases included nephritis (10 cases), edema of the face and palpitation of the heart (1), tuberculosis (1), mitral insufficiency (1), and two cases with healthy kidneys. He was able to verify increased diuresis 14 times in the 15 patients. In 12 patients with albuminuria there was a reduction of albumin in six cases, no effect in two, and in four cases the amount of albumin increased. Steinbrück did not observe an increase in sweating following doses of *Blatta.* He concluded that the principal effect of powdered cockroach was as a diuretic.

Bogomolow (1882) reported on 70 more cases of dropsy in which he administered *Blatta*. The edema was caused in 15 instances by heart failure, in 52 instances by kidney disease, and in 3 cases by liver disease. In 19 cases Bogomolow observed sweating; in 61 cases the volume of urine was increased significantly; in 13 instances diarrhea was increased by augmented transudation through the walls of the gut. No irritation or other unfavorable symptom was seen.

Tschernyschew (1882) investigated the physiological effects of an organic acid that he obtained from *Blatta orientalis*. In frogs there was an increasing retardation of heart action in which the heart remained in diastole with the ventricles distended with blood. The effect was not accomplished through the central nerve system but was a result of paralysis of the heart and its motor ganglion. In warm-blooded animals small doses retarded the pulse and large doses stopped heart action. The first effect appeared to depend on excitation of an inhibitory apparatus, but the latter appeared to depend on possible paralysis of the inhibitory apparatus, with some participation of the motor nerve of the heart. The acid effected strong diuresis in which the secretory elements of the kidney were stimulated.

The flurry of interest in cockroaches as a remedy for dropsy was confined to a relatively brief period. Although the professional medical papers describing this use appeared in Europe, interest in the subject was reflected in the lay press in the United States at the same time (Anonymous, 1877, 1877a, 1879, 1881; Landerer, 1879). After 1883, the medicinal use of cockroaches dropped from the literature, except for occasional references, until quite recently.

In 1933, in Helsinki, Vartiainen et al. reinvestigated the diuretic effects of *Blatta orientalis*. These workers examined the effects of the cockroach on the excretion of urine in rabbits. Powdered cockroach was administered by mouth and also subcutaneously as an infusion. Urine excretion was measured partly as excreted by rabbits kept in metabolic cages, partly by withdrawal by catheter from the bladder, and partly by taking urine from canulae inserted in the ureters of narcotized rabbits. Although some animals did not respond, there was sufficient increase in the excretion of urine in others to convince the authors that *B. orientalis* possesses diuresis-increasing effects, even though these may not have been particularly strong.

Apropos of the reputed diuretic properties of cockroaches, it is noteworthy that Stutinsky (1953) has reported evidence for an *antidiuretic* substance in the brain and retrocerebral complex of *Blaberus fuscus*. These organs from male cockroaches were ground to a powder. An extract of the powder, when injected into rats, caused a reduction in the quantity of urine eliminated. However, tests to determine possible oxytocic, vasopressor, or antidiuretic effects with corpora cardiaca from *Periplaneta* and *Leucophaea* were inconclusive (Vogt and Hild *in* Scharrer, 1955). Scharrer (1955) suggests that further tests seem necessary to substantiate the positive results obtained with extracts of *Blaberus*.

It is not out of place to mention the work of Scharrer (1945, 1949, 1951, 1953) on the development of cancer in *Leucophaea maderae*. She found that gastric cancer can be induced experimentally in this cockroach by severing the recurrent nerve; branches from this nerve innervate the foregut, stomach, salivary glands, and salivary reservoir. Roughly 75 percent of the operated insects developed tumors, the stomach being the most frequently affected organ. The digestive organs of an insect are structurally comparable to those of higher animals, and studies of this kind, employing the Madeira cockroach, may have significance in aiding our understanding of cancer in mammals.

> If a black beetle [*Blatta orientalis*] enters your room, or flies against you, severe illness and perhaps death will soon follow.
>
> Maryland superstition,
> COWAN (1865).

XIII. DISEASES INCORRECTLY ATTRIBUTED TO COCKROACHES

Cockroaches have been suspected of causing certain diseases or disseminating several disease agents which, on subsequent investigation, have been found to have other causes or vectors.

Beriberi.—Van der Scheer (1900, 1900a) believed that this vitamin-deficiency disease was caused by a parasite that lived in the intestine where it formed a toxin that caused degeneration of the nerves. He suspected that part of the life cycle of the parasite was passed in *Blatta orientalis*. Melville-Davison (1911) came to a similar conclusion. He believed that an amoeba which lived in the intestine of the cockroach caused the disease.

Bright's disease.—Caudell (1916) cited a case in which this disease was believed to have been caused by drinking soda water in which a cockroach had decayed.

Cancer.—Caudell (1916) quoted a Professor Nordlyset who claimed in 1913 that cancer was caused by drinking water in which cockroaches had oviposited. Fibiger (1913) and Fibiger and Ditlevsen (1914) demonstrated that *Periplaneta americana* is a vector of the rat nematode *Gongylonema neoplasticum* which they thought was in some way related to cancer in rats (see p. 27). Cordier (1933) suggested that *Entamoeba blattae,* an amoeba found in the intestines of cockroaches, was a causal agent of cancer.

Kala azar.—Before the vector of this leishmaniasis was believed to be the sand fly, cockroaches were suspected of being possible vectors (Young, 1924). Examinations of dissected cockroaches, including *Blatta orientalis,* taken in endemic areas in the Sudan (Archibald, 1923) and in southern India (Turkhud et al., 1926) were negative for the parasites.

Malaria.—Coronado (*in* Cao, 1898) stated without evidence in an 1897 paper that cockroaches, among other insects, spread this mosquito-borne disease.

Pellagra.—Jennings and King (1913) reported negative results in an attempt to incriminate cockroaches in the cause and spread of this deficiency disease.

Scurvy.—Melville-Davison (1911) attributed this deficiency disease to a gregarine found in the intestines of the cockroach. The symptoms of the disease, he thought, were caused by a toxin generated by the protozoan.

XIV. COCKROACHES VERSUS HOUSE FLIES

"The common housefly, loaded with all kinds of bacteria, benign and pathogenic, . . . offers no more danger from acute infectious diseases than does the common house roach. . ." (Longfellow, 1913). These words are as true today as they were when written. However, the domestic cockroaches have yet to achieve generally the unenviable reputation of the filth flies as carriers of infectious agents, in spite of this quotation from a recent U. S. Public Health Service publication (1952): "Equally important as disease carriers are flies and roaches." Yet both can and do carry similar disease-producing viruses, bacteria, protozoa, and helminths. Cockroaches and house flies are potential health hazards to man because they feed on both human feces and human food. Their relative importance as vectors is largely related to their abundance and the access each has to feces or other infective material and food or human contact. Flies, diurnal, more active, and at times apparently more numerous than cockroaches, frequently contaminate food during its preparation or after it has been served. Cockroaches, nocturnal, less active, and less obvious than house flies, usually contaminate unprotected food in dark storage areas or food left exposed overnight. Unfortunately it has always been easier to tolerate the cockroach, which shuns daylight, than to ignore the ubiquitous house fly, which breaks bread with us each meal.

In his discussion of the medical importance of flies, West (1951) stated that, "There is acceptable laboratory proof for the transmission of approximately thirty diseases (or parasitic organisms) by *Musca domestica* and related forms." This number was not increased in the more recent review by Lindsay and Scudder (1956) on nonbiting flies and disease. Cockroaches, by way of comparison, have been shown to harbor, naturally or experimentally, about 40 species of pathogenic bacteria alone; of these, at least 25 species are Enterobacteriaceae, organisms largely responsible for gastroenteritis in man. In addition, cockroaches have been shown to be intermediate hosts for many pathogenic helminths and to carry helminth eggs, viruses, protozoa, and fungi. Obviously, the number of disease agents transmitted is not alone a true measure of the relative importance of a vector. In citing these figures, we are not implying that cockroaches are medically more important than filth flies. Which vector is more important is academic, as there is little likelihood that the question can ever be resolved.

Although modern sewers do not promote fly breeding, they are ideal habitats for cockroaches where these insects may breed and become contaminated with feces and from which they may spread into nearby buildings (see pp. 10, 15). However, where the disposal of human waste is more primitive, filth flies may be the important vectors. Feces deposited on the soil certainly attract more flies than they do cockroaches. Feces deposited in privies may be visited more readily by cockroaches than by flies, according to the particular situation.

Sanitary pit privies have in the past reduced the fly menace, as flies in general tend to shun dark places and the deeper the pit, the fewer the flies (Fair *in* Rosenau, 1940). However, this is no longer wholly true. Kilpatrick and Bogue (1956) observed that, contrary to the general opinion prior to 1950, exceedingly heavy emergence of house flies has recently been recorded from active privy pits. This they attributed to a physiological change in house-fly behavior that they correlated with the development in the fly population of resistance to the insecticide dieldrin.

Dark privy pits might be expected to be ideal cockroach shelters, as attractive to these insects as sewers. Dow (1955) and Kilpatrick and Bogue (1956) have reported that in the southwest United States cockroaches were very prevalent in privy pits that had not been treated with insecticides. The ecology of cockroaches in privies has yet to be explored. Such a study should yield interesting information. Haines and Palmer (1955) observed seasonal fluctuations in populations of two species of *Periplaneta* in privies in southwestern Georgia.

The evidence for the transmission of infectious agents by both flies and cockroaches is largely circumstantial because most of the evidence is indirect. Rarely is either insect the only means of transmitting a disease agent, except when serving as an obligate intermediate host for an endoparasite (e.g., *Pycnoscelus surinamensis* as host of the chicken eyeworm). When other means of transmission are present it is difficult, if not impossible, to prove conclusively that specific outbreaks of disease were caused by pathogens transmitted by insects. Lindsay and Scudder (1956) cited only a few instances of proven correlations between disease morbidity and fly populations, but the experiments they discussed are highly convincing. It is obvious that closely controlled experiments are needed to prove the relationship between mechanical vectors and the morbidity of specific diseases. It is not our thesis that filth-bearing insects are the most important means of disseminating enteric disease organisms. We recognize that all sources of pathogens, including insects, play greater or lesser roles in epidemiology. Sabin (1951) has stressed that ". . . one cannot apply 'unitarian' epidemiological hypotheses and concepts in dealing with an infectious agent that is predominantly stool-borne." This statement applies with equal validity to the mechanical transmission of other infectious agents as well.

> There is sufficient direct and indirect evidence to warrant further study of the cockroach as a vector of disease and to initiate stronger measures designed to exterminate this insect, especially in hospitals and public eating establishments.
>
> JANSSEN and WEDBERG (1952).

XV. CONCLUSIONS

The existing evidence, which is presented in detail in the following appendices, should be sufficient to convince all but the most skeptical that cockroaches are highly dangerous, potential vectors of disease agents. At least 18 species of domiciliary cockroaches have been incriminated, naturally or experimentally, in the transmission of infectious agents or have been claimed to bite man. Most of these species will eat the feces of humans and domestic and exhibition animals. Several of the commonest species (*Periplaneta americana, P. australasiae, P. brunnea, P. fuliginosa, Blatta orientalis,* and *Blattella germanica*) have been captured repeatedly in sewers, cesspools, septic tanks, or privies. Several species have been found breeding in refuse dumps and have been found migrating from both sewers and dumps into nearby buildings. The predilection of cockroaches for human food and the contamination of food, dishes, and food preparation surfaces by cockroaches are notorious. Thus the mechanism exists for the transference of disease organisms by cockroaches to man and his animals.

Although natural transmission of viruses by cockroaches has not yet been proved, four strains of poliomyelitis virus have been found occurring naturally in wild-caught cockroaches. In addition, cockroaches can harbor experimentally four strains of poliomyelitis virus, Coxsackie, mouse encephalomyelitis, and yellow-fever viruses.

About 40 species of pathogenic bacteria have been isolated from naturally contaminated cockroaches. About 90 isolations of natural invasions in cockroaches with these organisms have been made. These and the following figures include only the reports by each investigator of the first isolation of an organism from each species of cockroach. Subsequent isolations of the same organism from the same species of cockroach by the same investigator are not included. In over 100 experimental inoculations of cockroaches with about 40 species of pathogenic bacteria, these organisms were recovered from the insects' feces, intestinal contents, or body surface. About 25 of the pathogenic bacteria are Enterobacteriaceae. A number of other bacteria of doubtful pathogenicity or of doubtful taxonomic status have also been isolated from naturally invaded cockroaches.

Two species of fungi that are sometimes associated with pathological conditions have been isolated from naturally contaminated cockroaches. One species of pathogenic fungus retained its pathogenicity after experimental passage through cockroaches.

So far, only one species of protozoa that is definitely pathogenic to man has been found occurring naturally in cockroaches. It was isolated three times by different investigators. Three species of pathogenic protozoa have been used at least 15 times to inoculate cockroaches experimentally.

The eggs of 7 species of pathogenic helminths have been found naturally in cockroaches 11 times. The eggs of 4 of these species and of 5 additional species have been fed experimentally to cockroaches 19 times. Cockroaches have been found to serve naturally as the intermediate hosts of 12 species of helminths in about 43 observations. Cockroaches were used successfully as intermediate hosts for 11 of these species and also for 11 other species in about 44 experiments.

There is no question about the ability of cockroaches to carry pathogens in or on their bodies. There is, however, some question about the epidemiological significance of this fact. Most of the evidence is circumstantial. The role of cockroaches as intermediate hosts of helminths has been established. Although cockroaches undoubtedly are vectors of the agents of viral and bacterial diseases, with very few exceptions their relations to specific outbreaks of disease have not been determined. This area of research has not received the attention it deserves. Demonstrating correlations between house flies and incidence of intestinal disease has been difficult (see Lindsay and Scudder, 1956). Linking cockroaches with the actual transmission of similar disease agents will be no easier.

Various workers have, as a result of their investigations, expressed their concern about cockroaches and disease. Morischita and Tsuchimochi (1926) stated, ". . . we are led to conclude that the cockroaches commonly found in our island [Formosa] may play a fairly important role in the dissemination of infectious diseases and helminthiasis and must not be overlooked from the sanitary point of view." Tejera (1926) concluded that cockroaches are insects which the hygienist must consider as possible disseminating agents of pathogenic germs, and, consequently, as transmitters of sickness to man.

Antonelli (1930) stated that from his investigations he was certain that considerable epidemiological importance should be attributed to the cockroach which, as a permanent danger, should be fought without quarter. Arizumi (1934) stated, "In my opinion the cockroaches, at least the two *Periplaneta* species examined, are eminently apt to spread, besides other pathogenic bacilli, also the Leprosis bacillus wherever they visit and deposit their feces." Mackerras and Pope (1948) concluded, "We have adduced sufficient evidence to justify intensive control measures in any area where both cockroaches and *Salmonella* infections are found."

Bitter and Williams (1949) concluded. "Because of the lack of conclusive evidence that roaches can transmit disease, these insects have been regarded with tolerance by a large portion of the population, especially in areas where roach control is difficult. The results cited above suggest that such tolerance is unwarranted and that every effort should be made to suppress the cockroach and to protect food and kitchen utensils from contact with its feces. Roach control is clearly of the highest importance in households that include infants."

Graffar and Mertens (1950) stated, "Up to the present time, cockroaches were generally considered repugnant but completely inoffensive insects. This opinion must be reformed, and it is expedient, in the hospitals at least, to waste no effort in destroying them." Eads et al. (1954) stated, "Both flies and cockroaches are outstanding among the omnivorous insects which are of significance in the contamination of food and water as a result of the intimacy and constancy of their association with both the food and the excreta of man and animals."

Cockroaches are tough, resilient insects with amazing endurance and the ability to recover rapidly from almost complete extermination. They will probably always be with us, and we can only temporarily reduce their numbers. But, as in all battles, recognition of a common enemy is essential to successful combat. We hope that this review has so strongly identified cockroaches with the dissemination of infectious agents that these insects will no longer be regarded as only minor annoyances. The acceptance of cockroaches as serious vectors of disease organisms is at least the first step in any organized campaign of extermination.

The specific measures to be taken to control cockroaches are beyond the scope of this review. However, the currently recommended chemical control measures and sanitary practices may be obtained from the following sources: the U. S. Department of Agriculture, U. S. Public Health Service, various state Agricultural Experiment Stations, and similar governmental agencies in other countries.

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> La *Periplaneta americana,* habitée par un nombre encore plus considérable de parasites végétaux et animaux, devient à ce point de vue encore plus digne d'être étudiée. . . . Le pauvre bête est une vraie ménagerie ambulante.
>
> MAGALHÃES (1900).

APPENDICES

The plants and animals are listed by phylum, class, order, and family in the order adopted by the taxonomic sources we have followed, but in alphabetical order by genus and species. In listing the authors of the species, we have followed the current usage of specialists in the field; for the helminths the original describer, the reviser, and the dates of both are given; for the bacteria and fungi the describer and reviser are listed; for the protozoa the original describer is given.

Each organism, in so far as we have been able to determine, is listed by its current name. To reduce the number of entries for each organism, we have synonymized the names reported by earlier authors with the names now in use. The only synonymy given is that which identifies the organism by the name used by the author of the paper cited; no attempt was made to prepare complete taxonomic synonymies.

Under the name of each organism the associated cockroaches are listed as being natural or experimental vectors. The name of each cockroach is followed by the country in which the observation was made, the authority, and comments on the invasion. Unidentified cockroaches associated with specific records are indicated by the word "Cockroaches." Question marks following the names of organisms or countries indicate tentative or questionable identifications.

APPENDIX A: VIRUSES

PATHOGENIC VIRUSES ASSOCIATED WITH COCKROACHES

POLIOMYELITIS VIRUSES

The disease caused by these viruses is usually mild, with upper respiratory or gastrointestinal symptoms. The central nervous system may be affected with an accompanying paralysis of voluntary muscles (Howe *in* Rivers, 1948).

Lansing strain

Experimental vectors.—Blattella germanica, U.S.A. (Hurlbut, 1949, 1950) : Mouse-adapted virus was inoculated into the hemocoeles of the insects. The virus was present in 22 surviving cockroaches after 15 days. Virus was not found in the cockroach feces or eggs. Emulsions of whole insects produced typical paralysis in mice when inoculated intracerebrally. The following authors incorrectly cited Hurlbut's host cockroach as *Periplaneta americana:* Syverton and Fischer (1950), Fischer and Syverton (1951a), Findlay and Howard (1951), and Hsiang et al. (1952).

Periplaneta americana, U.S.A. (Hsiang et al., 1952) : The virus was recovered from the feces of the cockroaches on the first day only, after they had been fed virus in an emulsion of cotton-rat brain. No virus could be detected in cockroach tissues within 24 hours after the virus meal. The authors suggest that virus inactivation might result from metabolic effect or from rapid excretion of the virus from the gut of the cockroach.

Brunhilde type, Minnesota and Mahoney strains

Experimental vectors.—Periplaneta americana, U.S.A. (Fischer and Syverton, 1951; Syverton et al., 1952) : After a single feeding this cockroach acquired, maintained, and excreted these viruses over a period of 16 days (7 to 15 days [Syverton et al., 1952]). Sufficient virus was recovered to paralyze and kill the recipient animals.

Columbia SK virus

Disease.—This virus is pathogenic for cotton rats, mice, golden hamsters, guinea pigs, and monkeys (Findlay and Howard, 1951).

Experimental vectors.—Blattella germanica and *Periplaneta americana* (Findlay and Howard, 1951): A suspension of mouse brain infected with this virus was injected into the hemocoeles of the cockroaches. After 72 hours and 120 hours, virus was detected in triturated bodies of *P. americana,* but not of *B. germanica,* up to 8 days after the viral meal.

Four unspecified strains

Natural vectors.—Blattella germanica (see below), *Periplaneta americana* (see below), and *Supella supellectilium,* U.S.A. (Syverton et al., 1952): Four strains of poliomyelitis virus were isolated from four lots of cockroaches captured on the premises of paralytic poliomyelitis patients from two States. The premises were representative of good and poor sanitary environments.

One lot of *Blattella* (identified to genus) from Pharr, Tex., may have included *B. vaga* as well as *B. germanica,* as both species are now known to be found there (R. P. Dow, p.c.). Of the two, *B. germanica* is the species most likely to be found in houses, but *B. vaga,* usually a field cockroach, may invade houses in great numbers during dry seasons (Flock, 1941). The specimens of one lot of *Periplaneta* caught in Pharr, Tex., although reported as *P. americana* (Syverton et al., 1952), may have included *P. brunnea* as well (Dow, 1955).

COXSACKIE VIRUSES

Type 4, subgroup A

Disease.—The Coxsackie or "C" viruses are responsible for human diseases diagnosed clinically as nonparalytic poliomyelitis, "summer grippe," aseptic meningitis, epidemic myalgia, pleurodynia, and, probably, Bornholm disease (Fischer and Syverton, 1951a).

Experimental vectors.—Periplaneta americana, U.S.A. (Fischer and Syverton, 1951a): After consuming a single meal containing this virus, the cockroaches excreted daily, over a period of 15 days, sufficient virus to paralyze and kill test mice.

MOUSE ENCEPHALOMYELITIS VIRUS

GD VII strain

Experimental vectors.—Periplaneta americana, U.S.A. (Syverton and Fischer, 1950): The insects were fed single meals containing this virus. Over a period of 7 days, sufficient virus was present daily in the cockroaches' feces to paralyze and kill test mice.

YELLOW-FEVER VIRUS

Disease.—An infection of the hemapoietic system; mosquitoes are the only blood-sucking arthropods that have been shown to play a part in the epidemiology of yellow fever (Theiler *in* Rivers, 1948).

Experimental vectors.—*Blatta orientalis* (Trop. Dis. Bull., 1942, p. 65, *in* Brumpt, 1949): According to Brumpt, the virus lasted less than 2 days in this insect. We have checked the reference given by Brumpt but found no mention of cockroaches and virus.

Blattella germanica (Findlay and MacCallum, 1939): Yellow-fever virus injected into the insects' abdomens retained its activity for at least 15 days. When yellow-fever virus was introduced into the stomachs of Indian monkeys (*Macaca mulatta*) and African monkeys (*Cercopithecus aethiops*), the virus passed into the blood stream and caused fatal infections in the Indian monkeys.

NEGATIVE FINDINGS

The following cockroaches (U.S.A., Texas) were examined for viral invasions, with negative results, by Eads et al. (1954): *Blatta orientalis, Blattella germanica, Periplaneta americana,* and *Supella supellectilium.*

NEWCASTLE DISEASE VIRUS

California strain No. NC 194-5-6-7

Disease.—Avian pneumoencephalitis.

Experimental vector.—*Periplaneta americana,* U.S.A. (Gallardo et al., 1957): The virus could not be recovered in the feces after feeding to the cockroaches.

APPENDIX B: BACTERIA

Most of the bacteria listed below are pathogenic to humans, but some are primarily of veterinary importance. Species that are normally nonpathogenic but which apparently acquired pathogenicity (to laboratory animals) on passage through the cockroach have also been included.

Where it has been possible to synonymize the names of the bacteria, as used in the references cited, we have followed Bergey's Manual of Determinative Bacteriology, sixth edition (Breed et al., 1948). The disease entity and habitat of each organism were obtained from Breed et al. (1948), Smith et al. (1948), and Dubos (1948), or other indicated sources. The taxonomic arrangement follows that of Breed et al. (1948).

Part I contains positive associations of cockroaches with valid species of bacteria. Part II contains positive associations of cockroaches with pathogenic bacteria whose taxonomic position is uncertain. Part III contains negative findings.

PART I. PATHOGENIC[8] BACTERIA ASSOCIATED WITH COCKROACHES

Phylum SCHIZOPHYTA

Class SCHIZOMYCETES

Order EUBACTERIALES

Family PSEUDOMONADACEAE

Pseudomonas aeruginosa (Schroeter) Migula

Synonymy.—Bacillus pyocyaneus.

Common name.—Blue pus organism.

Disease.—Cause of various lesions in humans and other animals, urinary tract infections. Habitat: Polluted water, sewage.

Natural vectors.—Blaberus craniifer, U.S.A. (Wedberg et al., 1949): Organism isolated from feces.

Blatta orientalis, U.S.A. (Olson and Rueger, 1950; T. A. Olson, p. c.): From laboratory-reared cockroaches.

Blattella germanica, U.S.A. (Janssen and Wedberg, 1952): Organ-

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[8] Certain of these bacteria are considered to be nonpathogenic or of doubtful or low pathogenicity by some authors.

ism isolated from feces and alimentary canal. (Olson and Rueger, 1950: T. A. Olson, p. c.): From laboratory-bred cockroaches.

Periplaneta americana, U.S.A. (Bitter and Williams, 1949, 1949a): Organism isolated from intestinal tract. (Olson and Rueger, 1950; T. A. Olson, p. c.): From laboratory-bred cockroaches.

Experimental vectors.—Blattella germanica, U.S.A. (Herms and Nelson, 1913): Cockroach picked up organism on tarsi and inoculated three agar plates, also transferred organism to sugar.

Cockroach, U.S.A. (Longfellow, 1913): Organism isolated from feet and viscera of cockroaches allowed to feed on inoculated food.

Pseudomonas eisenbergii Migula

Synonymy.—B. fluorescens non liquefaciens.

Disease.—Pathogenic to guinea pigs and rabbits (Cao, 1906). Nonpathogenic (Breed et al., 1948).

Natural vectors.—Blatta orientalis, Italy (Cao, 1906): Organism isolated from intestinal contents.

Experimental vectors.—Blatta orientalis, Italy (Cao, 1906): Strain D of the above organism, isolated from soil, acquired moderate virulence in the feces of the cockroaches and produced abscesses and death in guinea pig.

Pseudomonas fluorescens Migula

Synonymy.—Bacillus fluorescens liquefaciens.

Disease.—Strains B, C, D, and F reported by Cao to be pathogenic to guinea pigs. Normally found in soil, water, sewage, feces. Nonpathogenic (Breed et al., 1948).

Natural vectors.—Blatta orientalis, Italy (Cao, 1898, 1906): From intestinal contents. (Spinelli and Reitano, 1932): From intestinal tract.

Periplaneta americana, U.S.A. (Gier, 1947).

Experimental vectors.—Blatta orientalis, Italy (Cao, 1898, 1906): Insects that had fasted were fed bacterial colonies. Cultures from feces were pathogenic when injected into guinea pigs and rabbits.

Periplaneta americana, U.S.A. (Gier, 1947): Organism pathogenic to the cockroach when injected.

Vibrio comma (Schroeter) Winslow et al.

Synonymy.—"Vibrione del colèra" of Cao; *Vibrio cholerae.*

Disease.—Asiatic cholera. Habitat: Intestinal contents of cholera patients and carriers.

Experimental vectors.—Blatta orientalis, Italy (Cao, 1898; Spinelli and Reitano, 1932): After experimental feedings, the cholera vibrios passed unharmed through the digestive tract of the insect. Cholera vibrios survived in the insects' intestinal tracts for 15 days and were found in their feces 86 hours after being ingested (Spinelli and Reitano, 1932).

Blattella germanica, Orient (Toda, 1923): 94 cockroaches (collected from Japanese ocean liners) were fed *V. comma* in bread. The organism was recovered from 15 percent of the insects, from feces or from the intestines after death. The feces contained viable vibrios up to 3 days after the infective meal. Germany (Jettmar, 1927): Cockroaches fed cholera organisms showed a higher mortality than those fed plague bacilli.

Periplaneta americana, Philippine Islands (Barber, 1914): Feces containing vibrios were obtained from 8 cockroaches 6 hours after an experimental feeding with feces from a cholera patient. The organism appeared in enormous numbers in the feces for at least 2 days thereafter and in smaller numbers 79 hours after ingestion. There was no loss of virulence for guinea pigs after the vibrios had been in the insects' intestines 29 hours. Regurgitated food contained vibrios. Cholera vibrios in cockroach feces will survive on human food for at least 16 hours after discharge from the insect. Netherlands (Akkerman, 1933): In 12.7 percent of the cockroaches there were vibrios in the feces 24 hours after feeding. One insect excreted vibrios in its feces 3 days after feeding. Formosa (Morischita and Tsuchimochi, 1926): 25 insects were fed on a culture of cholera vibrios. Intestinal contents of groups of 5 were positive 3.5 and 12 hours after feeding. After 24 hours, 3 of 5 were positive; after 48 hours, 2 of 5 were positive; after 68 hours, all were negative. Fecal examinations of 10 cockroaches were positive 5 to 34 hours after feeding; feces excreted after 48 to 53 hours were partly positive; after 57 hours all feces were negative except 1 positive at 67 hours. The average ratio of positive feces was 16.3 percent. Intestines were negative for *V. comma* after 68 or 70 hours.

Periplaneta australasiae, Formosa (Morischita and Tsuchimochi, 1926): One specimen that was fed *V. comma* excreted feces positive for the organism.

Vibrio metschnikovii Gamaléia

Synonymy.—"Vibrione di Metschnikow" of Cao.

Disease.—Choleralike disease of chickens, pigeons, and other animals.

Experimental vectors.—Blatta orientalis, Italy (Cao, 1898, 1906): The organism passed unchanged through the gut of this cockroach and was excreted in the feces. In some experiments, attenuated cultures of this organism regained their full virulence on passage through the cockroach (Cao, 1906).

Family MICROCOCCACEAE

Micrococcus aurantiacus (Schroeter) Cohn

Source.—Usually isolated from infections; may be pathogenic; found in milk, cheese, and dust.

Natural vectors.—Blattella germanica, U.S.A., Connecticut (Janssen and Wedberg, 1952): Organism isolated from feces and alimentary canal.

Micrococcus citreus Migula

Synonymy.—Staphylococcus citreus.

Disease.—Pathogenic; isolated from pus; found on skin and mucous membranes of vertebrates (Breed et al., 1948). Nonpathogenic (Wilson and Miles, 1955).

Natural vectors.—Cockroaches, U.S.A. (Longfellow, 1913): Organism isolated from legs and feces.

Experimental vectors.—Blatta orientalis, Italy (Cao, 1898): Organism not recovered in the feces.

Micrococcus epidermidis (Winslow and Winslow) Hucker

Disease.—Parasitic rather than pathogenic; found on skin and mucous membranes.

Natural vectors.—Blattella germanica, U.S.A., Connecticut (Janssen and Wedberg, 1952): Organism isolated from feces and alimentary canal.

Micrococcus pyogenes var. albus (Rosenbach) Schroeter

Synonymy.—Staphylococcus albus.

Disease.—Occurs in wounds, boils, abscesses. Pathogenic. Habitat: Skin and mucous membranes.

Natural vectors.—Blaberus craniifer, U.S.A., Connecticut (Wedberg et al., 1949): Organism isolated from feces.

Blatta orientalis, U.S.A., Iowa, (Tauber, 1940; Tauber and Griffiths, 1942): Organism isolated from hemolymph.

Blattella germanica, U.S.A. (Herms and Nelson, 1913; Herms, 1939; Janssen and Wedberg, 1952): Organism isolated from the legs, antennae, and feces.

Experimental vectors.—Blatta orientalis, Italy (Cao, 1898): Failed to recover the organism. U.S.A. (Tauber and Griffiths, 1942): Organism toxic to the cockroach when injected.

Micrococcus pyogenes var. aureus (Rosenbach) Zopf

Synonymy.—Staphylococcus aureus.

Disease.—Pathogenic. The cause of boils, abscesses, suppuration in wounds. Habitat: Skin and mucous membranes.

Natural vectors.—Blaberus craniifer, U.S.A., Connecticut (Wedberg et al., 1949): Organism isolated from feces.

Blatta orientalis, Italy (Cao, 1906): Organism isolated from intestinal contents. Cao in an earlier work (1898) failed to recover this organism from the cockroach.

Blattella germanica, U.S.A. (Herms, 1939): Organism isolated from the antennae.

Cockroaches, U.S.A. (Longfellow, 1913): Organism isolated from the legs.

Micrococcus spp.

Disease.—These organisms were obtained from pus or were designated as staphylococci (i.e., pathogenic micrococci [Blair *in* Dubos, 1948]).

Natural vectors.—Blatta orientalis, Italy (Spinelli and Reitano, 1932). Germany (Jettmar, 1935): Organisms isolated from intestinal tract.

Blattella germanica, Germany (Jettmar, 1935): Hemolytic staphylococci were isolated from the outer surfaces of 19 insects captured in a hospital operating room.

Experimental vectors.—Blattella germanica, on shipboard (Morrell, 1911): Two specimens were fed staphylococcic pus. The organisms were recovered in the feces, and cultures on agar were obtained from these. Germany (Vollbrechtshausen, 1953): Cultures of staphylococci (obtained from the clothing louse) were injected, orally and anally, into cockroaches. Colonization and propagation in the intestines of the cockroaches lasted up to 6 to 8 weeks after heavy injections. The organism was recovered from the feces of one insect 180 days after the injection.

Family NEISSERIACEAE

Neisseria meningitidis (Albrecht and Ghon) Holland

Common name.—Meningococcus.

Disease.—Cerebrospinal fever.

Experimental vectors.—Cockroaches, U.S.A. (Longfellow, 1913): After feeding, the organism was recovered in a few cases from the viscera and outer surface of the body; however, the results were not as conclusive as were Longfellow's findings with pneumococcus.

Veillonella parvula (Veillon and Zuber) Prévot

Synonymy.—*Micrococcus parvulus.*

Disease.—Normally a harmless parasite in natural cavities of man and other animals, but it may occasionally be pathogenic.

Natural vectors.—*Periplaneta americana,* U.S.A. (Hatcher, 1939): Organism isolated from feces.

Family LACTOBACTERIACEAE

Diplococcus pneumoniae Weichselbaum

Synonymy.—"Diplobacillo di Fränkel" of Cao.

Common name.—Pneumococcus.

Disease.—Commonest cause of lobar pneumonia. Habitat: Respiratory tract of man and animals.

Experimental vectors.—*Blatta orientalis,* Italy (Cao, 1898): Organism killed in the cockroach's gut.

Cockroaches, U.S.A. (Longfellow, 1913): After feeding on the organism, 3 out of 10 cockroaches had the bacterium on legs or abdomens. Smears of the opened bodies of all 10 insects showed from a few to a number of pneumococcus colonies in each.

Pneumococcus, Type I, No. 1231

Disease.—Pathogenic to mice (Vollbrechtshausen, 1953).

Experimental vectors.—*Blattella germanica,* Germany (Vollbrechtshausen, 1953): 25 cockroaches injected orally or anally with pneumococci in a serum bouillon. Pneumococci appeared in the feces within 5 hours after the injection and were excreted over a period of 3 days. Experiment repeated with 50 cockroaches. The number of introduced pneumococci decreased in the intestines until, after 5 days, the test insects no longer showed such bacteria.

Streptococcus faecalis Andrewes and Horder

Source.—Occurs in inflammatory exudates; in blood stream in subacute endocarditis; European foul-brood of bees. Found in milk and milk products, especially cheese.

Natural vectors.—*Blatta orientalis,* Poland (Nicewicz et al., 1946): Organism isolated from the alimentary tract.

Blattella germanica, U.S.A. (Steinhaus, 1941): Organism isolated from the midintestine.

Periplaneta americana, England (Shrewsbury and Barson, 1948): Organism cultivated from the alimentary tract.

Cockroaches (presumably *B. orientalis, B. germanica,* and/or *P. americana*), Egypt (El-Kholy and Gohar, 1945): Organism isolated from outer body surfaces, intestines, and suspensions of macerated insects.

Streptococcus liquefaciens Sternberg emend. Orla-Jensen

Source.—Found in blood in subacute endocarditis. Foul-brood of bees. Found in feces, and in dairy and other food products.

Natural vectors.—*Blatta orientalis,* Poland (Nicewicz et al., 1946): Organism isolated from alimentary tract.

Streptococcus pyogenes Rosenbach

Synonymy.—*Streptococcus pyogenes longus;* "Streptococco piogene" of Cao.

Disease.—Organism occurs in human infections of many varied types.

Natural vectors.—*Blatta orientalis,* Italy (Cao, 1906): Organism isolated from feces; in pure culture it caused only local suppuration in guinea pigs or rabbits.

Experimental vectors.—Cockroaches, U.S.A. (Longfellow, 1913): Organism isolated from legs and viscera.

Streptococcus sp. (pyogenic group)

Synonymy.—The exact species used by Jettmar (1935) is not known, but he refers to a hemolytic *Streptococcus* of the beta type. According to Breed et al. (1948), such an organism would probably fall in the pyogenic group.

Disease.—Streptococci of the pyogenic group occur in human infections of many varied types.

Experimental vectors.—*Blatta orientalis,* Germany (Jettmar, 1935): On the second day after ingesting an infective meal, the cockroaches excreted hemolytic streptococci in their feces.

Streptococcus sp. (viridans group)

Synonymy.—The species used by Jettmar (1935) is not known, but he refers to a *Streptococcus* of the alpha type which formed colonies with green patches on blood agar. According to Breed et al.

(1948), and Smith et al. (1948), streptococci like the above would probably fall in the *viridans* group.

Disease.—Streptococci of the *viridans* group occur in pus, abscesses, and in the human mouth, throat, and nasopharynx.

Experimental vectors.—*Blatta orientalis,* Germany (Jettmar, 1935): Organism isolated from the hindgut and feces in almost pure culture. A mouse was successfully infected through subcutaneous injection.

Streptococcus spp.

Disease.—Some species of *Streptococcus* are highly pathogenic, and for that reason these undetermined species are listed here.

Natural vectors.—*Blatta orientalis,* Germany (Jettmar, 1935): Cultures from the hindgut contained short chains of streptococci.

Blattella germanica, U.S.A. (Janssen and Wedberg, 1952): Organism isolated from the feces and alimentary canal. Germany (Jettmar, 1935): 19 specimens, captured in the operating room of a hospital, were found to be externally contaminated with streptococci which produced green colonies on blood agar.

Cockroaches, U.S.A. (Longfellow, 1913): A streptococcus that hemolyzed human blood was isolated from the insects' viscera.

Experimental vectors.—*Blatta orientalis,* Italy (Cao, 1898): The streptococci did not pass through the gut of this insect after an infective feeding.

Family CORYNEBACTERIACEAE

Corynebacterium diphtheriae (Flügge) Lehmann and Neumann

Synonymy.—"Bacillus Klebs-Loeffler" of Longfellow; "Bacillo di Löffler" of Cao.

Disease.—Diphtheria in man.

Experimental vectors.—*Blatta orientalis,* Italy (Cao, 1898): Organism could not be recovered from the feces.

Cockroaches, U.S.A. (Longfellow, 1913): Organism recovered from legs of cockroaches exposed to sterile food that Longfellow had inoculated with *C. diphtheriae.*

Family ENTEROBACTERIACEAE

Escherichia coli (Migula) Castellani and Chalmers

Synonymy.—*Bacillus coli; B. coli communis; Bacterium coli.*

Disease.—Causes infections of genitourinary tract. Invades circulation in agonal stages of diseases. Habitat: Intestine of man and other vertebrates.

Natural vectors.—Blatta orientalis, Italy (Cao, 1898, 1906). France (Sartory and Clerc, 1908). Italy (Spinelli and Reitano, 1932). Europe (Jettmar, 1935). Poland (Nicewicz et al., 1946).

Blattella germanica, U.S.A. (Steinhaus, 1941).

Periplaneta americana, U.S.A., Texas (Bitter and Williams, 1949, 1949a).

Cockroach, U.S.A. (Longfellow, 1913).

Cockroaches (presumably *B. orientalis, B. germanica,* and/or *P. americana*), Egypt (El-Kholy and Gohar, 1945).

Organism isolated from feces of *B. orientalis,* from intestinal contents of all hosts, and from outer surfaces of bodies or suspensions of whole, undetermined cockroaches.

Experimental vectors.—Blattella germanica, Germany (Vollbrechtshausen, 1953); Organisms injected into the insects' intestinal tracts in a serum and salt solution. Highest concentrations of bacteria killed the insects, but most insects survived the lowest concentration. The test organism was recovered from the feces during the first 14 days.

Klebsiella pneumoniae (Schroeter) Trevisan

Synonymy.—"Bacillo di Friedländer" of Cao.

Disease.—Pneumonia. Associated with infections of respiratory, intestinal, and genitourinary tracts of man. Has been isolated from soil, water, and milk.

Experimental vectors.—Blatta orientalis, Italy (Cao, 1898): This organism passed through the insects' guts unchanged in virulence.

Paracolobactrum aerogenoides Borman, Stuart and Wheeler

Source.—Human gastroenteritis. Habitat: Surface water, soils, intestine of man and other animals.

Natural vectors.—Blattella germanica, U.S.A. (Janssen and Wedberg, 1952): Organism isolated from feces and alimentary canal.

Periplaneta americana, U.S.A. (Bitter and Williams, 1949): Organism isolated from intestinal tract. Doubtful pathogenicity.

Paracolobactrum coliforme Borman, Stuart and Wheeler

Source.—Human gastroenteritis. Habitat: Soils, surface water, intestinal tract of man and other animals.

Natural vectors.—Blattella germanica, U.S.A. (Janssen and Wedberg, 1952): Organism isolated from feces and alimentary canal.

Periplaneta americana, U.S.A. (Bitter and Williams, 1949): Organism isolated from intestinal tract.

Paracolobactrum spp.

Source.—All species of this genus isolated from human gastroenteritis. Habitat: As preceding species.

Natural vectors.—*Blatta orientalis, Blattella germanica,* and *Periplaneta americana,* U.S.A. (Olson and Rueger, 1950; T. A. Olson, p. c.): The organisms were isolated from laboratory-reared cockroaches.

Periplaneta americana, U.S.A. (Bitter and Williams, 1949a).

Proteus mirabilis Hauser

Source.—Gastroenteritis. Habitat: Putrefying materials, infusions, abscesses (Breed et al., 1948). *Proteus* bacilli appear to be responsible for a number of inflammatory and suppurative processes in man (Wilson and Miles, 1955).

Natural vectors.—*Periplaneta americana,* U.S.A. (Bitter and Williams, 1949, 1949a): Organism isolated from intestines. Doubtful pathogenicity.

Proteus morganii (Winslow et al.) Rauss

Synonymy.—"Bacillus Morgan" of El-Kholy and Gohar.

Source.—Summer diarrhea in infants.

Natural vectors.—*Periplaneta americana,* U.S.A. (Bitter and Williams, 1949, 1949a): Organism isolated from the intestine. Doubtful pathogenicity.

Cockroaches (presumably *Blatta orientalis, Blattella germanica,* and/or *P. americana*), Egypt (El-Kholy and Gohar, 1945): Organism isolated from suspensions of whole cockroaches.

Proteus rettgeri (Hadley et al.) Rustigian and Stuart

Source.—Sporadic and epidemic gastroenteritis. Some choleralike diseases of birds, fowl typhoid.

Natural vectors.—*Periplaneta americana,* U.S.A. (Bitter and Williams, 1949, 1949a): Organism isolated from intestines. Doubtful pathogenicity.

Proteus vulgaris Hauser

Synonymy.—*Bacillus proteus vulgaris.*

Source.—Urinary-tract infections, abscesses. Habitat: Feces, putrefying materials.

Natural vectors.—*Blaberus craniifer,* U.S.A. (Wedberg, et al., 1949): Organism isolated from feces.

Blatta orientalis, Italy (Spinelli and Reitano, 1932): Organism isolated from intestinal tract.

Periplaneta americana, U.S.A. (Bitter and Williams, 1949, 1949a): Organism isolated from intestinal tract. Doubtful pathogenicity.

Cockroaches, U.S.A. (Longfellow, 1913): Organism isolated from the legs.

Proteus spp.

Disease.—All four species of this genus are possibly pathogenic; see preceding species.

Natural vectors.—*Blatta orientalis* and *Periplaneta americana,* U.S.A. (Olson and Rueger, 1950; T. A. Olson, p. c.). These organisms were isolated from laboratory-reared cockroaches.

P. americana, U.S.A. (Bitter and Williams, 1949): Organisms isolated from intestines. Doubtful pathogenicity.

Salmonella anatis (Rettger and Scoville) Bergey et al.

Synonymy.—*Salmonella anatum.*

Disease.—Intestinal infections in chickens and man. Widely distributed in man and domestic animals.

Natural vectors.—*Periplaneta americana,* U.S.A. (Eads et al., 1954): Organism isolated from cockroaches collected in sewer manholes.

Salmonella choleraesuis (Smith) Weldin

Synonymy.—*B. suipestifer* of Pavlovskii.

Disease.—Occasionally causes acute gastroenteritis and enteric fever in man.

Experimental vectors.—*Polyphaga saussurei,* U.S.S.R. (Zmeev *in* Pavlovskii, 1948): The organism, when fed in bread and human feces, passed through the insects unchanged.

Salmonella enteritidis (Gaertner) Castellani and Chalmers

Synonymy.—*B. Gärtneri* of Pavlovskii.

Disease.—First isolated from human feces in an epidemic of food poisoning. Also a pathogen of domestic and wild animals.

Experimental vectors.—*Blatta orientalis,* U.S.S.R. (Rozengolts and I͡udina *in* Pavlovskii, 1948): Cockroaches were infected per os. The organism could be observed in the intestinal tracts and feces up to the fourth day. In the insects' intestinal canals, the organism changed under influence of the host, but after it was subcultured or passed through mice, the modified strain regained its original properties.

Blattella germanica, U.S.A. (Olson and Rueger, 1950; T. A. Olson, p. c.): The organism was recovered from the feces within 2 days after feeding. U.S.S.R. (Rozengolts and I͡udina *in* Pavlovskii, 1948): See comments under *B. orientalis.*

Polyphaga saussurei, U.S.S.R. (Zmeev *in* Pavlovskii, 1948): The organism was fed in bread and human feces; it passed through the cockroach unchanged.

Salmonella morbificans (Migula) Haupt

Synonymy.—Salmonella bovis-morbificans.

Disease.—Gastroenteritis, septicemia in cattle.

Natural vectors.—Periplaneta americana, Australia (Mackerras and Mackerras, 1948): This record may have included *Periplaneta ignota* which was not recognized at that time as distinct from *P. americana* (Mackerras and Pope, 1948). Organism isolated from the guts of cockroaches captured in hospital wards in which cases of gastroenteritis were occurring. During the epidemic, there were three invasions in 16 cockroaches collected in childrens' wards, but none in 146 cockroaches from other hospitals or outside in the same period, or in flies (Mackerras and Mackerras, 1949). Dr. I. M. Mackerras (p. c.) has confirmed that the isolations attributed to "cockroaches" in the 1949 paper are the same as those that were reported for *P. americana* in the 1948 paper.

Experimental vectors.—Nauphoeta cinerea, Periplaneta australasiae Periplaneta ignota, and *Supella supellectilium,* Australia (Mackerras and Pope, 1948): All the above cockroaches were invaded by this organism after feeding on sucrose broth cultures. Isolation of the organism was made from the feces or guts after death. The longest period of infection was 19 days, in *P. ignota.*

Salmonella paratyphi (Kayser) Castellani and Chalmers

Synonymy.—"Paratifa A" of Pavlovskii.

Disease.—Enteric fever in man.

Experimental vectors.—Polyphaga saussurei, U.S.S.R. (Zmeev *in* Pavlovskii, 1948): The organism, when fed in bread and human feces, passed through the insect unchanged.

Salmonella schottmuelleri (Winslow et al.) Bergey et al.

Synonymy.—Bacillus para-typhosus, B. "Paratifa B" of Pavlovskii.

Disease.—Natural pathogen of man which causes enteric fever.

Natural vectors.—Periplaneta americana, U.S.A. (Bitter and Williams, 1949, 1949a): Organism isolated from intestinal tract of cockroaches captured either at sewer manholes or in a private home.

Experimental vectors.—Periplaneta americana, Gold Coast Colony (Macfie, 1922): Organism was not recovered from feces after feeding to cockroach.

Polyphaga saussurei, U.S.S.R. (Zmeev *in* Pavlovskii, 1948): The organism, when fed in bread and human feces, passed through the insect unchanged.

Salmonella sp. (Type Adelaide)

Synonymy.—Salmonella adelaide.

Disease.—Isolated from two fatal cases resembling typhoid fever.

Experimental vectors.—Nauphoeta cinerea, Periplaneta australasiae, Periplaneta ignota, and *Supella supellectilium,* Australia (Mackerras and Pope, 1948): The above organism was recovered from the feces or guts of all these cockroaches. The longest invasion encountered was 42 days in *N. cinerea.*

Salmonella sp. (Type Bareilly)

Synonymy.—Salmonella bareilly.

Disease.—Natural pathogen of man; causes gastroenteritis and enteric fever. Widely distributed in fowls.

Natural vectors.—Periplaneta americana, U.S.A. (Eads et al., 1954): Organism isolated from macerated suspensions of cockroaches that had been captured in sewer manholes.

Salmonella sp. (Type Bredeny)

Synonymy.—Salmonella bredeny.

Disease.—Human gastroenteritis, abscesses. Also found in hogs and chickens.

Natural vectors.—Periplaneta americana, U.S.A. (Bitter and Williams, 1949, 1949a): Organism isolated from the intestinal tracts of cockroaches captured either at sewer manholes or in a private home.

Salmonella sp. (Type Derby)

Synonymy.—Salmonella derby.

Disease.—Isolated from human feces; presumably it could cause gastroenteritis as all known species of *Salmonella* are pathogenic for warm-blooded animals, including man (Breed et al., 1948).

Experimental vectors.—Nauphoeta cinerea, Periplaneta australasiae, and *Supella supellectilium,* Australia (Mackerras and Pope, 1948): This organism was recovered from the feces or guts of these cockroaches. The longest invasions lasted 20 days in *N. cinerea* and 30 days in *S. supellectilium.*

Salmonella sp. (Type Kentucky)

Synonymy.—Salmonella kentucky.

Disease.—Isolated from chicken with coccidiosis and ulcerative enteritis; also found in many species of fowl and in hogs and man.

Natural vectors.—Periplaneta americana, U.S.A. (Eads et al., 1954): Organism isolated from cockroaches captured in sewer manholes.

Salmonella sp. (Type Kottbus)

Synonymy.—Salmonella kottbus.

Disease.—Acute gastroenteritis.

Experimental vectors.—Periplaneta australasiae, Australia (Mackerras and Pope, 1948): Three cockroaches were contaminated in the laboratory during tests with other species of *Salmonella.* The invasion lasted 18 days in one cockroach.

Salmonella sp. (Type Meleagris)

Synonymy.—Salmonella meleagridis Brunner and Edwards.

Disease.—Isolated from man, fowl, snakes.

Natural vectors.—Periplaneta americana, U.S.A. (Eads et al., 1954): Organism isolated from cockroaches captured in sewer manholes.

Salmonella sp. (Type Montevideo)

Synonymy.—Salmonella montevideo.

Disease.—Organism isolated from humans, from an ape with fatal enterocolitis, and from chickens and powdered eggs.

Experimental vectors.—Periplaneta americana, U.S.A. (Jung and Shaffer, 1952): The organism survived in the gut fairly regularly and persisted for at least 7 days when the insects had ingested feces containing approximately 10^4 or more viable *S. montevideo* (strain B-33). A second strain of this organism (5327) had less ability to persist in the cockroaches' guts.

Salmonella sp. (Type Newport)

Synonymy.—Salmonella newport.

Disease.—Food poisoning in man. Widely distributed in man, cattle, hogs, chickens, snakes.

Natural vectors.—Periplaneta americana, U.S.A. (Eads et al., 1954): Organism isolated from cockroaches captured in sewer manholes.

Salmonella sp. (Type Oranienburg)

Synonymy.—Salmonella oranienburg.

Disease.—Gastroenteritis in man. Also from chickens, quail, powdered eggs, hogs.

Natural vectors.—Periplaneta americana, U.S.A. (Bitter and Williams, 1949, 1949a): Organism isolated from intestinal tracts of two cockroaches captured either at sewer manholes or in a private home. U.S.A. (Eads et al., 1954): Organism isolated from cockroaches captured in sewer manholes.

Experimental vectors.—Blatta orientalis, Blattella germanica, and *Periplaneta americana,* U.S.A. (Olson and Rueger, 1950): From fecal isolations, the organism was found to survive for 20 days in *B. orientalis,* 12 days in *B. germanica,* and 10 days in *P. americana.* However, the oriental cockroach was positive (post mortem examination) 42 days after an experimental feeding, even though the feces were contaminated only during the first 20 days. The *Salmonella* remained viable on the pronotal surface of *P. americana* for as long as 78 days. Fecal pellets from an experimental American cockroach remained infective 199 days. In a recent letter, Dr. Olson informed us that *S. oranienburg* had survived in feces of *P. americana* for 4 years and 115 days.

Salmonella sp. (Type Panama)

Synonymy.—Salmonella panama.

Disease.—Human food poisoning. Habitat: Widely distributed; found in reptiles, hogs, chickens, as well as man.

Natural vectors.—Periplaneta americana, U.S.A. (Eads et al., 1954): Organism isolated from cockroaches captured in sewer manholes.

Salmonella sp. (Type Rubislaw)

Synonymy.—Salmonella rubislaw.

Disease.—Enteritis in child. Also found in snakes.

Natural vectors.—Periplaneta americana, U.S.A. (Eads et al., 1954): Organism isolated from cockroaches captured in sewer manholes.

Salmonella sp. (Type Tennessee)

Synonymy.—Salmonella tennessee.

Disease.—Presumably a cause of food poisoning. Found in turkeys, powdered eggs, man.

Natural vectors.—Periplaneta americana, U.S.A. (Eads et al., 1954): Organism isolated from cockroaches captured in sewer manholes.

Salmonella typhimurium (Loeffler) Castellani and Chalmers

Synonymy.—Bac. Breslau of Pavloskii.

Disease.—Food poisoning in man. Found in mice, snakes.

Natural vectors.—Blattella germanica, Belgium (Graffar and Mertens, 1950): Isolated from a cockroach captured in a hospital ward during an epidemic of gastroenteritis. The epidemic was stopped by extermination of the cockroaches.

Nauphoeta cinerea, Australia (Mackerras and Mackerras, 1948): Organism isolated from the gut of an insect captured in hospital wards where cases of *Salmonella* infection were occurring.

Experimental vectors.—Blaberus craniifer, U.S.A. (Wedberg et al., 1949): Massive amounts of this organism passed through the digestive tract and were recovered in the feces up to 12 days thereafter.

Blatta orientalis, U.S.S.R. (Rozengolts and I͡udina *in* Pavlovskii, 1948): After the organism was fed to the cockroaches, it was found in the intestinal tracts and feces up to the fourth day. The organism in the insects' intestinal tracts was changed, but after it was subcultured or passed through mice it regained the properties of the original strain.

Blattella germanica, Belgium (Graffar and Mertens, 1950): After a meal containing *S. typhimurium,* the digestive tracts of the cockroaches contained numerous *Salmonella* up to 10 days and some still contained pathogens on the fourteenth day. The presence of the pathogens on the exoskeleton was irregular after the fourth day, but many were still present up to the tenth day. U.S.A. (Olson and Rueger, 1950): The organism was recovered from the digestive tract 9 days after the original inoculative feeding. U.S.A. (Janssen and Wedberg, 1952): When *S. typhimurium* was fed to the cockroaches in sufficient numbers, positive cultures could be obtained from the feces up to the seventh day and from the alimentary canals up to the eleventh day after feeding. U.S.A. (Beck and Coffee, 1943): These workers reported that *B. germanica* did not disseminate the organism.

U.S.S.R. (Rozengolts and I͡udina *in* Pavlovskii, 1948): Same comments as reported by these workers under *B. orientalis.*

Nauphoeta cinerea, Australia (Mackerras and Pope, 1948): Viable *Salmonella* excreted in the cockroach feces up to 16 days after inoculative feeding. In a laboratory colony of this cockroach, which had been fed on a culture of *S. typhimurium,* the entire immature insect and the intestines of adults were positive on the third, fifteenth, and twenty-fifth days after feeding. The organism was also isolated from paper from the culture jar, and from agar plates on which some of the cockroaches were allowed to walk.

Periplaneta americana, U.S.A. (Beck and Coffee, 1943): The organism is capable of being disseminated by this cockroach which apparently harbors it in the intestine as well as mechanically on the appendages. (Jung and Shaffer, 1952): This organism survived in the gut of *P. americana* fairly regularly and persisted for at least 7 days when the insects had ingested human feces containing approximately 10^4 or more viable *S. typhimurium* (strain 5609).

Periplaneta australasiae and *Supella supellectilium,* Australia (Mackerras and Pope, 1948): Organism recovered from the feces or guts from two of three *P. australasiae* and from two of two *S. supellectilium.*

Polyphaga saussurei, U.S.S.R. (Zmeev *in* Pavlovskii, 1948): The organism was fed mixed with bread and human feces. It passed unchanged through the insect. Mice fed with the intestines of *P. saussurei,* which had been infected per os, died and the organism was reisolated from the mice.

Salmonella typhosa (Zopf) White

Synonymy.—"Bacillo del tifo" of Antonelli (1930). *Bacillus typhosus.* Eberth's bacillus. "Palochki bri͡ushnogo tifa" of Pavlovskii.

Disease.—Typhoid fever.

Natural vectors.—Blatta orientalis, Italy (Antonelli, 1930, 1943): The organism was isolated from the legs of cockroaches captured in the homes of people who had contracted typhoid. The cockroaches had easy access to open latrines in which typhoid patients voided feces. The organism was also recovered from cockroach feces on bread and cheese collected in the same homes.

Cockroaches, U.S.A. (Englemann, 1903): Englemann described an outbreak of typhoid in Chicago and presumed cockroaches to be carriers; however, no evidence was given to support this view.

Experimental vectors.—Blaberus craniifer, U.S.A. (Wedberg et al., 1949): Attempts to pass the typhoid organism through this cockroach were unsuccessful. Massive doses of the organism were fed, but in no instance could it be isolated from the feces or digestive tract.

Blatta orientalis, Italy (Spinelli and Reitano, 1932): The organism was isolated from the feces and intestinal tract; it survived in the insect's gut for 9 days. Some of the organisms were recovered from the feces 3 days after the experimental meal had been ingested. U.S.A. (McBurney and Davis, 1930): Cockroaches, starved under sterile conditions for 72 hours and then fed *S. typhosa* for 120 hours, gave colonies which only once could be confirmed as *S. typhosa* by the agglutination test and reactions on sugar broths. However, organisms resembling *S. typhosa* were obtained from cockroaches fed *S. typhosa;* no such organisms were obtained prior to the experimental feeding. No tests were made to determine the virulence of *S. typhosa* that had passed through the cockroaches' intestines. U.S.S.R. (Rozengolts and I͡udina *in* Pavlovskii, 1948): The organism was found in the intestines of insects up to the twenty-third day and in the feces up to the eleventh day. However, after the third day the organism became less frequent.

Blattella germanica, U.S.A. (Janssen and Wedberg, 1952): Controlled feeding of massive doses of *S. typhosa* failed to produce a single positive stool after 24 hours in all cockroaches tested. Only 2 of 45 stools passed within the first 18 hours after the feeding were positive. The presence of a lethal agent responsible for the destruction of *S. typhosa* could not be revealed. Germany (Jettmar, 1927): Cockroaches fed typhoid cultures showed a higher mortality than those fed plague bacilli. U.S.S.R. (Rozengolts and I͡udina *in* Pavlovskii, 1948): Same comments as reported by these authors under *B. orientalis.*

Periplaneta americana, Gold Coast Colony (Macfie, 1922): The organism could not be recovered after feeding. Netherlands (Akkerman, 1933): Organism isolated from the gut, up to 2 days, and in the feces up to 3 days after feeding. Formosa (Morischita and Tsuchimochi, 1926): The feces of 40 out of 50 cockroaches fed *S. typhosa* contained this organism within 3 hours after feeding and for about 3 days thereafter. U.S.A. (T. Olson, p. c.): Organisms recovered in feces 5 days after feeding; water in containers was contaminated by mouth contact after 5 days.

Periplaneta australasiae, Formosa (Morischita and Tsuchimochi, 1926): All three insects that were fed *S. typhosa* excreted this organism in their feces within 3 hours and for about 3 days thereafter.

Polyphaga saussurei, U.S.S.R. (Zmeev *in* Pavlovskii, 1948): The organism was fed together with bread and human feces. It passed through the insect unchanged.

Cockroaches (presumably *Blatta orientalis, Blattella germanica,* and/or *Periplaneta americana*), Egypt (El-Kholy and Gohar, 1945): *S. typhosa* isolated from macerated insects and from plates over which the cockroaches had walked after they had received an inoculated meal.

Cockroaches, U.S.A. (Coplin, 1899): Cockroaches, which were allowed to walk over a culture of the organism, transferred *S. typhosa* to agar plates both from the feet and the ventral surface of the body. U.S.A. (Longfellow, 1913): Organism isolated from intestine and outer surface of body. Venezuela (Tejera, 1926): Typhoid organism isolated from feces 24 and 48 hours after the cockroaches had eaten an inoculated meal.

Serratia marcescens Bizio

This species of bacteria is normally found in water, soil, milk, foods, and insects. It has been isolated from cockroaches several times and is known to be toxic to insects. Dr. T. Olson (p. c.) isolated, from a species of *Periplaneta* received in a shipment from the south, a strain of *S. marcescens* which was toxic to mice when administered intraperitoneally.

Shigella alkalescens (Andrewes) Weldin

Disease.—Dysentery in man.

Natural vectors.—Periplaneta americana, U.S.A. (Bitter and Williams, 1949, 1949a): Organism isolated from the intestinal tract.

Shigella dysenteriae (Shiga) Castellani and Chalmers

Synonymy.—B. dysenteriae Shiga of Pavlovskii.

Disease.—Dysentery in man and monkeys.

Experimental vectors.—Blatta orientalis, Italy (Spinelli and Reitano, 1932): The dysentery organisms passed unharmed through the digestive tract and were isolated from the intestinal tract and feces 6 days and 96 hours, respectively, after an experimental meal; the organism was also regurgitated.

Periplaneta americana, Formosa (Morischita and Tsuchimochi, 1926): Feces of 30 cockroaches fed a culture of this organism were 100 percent contaminated. Feces excreted 48 hours after feeding were mostly positive, and those after 58 hours were entirely negative. At dissection after 70 hours, the contents of the digestive tracts were all sterile. Cockroaches killed after 48 hours still contained the organism.

Polyphaga saussurei, U.S.S.R. (Zmeev *in* Pavlovskii, 1948): The organism was fed mixed with bread and human feces. It passed through the insect unchanged.

Shigella paradysenteriae (Collins) Weldin

Synonymy.—Bacillus dysenteriae (Flexner) of Macfie. *B. flexneri* of Pavlovskii.

Disease.—Dysentery in man; summer diarrhoea in children.

Natural vectors.—Shelfordella tartara, Tadzhikistan (Zmeev, 1940): The organisms were isolated in a viable state from the stomach of the cockroach. This cockroach occurs in houses in Central Asia where it may play some part in maintaining domestic foci of the disease. Pavlovskii (1948) stated that Zmeev isolated Flexner's dysentery bacillus from four cockroaches of this species caught in a food cupboard in a hospital.

Experimental vectors.—Periplaneta americana, Gold Coast Colony (Macfie, 1922): The organism was not recovered in the feces. *Polyphaga saussurei,* U.S.S.R. (Zmeev *in* Pavlovskii, 1948): When the organism was fed in bread and human feces, it passed through the insect unchanged.

Cockroaches, Venezuela (Tejera, 1926): The organism was recovered from feces 24 hours after an experimental feeding but not after 4 days.

Family PARVOBACTERIACEAE

Brucella abortus (Schmidt and Weis) Meyer and Shaw

Disease.—Cause of infectious abortion in cattle, mares, sheep, rabbits, guinea pigs, and all other domestic animals except hogs. Causes undulant fever in man.

Experimental vectors.—Periplaneta americana, U.S.A. (Ruhland and Huddleson, 1941): Organism did not remain alive in intestinal tract of cockroach for more than 24 hours.

Malleomyces mallei (Zopf) Pribram

Synonymy.—"Bacillo della morva" of Cao.

Disease.—Glanders in horses, other domestic animals, and man.

Experimental vectors.—Blatta orientalis, Italy (Cao, 1898): This organism passed unchanged through the gut with the feces and retained its virulence.

Pasteurella multocida (Lehmann and Neumann) Rosenbusch and Merchant

Synonymy.—"B. del colera dei polli" of Cao (1906) was interpreted by Pierce (1921) and Steinhaus (1946) as *Bacterium cholerae gallinarum.* Hühnercholerabacterien. *Pasteurella avicida.*

Disease.—The cause of hemorrhagic septicemia in birds and mammals; chicken cholera.

Experimental vectors.—Blatta orientalis, Germany (Küster, 1902, 1903): In 1902 Küster found that the organism passed through the intestine of the insect without losing its virulence; but in 1903, after he fed the organism to cockroaches it was not recovered. Italy (Cao, 1906): Cao found that the bacterium of chicken cholera, which had lost virulence, regained part of its virulence after passage through the cockroach's intestine.

Pasteurella pestis (Lehmann and Neumann) Holland

Synonymy.—"Bacillo della peste bubbonica di Kitasato e Yersin" of Cao.

Disease.—Causative organism of plague in man, rats, other rodents. Infectious for mice, guinea pigs, and rabbits.

Natural vectors.—Blatta orientalis, Hong Kong (Hunter, 1906): Insects collected from plague-infected foci contained *P. pestis.* Transmission of plague by flea bites and feces is now well established. Presumably for cockroaches to serve as vectors of this disease, they would have to contaminate wounds (bites?) with infected, regurgitated material or infected feces, or be eaten by the host.

Experimental vectors.—Blatta orientalis, Italy (Cao, 1898). Germany (Küster, 1903). Cao found that the organism passed through the gut of the insect unchanged in virulence. Küster found that after fresh cockroach feces had been injected into a rat, the animal died of plague; feces over 24 hours old were not infectious.

Blattella germanica, Germany (Jettmar, 1927): Cockroaches remained alive while being fed *P. pestis* for one month. The organism lost its virulence in the intestine of the insect, and it was not possible to infect guinea pigs with fresh feces from bacteria-fed cockroaches.

Leucophaea maderae and *Periplaneta americana,* Philippine Islands (Barber, 1912): In one experiment, 11 *P. americana* and 15 *L. maderae* were inoculated in the leg with a virulent strain of *P. pestis.* Eleven of these insects died within 2 days; six of the dead insects showed pure *P. pestis* cultures. In another experiment, 61 cockroaches were inoculated with virulent *P. pestis.* Nine of these showed, at necropsy, pure cultures of bacilli morphologically resembling *P. pestis.*

Massive doses of *P. pestis* failed to infect most of the insects when injected into the body.

Cockroaches, Australia (Pound, 1907): Pound suspected that control guinea pigs in his laboratory became infected with plague by eating food contaminated by cockroaches. In the laboratory, rats may be infected with plague by ingesting the bacteria (Rosenau, 1940).

Family BACILLACEAE

Bacillus anthracis Cohen emend. Koch

Synonymy.—"Bacillo del carbonchio" of Cao. Milzbrandbacillen of Küster.

Disease.—Cause of anthrax in man, cattle, sheep, and swine.

Experimental vectors.—*Blatta orientalis,* Italy (Cao, 1898, 1906): Organism passed through the gut unchanged. It was excreted in the feces for a month after a single feeding. Attenuated *B. anthracis* regained full virulence in some experiments but not in others (Cao, 1906). Germany (Küster, 1903): Virulence was proved by injection of recovered organism into white mice.

Bacillus subtilis Cohn emend. Prazmowski

Disease.—After passage through the cockroach's intestine, the bacterium became pathogenic to laboratory animals (Cao, 1898). Normally found in soil and decomposing organic matter.

Natural vectors.—*Blaberus craniifer,* U.S.A. (Wedberg et al., 1949): From feces.

Blatta orientalis, Italy (Cao, 1898, 1906): From intestinal contents. (Spinelli and Reitano, 1932): Feces. France (Sartory and Clerc, 1908): Feces. Poland (Nicewicz et al., 1946): Feces.

Cryptocercus punctulatus, U.S.A. (Hatcher, 1939): From feces.

Periplaneta americana, England (Shrewsbury and Barson, 1948): Intestinal tract.

Cockroaches, U.S.A. (Longfellow, 1913): Outer part of body and intestinal tract.

Experimental vectors.—*Blatta orientalis,* Italy (Cao, 1898, 1906): Organism recovered from intestinal tract.

Clostridium feseri Trevisan

Synonymy.—"Bacillo del carbonchio sintomatico" of Cao.

Disease.—Cause of black leg or symptomatic anthrax in cattle and other animals. Habitat: Probably manured soil.

Experimental vectors.—Blatta orientalis, Italy (Cao, 1898): Organism passed unchanged through the gut with the feces and retained its virulence.

Clostridium novyi (Migula) Bergey et al.
or
Clostridium sporogenes (Metchnikoff) Bergey et al.

Synonymy.—"Bacillo dell'edema maligno" of Cao. Steinhaus (1946) considered Cao's organism to be *C. sporogenes.* Smith et al. (1948) stated that *C. novyi* was isolated in 1894 from guinea pigs with "malignant edema" and that it will probably never be settled whether *C. sporogenes* is identical with Koch's bacillus of malignant edema. Obviously there is no way of properly identifying Cao's bacillus of malignant edema.

Source.—Gaseous gangrene; "malignant edema." Habitat: Probably manured soil.

Natural and experimental vectors.—Blatta orientalis, Italy (Cao, 1898): Isolated from feces of naturally invaded cockroach. Experimentally the organism also passed unchanged through the gut with feces and retained its virulence.

Clostridium perfringens (Veillon and Zuber) Holland

Synonymy.—Clostridium welchii.

Disease.—Gaseous gangrene. Habitat: Feces, sewage, soil.

Natural vectors.—Cockroaches (presumably *Blatta orientalis, Blattella germanica,* and/or *Periplaneta americana*), Egypt (El-Kholy and Gohar, 1945): Isolated from whole suspensions of the cockroaches. The organism that was isolated from the insects killed inoculated guinea pigs.

Clostridium tetani (Flügge) Holland

Synonymy.—"Bacillo del tetano" of Cao.

Disease.—Lockjaw or tetanus. Habitat: Soils, human and horse feces.

Experimental vectors.—Blatta orientalis, Italy (Cao, 1898): Organism passed through the gut unchanged in virulence, but the tetanus-toxin itself was destroyed in the intestine.

Clostridium spp.

Disease.—About half the derived species of *Clostridium* are pathogenic (Reed *in* Dubos, 1948).

Natural vectors.—Periplaneta americana, England (Shrewsbury and Barson, 1948): Seven strains of *Clostridium* spp. were isolated from the alimentary tract.

Order ACTINOMYCETALES

Family MYCOBACTERIACEAE

Mycobacterium avium Chester

Common name.—Avian tubercle bacillus.

Synonymy.—"Tuberkuleznykh kultur (ptichii)" of Pavlovskii.

Disease.—Tuberculosis in chickens, other birds, and less frequently in pigs.

Experimental vectors.—Blatta orientalis, U.S.S.R. (Ekzempliarskaia *in* Pavlovskii, 1948): When fed a culture of *M. avium,* the cockroaches voided the organism in their feces for up to 2 months. The organism aparently increased in virulence to guinea pigs by passage through the cockroach.

Mycobacterium lacticola Lehmann and Neumann (?)

Disease.—The organism gave a slight reaction when inoculated into the skin of a guinea pig (Leibovitz, 1951).

Natural vectors.—Periplaneta americana, U.S.A., Texas (Leibovitz, 1951): Organism, tentatively identified as *M. lacticola,* was isolated from macerated intestines of cockroaches that had been captured in sewers.

Mycobacterium leprae (Armauer-Hansen) Lehmann and Neumann

Disease.—Hansen's disease, leprosy. Habitat: Skin of man, leprous nodules, nasal mucosa.

Natural vectors.—Blattella germanica, Southern Rhodesia and Kenya (Moiser, 1945, 1946, 1946a; Anonymous, 1946): Of 230 cockroaches, mostly *B. germanica,* caught in native huts in Rhodesia, 55 were positive for Hansen's bacilli. Hansen's bacilli lasted an average of 14¾ days in the cockroach, though they remained unchanged in the feces for much longer, up to 16 months. Moiser observed small, acid-fast, oval bodies in about 70 percent of the cockroaches examined. Similar bodies have been observed in man, and Moiser thinks that they may be a stage in the development of *M. leprae* in the cockroach.

Periplaneta americana and *Periplaneta australasiae,* Formosa (Arizumi, 1934, 1934a): Of 67 cockroaches caught in serious-case wards in the leprosy sanatorium near Taihoku, 26.8 percent carried *M.*

leprae-like, acid-fast bacilli in their guts. Of 105 cockroaches caught in the slight-case wards, 12.3 percent carried this bacillus.

Cockroaches, Venezuela (Tejera, 1926): Acid-resistant bacteria similar to *M. leprae* were found in cockroaches captured in leprosy colony at Cabo Blanco, but this bacterium was never encountered in cockroaches captured elsewhere. Belgian Congo (Radna, 1939): Three of eight cockroaches captured in the hut of a leprosy patient were found to excrete *M. leprae* in their feces over a period of 10 days after capture.

Experimental vectors.—Blatta orientalis, Europe (Paldrock *in* Klingmüller, 1930): After 14 days, leprous bacilli were still abundant in the feces. Nyasaland (Lamborn, 1940): In one experiment, 38 cockroaches were fed for 9 days on a crust removed 6 months earlier from the ear of a leprous patient. Feces, passed immediately after this food was removed, contained large clusters of short filamentous bacilli, presumably the leprous organism. Ten additional cockroaches were allowed to feed on a dressing just removed from a leprous sore. *M. leprae* was definitely found in feces passed on the third day after removal of this food. Acid-fast particles were recovered on the fifth, eighth, twelfth, fourteenth, and twenty-first days.

Blattella germanica, Europe (Paldrock *in* Klingmüller, 1930): The cockroaches still excreted the bacilli in the feces 14 days after feeding on leprous nodules. Southern Rhodesia and Kenya (Moiser, 1945, 1946, 1946a, 1947; Anonymous, 1946): Cockroaches were fed corn meal inoculated with material from ulcerating nodules containing *M. leprae.* These bacilli were recovered in large numbers from the guts (up to the nineteenth day after feeding) and from dried feces of the insects. The bacilli remained morphologically unchanged in dried feces for several months. The bacilli were found in the feces of a series of five cockroaches, each fed the powdered dry feces of its predecessor.

Nauphoeta cinerea, Nyasaland (Lamborn, 1940): Thirty-four newly born cockroaches fed for 3 days on a dressing removed from a leprous sore. Globi were found in abundance in feces passed on the third day. Acid-fast organisms were recovered at intervals over a period of 66 days. Similar results were obtained with 10 other cockroaches. Feces of a control series of cockroaches remained free of acid-fast organisms.

Periplaneta americana, Gold Coast Colony (Macfie, 1922): The insects were fed scrapings from the nose of a leper. *M. leprae* appeared in the feces for 2 days after the meal. The organism appeared to pass unharmed through the intestine of the cockroach.

Periplaneta americana and *Periplaneta australasiae,* Formosa (Arizumi, 1934, 1934a): When fed an emulsion of leprous nodules, the cockroaches began to excrete *M. leprae* in their feces within 8 hours. This excretion of bacilli continued for 94 hours, but showed the highest positive infection 20, 32, and 44 hours after feeding. Morphologically the bacilli appeared to be unharmed by passage through the gut.

Cockroaches, Belgian Congo, Pawa (Radna, 1939): Three cockroaches were fed on leprous material and Hansen's bacilli were isolated from their feces. Venezuela (Tejera, 1926): Cockroaches were fed with material containing a large quantity of *M. leprae;* the intestinal contents were positive up to the eleventh day for acid-fast bacilli morphologically identical to *M. leprae.* India, Calcutta (Leprosy Research Department, 1948): Cockroaches whose feces were free of acid-fast bacilli for 3 consecutive days were fed leprous material. Acid-fast bacilli were obtained in decreasing number for 2 weeks thereafter.

Mycobacterium lepraemurium Marchoux and Sorel

Common name.—Rat leprosy bacillus.

Disease.—Endemic disease of rats in various parts of world.

Experimental vectors.—Cockroaches, Belgian Congo (Radna, 1939): The day after feeding on infectious material, the insects excreted acid-fast bacteria in their feces. The feces were diluted in physiological saline and injected into five wild rats. Two of the rats died after 134 and 156 days, respectively. Both had general visceral and ganglionic leprosy.

Mycobacterium phlei Lehmann and Neumann

Disease.—Injection into guinea pigs results in local abscesses. Widely distributed in soils, dust.

Natural vectors.—*Periplaneta americana,* U.S.A., Texas (D. W. Micks, p. c.): Organism isolated from batches of intestinal tracts of these cockroaches taken at random. Micks also found *Mycobacterium* spp. and *M. friedmanii* on the cockroaches. The latter is apparently pathogenic only to cold-blooded animals. U.S.A., Texas (Leibovitz, 1951): Leibovitz isolated an organism that he tentatively identified as *M. phlei* from the macerated intestines of cockroaches collected in sewers.

Mycobacterium piscium Bergey et al.

Synonymy.—"Tuberkuleznykh kultur (rybii)" of Pavlovskii, 1948.

Disease.—Infectious for carp, frogs, lizards, but not for guinea pigs and pigeons (Breed et al., 1948). Leibovitz (1951) found that the organism he isolated produced a marked reaction when inoculated into the skin of a guinea pig.

Natural vectors.—*Periplaneta americana,* U.S.A., Texas (Leibovitz, 1951): Organism, tentatively identified as *M. piscium,* was isolated from macerated intestines of cockroaches captured in sewers.

Experimental vectors.—*Blatta orientalis,* U.S.S.R. (Ekzempliarskaia *in* Pavlovskii, 1948): The organism was excreted in the feces for up to 2.5 months after it was fed to the cockroach. The virulence to guinea pigs increased on passage through the cockroach.

Mycobacterium tuberculosis (Schroeter) Lehmann and Neumann

Synonymy.—"Bacillo di Koch" of Cao. "Tuberkuleznykh kultur (chelovecheskii, bychii)" of Pavlovskii.

Common name.—Human tubercle bacillus.

Disease.—Tuberculosis in man; transmissible to rabbits and guinea pigs.

Experimental vectors.—*Blatta orientalis,* Italy (Cao, 1898): The organism passed unchanged in virulence through the insect with the feces. Germany (Küster, 1903): Küster fed the insects pure culture of tubercle bacillus in potato mash. After 2 days, he recovered a great mass of *M. tuberculosis* in the feces. He injected some of this excreted material into guinea pigs 3 and 9 days after a feeding. Both died of typical tuberculosis after 2 months. U.S.S.R. (Ekzempliarskaia *in* Pavlovskii, 1948): *M. tuberculosis* var. *hominis* and *M. tuberculosis* var. *bovis,* when fed in culture, were excreted in the feces for up to 2 months thereafter. The virulence (tested in guinea pigs) of these organisms was somewhat weakened by passage through the cockroach.

Blattella germanica, on shipboard (Morrell, 1911): *M. tuberculosis* was present in the feces within 24 hours after the insect had fed on sputum from a tuberculous patient.

Periplaneta americana, Gold Coast Colony (Macfie, 1922): The feces of cockroaches fed tuberculous sputum were examined daily. Feces passed from the second to fifth day contained tubercle bacilli; from the sixth to the fourteenth day, when examinations were stopped, no more tubercle bacilli were detected.

Cockroaches, Venzeuela (Tejera, 1926): A group of 30 cockroaches were fed sputum containing *M. tuberculosis,* over a 3-day period. Ninety percent of the feces excreted over several days contained typical acid-fast bacilli. Some of these insects, when killed 40 days later, contained bacilli morphologically identical to *M. tuberculosis.* U.S.A. (Read, 1933): The insects were fed tuberculosis sputum for 48 hours. After the insects had been fed, their digestive tracts were ground and injected into guinea pigs; these animals developed typical tuberculous lesions.

Mycobacterium spp.

Disease.—Most species in this genus are animal parasites.

Natural vectors.—Periplaneta americana, U.S.A., Texas (D. W. Micks, p. c.; Liebovitz, 1951): Organism isolated from intestinal tract.

Family ACTINOMYCETACEAE

Nocardia sp. (?)

Disease.—Nocardiosis is an infection, caused by various species of this genus, with symptoms similar to peritonitis, pneumonitis, pseudotuberculosis, meningitis, abscesses.

Natural vectors.—Periplaneta americana, U.S.A., Texas (Leibovitz, 1951): Organism, tentatively identified as *Nocardia* sp., was isolated from macerated intestines of cockroaches that had been captured in sewers.

PART II. PATHOGENIC BACTERIA WHOSE TAXONOMIC POSITION IS UNCERTAIN

The following organisms are either not listed in Breed et al. (1948) or are stated by them to be difficult to classify.

"B. aerobio del pseudoedema maligno" of Cao

Disease.—Pathogenic to rabbits.

Natural vectors.—Blatta orientalis, Italy (Cao, 1906): Isolated from feces.

"B. del pseudoedema maligno" of Cao

Disease.—Pathogenic to guinea pigs.

Natural vectors.—Blatta orientalis, Italy (Cao, 1906): Organism isolated from feces.

"Bacillo proteisimile" of Cao

Disease.—A *Proteus*-like organism pathogenic to guinea pigs and rabbits.

Natural vectors.—*Blatta orientalis,* Italy (Cao, 1898, 1906): Isolated from the intestinal contents.

Experimental vectors.—*Blatta orientalis,* Italy (Cao, 1906): Organism that was recovered from feces after being fed to the insects was lethal to guinea pigs within 48 to 60 hours.

"Bacillo del barbone dei bufali" of Cao

Experimental vectors.—*Blatta orientalis,* Italy (Cao, 1898): The bacillus of buffalo cholera retained its virulence after ingestion and passage through the insect.

"Bacillo similcarbonchio" of Cao

Disease.—An anthraxlike bacterium pathogenic to guinea pigs, rabbits, and pigeons.

Natural vectors.—*Blatta orientalis,* Italy (Cao, 1898, 1906): Isolated from the intestinal contents.

Experimental vectors.—*Blatta orientalis,* Italy (Cao, 1906): Strains C and D of this organism killed guinea pigs when reisolated from the cockroach's feces.

"Bacillo similtifo" or "Bacillo tifosimile" of Cao

Disease.—A typhoidlike bacterium pathogenic to guinea pigs and rabbits.

Natural vectors.—*Blatta orientalis,* Italy (Cao, 1898, 1906): Isolated from the intestinal contents.

Experimental vectors.—*Blatta orientalis,* Italy (Cao, 1906): Organism acquired pathogenicity on passage through intestinal tracts of cockroaches after being fed to the insects in a liver infusion. The bacteria survived in the intestines for 2 to 3 months.

Paracolon bacilli

Source.—May cause clinical dysentery. Strains of paracolon bacilli have been isolated from cases of enteritis in man, food poisoning, infections of genitourinary tract, powdered eggs, and fatal infections in chickens, turkeys, and snakes.

Natural vectors.—Cockroaches (presumably *Blatta orientalis, Blattella germanica,* and/or *Periplaneta americana*), Egypt (El-Kholy and Gohar, 1945): Organisms isolated from suspensions of macerated whole insects.

Sarcina alba "patogena" of Cao

Disease.—Pathogenic to guinea pigs and rabbits. The organism differed from *Sarcina alba* only in its pathogenic properties.

Natural vectors.—Blatta orientalis, Italy (Cao, 1898, 1906): Organism isolated from the intestinal contents; it retained its virulence after passage through the cockroach.

Sarcina "bianca" and "gialla" of Cao

Disease.—After passage through the gut of the cockroach, the white and yellow *Sarcina* became pathogenic to guinea pigs and rabbits.
Experimental vectors.—Blatta orientalis, Italy (Cao, 1898).

Spirochaeta periplanetae Laveran and Franchini

Disease.—Possibly pathogenic to white mice.
Natural vectors.—Blatta orientalis, France (Laveran and Franchini, 1920a): Of five white mice inoculated with the contents of the digestive tubes of cockroaches inoculated with the spirochaete, one died 24 hours and another 48 hours after inoculation; two others became infected and one was unaffected. However, the pathogenicity of this organism is questionable, inasmuch as the entire intestinal contents of the insect were inoculated into the mice.

Streptococcus microapoika Cooper, Keller, and Johnson

Disease.—From throat and feces of children with enteritis.
Natural vectors.—Blatta orientalis, Poland (Nicewicz et al., 1946): Organism isolated from alimentary tract.

Streptococcus non-hemolyticus II Holman

Disease.—Isolated from various human and animal infections.
Natural vectors.—Periplaneta americana, England (Shrewsbury and Barson, 1948): Organism isolated from alimentary tract.

PART III. NEGATIVE FINDINGS

The following organisms were not recovered after they were fed to cockroaches.

Actinomyces asteroides (Eppinger) Gasperini

[=*Streptothrix eppingeri* Rossi-Doria (Dodge, 1935).]
Disease.—Organism found in brain abscess and in peritonitis (Dodge, 1935).
Cockroach.—Blatta orientalis (Cao, 1898).

Actinomyces carneus (Rossi-Doria) Gasperini

Disease.—Organism reported from a case of chronic bronchitis; pathogenic to rabbit and guinea pig (Dodge, 1935).

Cockroach.—*Blatta orientalis* (Cao, 1898).

Neisseria gonorrhoeae Trevisan

Disease.—Gonorrhoea and other infections in man.

Cockroach.—*Periplaneta americana* (Macfie, 1922).

Spirochaeta crocidurae Leger (I) and Spirochaeta hispanica de Buen (II)

Diseases.—(I) Blood parasite of a shrew-mouse in Senegal; (II) cause of Spanish and Moroccan relapsing fever.

Cockroaches, Tunisia(?) (Wollman, 1927; Wollman et al., 1928): Cockroaches externally contaminated with the blood parasites were macerated and injected into peritoneum of a rat. No spirochaetes were found in the blood of this rat.

The following cockroaches were examined for pathogenic bacterial infections, with negative results, by Eads et al. (1954) in Texas:

Blatta orientalis, 54 insects in 15 pools from sewer manholes.

Blattella germanica, 118 insects in 5 pools from food establishments.

Periplaneta americana, 70 insects in 5 pools from food establishments.

Supella supellectilium, 235 insects in 11 pools from food establishments.

APPENDIX C: FUNGI

PATHOGENIC FUNGI ASSOCIATED WITH COCKROACHES

Phylum THALLOPHYTA

Class FUNGI IMPERFECTI

Order MONILIALES

Family MONILIACEAE

Aspergillus fumigatus Fresenius

Disease.—Aspergillosis, an inflammatory infection of the sinuses, bronchi, lungs, and sometimes other parts of the body (Smith et al., 1948).

Natural vectors.—Blatta orientalis, France (Sartory and Clerc, 1908): Organism isolated from the insects' intestinal contents.

Aspergillus niger van Tieghem

Disease.—This species is predominantly saprophytic but is occasionally parasitic in the human ear (Dodge, 1935).

Natural vectors.—Periplaneta americana, U.S.A., Texas (O. B. McShan, 1953): Organism isolated from the feces of cockroaches collected in a grain elevator basement at the Galveston docks.

Experimental vectors.—Blatta orientalis, Italy (Cao, 1898): The organism passed unchanged through the gut of the insects.

Geotrichum candidum Link

Synonymy.—Oidium lactis (Dodge, 1935).

Disease.—Geotrichosis, an infection producing lesions in the mouth, intestinal tract, bronchi, and lungs (Conant et al., 1954).

Experimental vectors.—Blatta orientalis, Italy (Cao, 1898): The organism retained its pathogenicity after passing through the gut.

NEGATIVE FINDINGS

The following organism was not recovered in the cockroaches' feces after feeding experiments.

Histoplasma capsulatum Darling

Disease.—Histoplasmosis, an infectious mycosis that usually results in a pulmonary disease of man.

Cockroach.—*Periplaneta americana,* U.S.A., Texas (O. B. McShan, 1953): 24 hours after the insects had been fed an inoculated meal, they showed no evidence of fungus invasion as determined by fecal cultures and inoculation into mice. The organism could be detected in the cockroaches' intestinal contents 30 minutes after inoculation, but thereafter all pools were negative.

APPENDIX D: PROTOZOA

PATHOGENIC PROTOZOA ASSOCIATED WITH COCKROACHES

Information on the diseases caused by protozoa was taken from Chandler (1949) and Faust (1955). The classification follows Kudo (1954).

Phylum PROTOZOA

Class MASTIGOPHORA

Order PROTOMONADINA

Family TRYPANOSOMATIDAE

Herpetomonas periplanetae Laveran and Franchini

Disease.—Possibly pathogenic to white mice.

Natural vectors.—Blatta orientalis, Italy (Laveran and Franchini, 1920): The contents of the digestive tract of *B. orientalis,* containing *H. periplanetae,* were injected into eight white mice; five mice died. The pathogenicity of this organism is questionable, inasmuch as the entire intestinal contents were injected rather than a pure culture of the protozoan.

Order POLYMASTIGINA

Family TRICHOMONADIDAE

Trichomonas hominis (Davaine)

Disease.—The pathogenicity of *T. hominis* has not been proved, but it is often associated with persistent diarrhea, for which it may or may not be responsible.

Experimental vectors.—Blatta orientalis, South Africa (Porter, 1918): The cockroaches ingested this organism by feeding on infected human feces. *T. hominis* passed unchanged through the insects' intestines and was successfully transferred to rats. Italian Somaliland (Mariani and Besta, 1936): Human *Trichomonas,* presumably *T. hominis,* and *Chilomastix* were fed to cockroaches on bread. The flagellates were present in 60 percent of the cockroaches examined in the first 48 hours, in 25 percent of the insects after 10 days, and in 10 percent after 20 days. In a second experiment these flagellates were present in 66 percent of the cockroaches after 3 days, and in 33 percent after 10 days.

Periplaneta americana, South Africa (Porter, 1918): See comments under *B. orientalis.* U.S.A. (Hegner, 1928): *T. hominis,* ingested with human feces, was destroyed in the crop of the insect within 2 to 5½ hours. No flagellates were found in the insects after 2 days; very few survived until they reached the intestine.

Family HEXAMITIDAE

Giardia intestinalis (Lambl)

Synonymy.—Giardia lamblia; Lamblia intestinalis.

Disease.—Although a majority of persons harboring *G. intestinalis* are asymptomatic, others have a persistent diarrhea.

Experimental vectors.—Blatta orientalis, South Africa (Porter, 1918): The cockroaches were fed on human excrement that contained *G. intestinalis.* Cysts of this protozoan passed unchanged through the cockroaches and were recovered from their feces. These same cysts, when fed to rats, caused diarrhea.

Blattella germanica, Brazil (Pessoa and Correa, 1927): Adults and nymphs were fed cysts of *G. intestinalis.* These cysts were recovered from feces up to 5 days after feeding. The greatest number of living cysts was found 48 hours after feeding.

Eurycotis floridana, U.S.A. (Young, 1937): Experiments showed that cysts fed to adults and nymphs reached the insects' colons within 2 hours.

Leucophaea maderae, Brazil (Pessoa and Correa, 1927): Nymphs only of this species were used. Thirty-four living cysts were found in the feces up to 7 days after feeding.

Periplaneta americana, South Africa (Porter, 1918): See comments following *B. orientalis.* Gold Coast Colony (Macfie, 1922): In two experiments, cysts of *G. intestinalis,* fed in human feces, passed through the cockroaches' intestines apparently unharmed and unchanged. Brazil (Pessoa and Correa, 1927): Live cysts were found in the feces up to 5 days after feeding. Two specimens regurgitated a milky fluid, up to one-half hour after feeding, that contained live cysts. U.S.A. (Young, 1937): See comments under *E. floridana.* Cysts remained in the insects' intestines as long as 12 days, but the viability of these cysts was not tested.

Periplaneta brunnea, U.S.A. (Young, 1937): See comments under *E. floridana* and after Young under *P. americana.*

Cockroaches, Venezuela (Tejera, 1926): A group of 30 cockroaches were fed human feces containing many cysts and mobile forms of *G. intestinalis.* Within 24 hours the feces of 8 of 10 cockroaches contained cysts. Cysts were present in the feces of all insects examined after 48 hours. Of 10 cockroaches killed after 8 days, 2 had mobile *G. intestinalis* in the intestines. Argentina (Bacigalupo *in* Tejera, 1926, p. 256): Cysts of *G. intestinalis* were eliminated by cockroaches in the same form as ingested.

Giardia sp.

Natural vectors.—Cockroaches, Venezuela (Tejera, 1926): Cysts morphologically identical to those of *Giardia* (species not determined) were found in the intestinal contents of 5 percent of the cockroaches captured in latrines.

Class SARCODINA

Order AMOEBINA

Family ENDAMOEBIDAE

Entamoeba histolytica Schaudinn

Synonymy.—Endamoeba histolytica; Entamoeba dysenteriae. (Kudo, 1954, separated *Entamoeba* from *Endamoeba* by nuclear characteristics.)

Disease.—Amoebic dysentery in man.

Natural vectors.—Periplaneta americana and/or *Blattella germanica,* Cairo, Egypt (DeCoursey and Otto, 1956): 9 of 217 cockroaches collected in restaurants contained cysts morphologically resembling *E. histolytica.* Of 44 cockroaches collected in 2 villages, 5 contained this protozoan.

Cockroaches, Venezuela (Tejera, 1926): Cysts resembling those of *E. histolytica* were found in the intestinal contents of cockroaches captured in the sewer of a hospital and in a kitchen near a latrine. Two young cats were fed milk containing feces from some of these cockroaches; both cats in a few days passed feces which contained amoebae of the Schaudinn type.

Cockroaches (presumably including *Blatta orientalis, Blattella germanica, Periplaneta americana, Periplaneta australasiae,* and *Supella supellectilium*). Peru (Schneider and Shields, 1947): One hundred cockroaches were captured and the legs and intestinal contents of each were cultured. No protozoa were found on the legs, but *E. histolytica* was found in 7 percent of the cultures of intestinal tracts.

Experimental vectors.—Blatta orientalis. Italian Somaliland (Mariani and Besta, 1936): Vegetative and precystic forms of *E. histolytica* were found in 33 percent of the cockroaches examined 24 to 48 hours after they had fed on bread inoculated with this organism. A few cystic forms were found in one of the cockroaches after 10 days.

Periplaneta americana, Gold Coast Colony (Macfie, 1922). Cockroaches used in this experiment were carefully examined for amoebic invasions because some of these insects at Accra had been found naturally invaded (whether by *E. histolytica, E. coli,* or both is not clear). Cysts of *E. histolytica* were found in the feces of seven of nine cockroaches fed human feces containing cysts of this organism. The cysts appeared to be unharmed by passage through the insects; they were seen in the feces for only 1 to 3 days. U.S.A. (Frye and Meleney, 1936): The cockroaches were fed on a culture of cysts mixed with rice flour and sugar. Cysts were first found in the feces 16 to 20 hours after the cysts had been eaten. Development of this protozoan was obtained from cysts collected in cockroach feces after 48 hours.

Cockroaches, Venezuela (Tejera, 1926): Nymphal cockroaches were fed feces containing numerous cysts and mobile forms of *E. histolytica.* After 24 hours, the feces of 6 of 20 cockroaches contained cysts. After 48 hours, the feces of 8 of another 20 cockroaches contained cysts. Three days later, 6 cockroaches of another group produced cysts. The cysts were verified as dysenteric amoebae by feeding contaminated cockroach feces to three kittens. A few days latter, the kittens showed unmistakable signs of dysentery and typical dysenteric amoebae were found in their feces.

Class CILIATA

Order SPIROTRICHA

Family BURSARIIDAE

Balantidium coli (Malmsten)

Disease.—Dysentery and diarrhea in man and monkeys.

Experimental vectors.—Cockroaches, Venezuela (Tejera, 1926): 30 cockroaches were fed hog feces containing many *B. coli* cysts. After 24 hours, 4 of 10 cockroaches passed cysts in their feces. After 48 hours, the feces of 8 of 10 cockroaches contained cysts. Typical *B. coli* cysts were found in the intestines of the remaining 10 insects. A monkey (*Cebus capucinus*) was infected with *B. coli* by eating cockroach intestinal contents that contained cysts. Dysentery developed with attendant diarrhea. Numerous *B. coli* were recovered from the contents of the monkey's colon.

APPENDIX E: HELMINTHS

Information on the helminthic diseases was taken from Chandler (1949) and Faust (1955). The classification follows Hyman (1951, 1951a).

Parts I and II contain positive associations of cockroaches with helminths. Part III contains doubtful records, and Part IV contains negative findings.

PART I. PATHOGENIC HELMINTHS WHOSE EGGS HAVE BEEN CARRIED BY COCKROACHES

Phylum PLATYHELMINTHES

Class TREMATODA

Order DIGENEA

Family SCHISTOSOMATIDAE

Schistosoma haematobium (Bilharz, 1852) Weinland, 1858

Common name.—The vesical blood fluke.

Disease.—Vesical schistosomiasis or vesical bilharziasis, endemic hematuria.

Experimental vectors.—Periplaneta americana, Gold Coast Colony (Macfie, 1922): The eggs passed unharmed through the insect and appeared in the feces the following day.

Class CESTODA

Order TAENIOIDEA

Family HYMENOLEPIDIDAE

Hymenolepis sp.

Disease.—Tapeworm infections.

Natural vectors.—Periplaneta americana, Formosa (Morischita and Tsuchimochi, 1926): Eggs of this worm were often found in feces and intestinal contents of cockroaches captured in the animal house of the Government Research Institute.

Polyphaga saussurei, Tadzikhistan (Zmeev, 1936): In two instances, a single egg of *Hymenolepis* sp. was found in the cockroaches' intestines. In one, the egg was deformed while in the other it was undamaged. In the area where these insects were collected, numerous rats (*Nesokia indica*) were commonly infected with *Hymenolepis diminuta.*

Family TAENIIDAE

Taenia saginata Goeze, 1782

Common name.—The beef tapeworm.

Disease.—Beef tapeworm infections.

Experimental vectors.—Periplaneta americana, Gold Coast Colony (Macfie, 1922): The eggs passed unharmed through two of four cockroaches; in one only shrunken eggs were seen, and in the fourth no eggs were found. There were few eggs in the human feces used in these experiments.

Family Unknown

Undetermined tapeworm eggs

Natural vectors.—Polyphaga saussurei, Tadzhikistan (Zmeev, 1936): Eggs similar to cestode eggs (Taenioidea) found in humans were found in the intestine and appeared to be uninjured. Several cestode eggs were found in 2 of 154 cockroaches which had been collected in ruined houses heavily contaminated with feces.

Phylum ASCHELMINTHES

Class NEMATODA

Order OXYUROIDEA

Family OXYURIDAE

Enterobius vermicularis (Linnaeus, 1758) Leach in Baird, 1853

Common name.—Human pinworm or seatworm.

Disease.—Enterobiasis or oxyuriasis.

Natural vectors.—Blatta orientalis, U.S.S.R. (Sondak, 1935): In the 412 cockroaches examined, one egg was isolated from the rectum of a specimen caught in a buffet.

Blattella germanica, U.S.S.R. (Sondak, 1935): In the 788 cockroaches examined, one egg was isolated from the rectum of a specimen caught in a bakery and another in a specimen caught in a factory kitchen.

Order ASCAROIDEA

Family ASCARIDAE

Ascaris lumbricoides Linnaeus, 1758

Common name.—Giant intestinal roundworm.

Disease.—Ascariasis.

Natural vectors.—*Periplaneta americana,* South Africa, Vrededorp (Porter, 1930): One specimen contained ova of *Ascaris lumbricoides* or *Ascaris suum* Goeze, 1782 (=*Ascaris suilla*), which indicates the ingestion of human or pig feces by the cockroach.

Experimental vectors.—*Periplaneta americana,* Gold Coast Colony (Macfie, 1922): The eggs passed unharmed with the feces of the insects for a day or two after feeding. In one experiment, feces passed 4 days after ingestion of the inoculated meal contained eggs which had developed slightly. India, Western Bengal (Chandler, 1926): The cockroaches were fed human feces containing eggs of *Ascaris* (species not mentioned but presumably *lumbricoides*). Small numbers of eggs were recovered in the feces.

Periplaneta americana, Periplaneta australasiae, Neostylopyga (=*Dorylaea*) *rhombifolia,* Formosa (Morischita and Tsuchimochi, 1926): Human feces containing *Ascaris* eggs were fed to these cockroaches; 15 of 32 *P. americana,* 6 *P. australasiae,* and 6 *N. rhombifolia* excreted viable eggs 1 to 4 days (*P. americana*) or 1 or 2 days after the inoculated meal. Eggs in cockroach feces that had remained dry for some hours developed when cultured.

Ascaris sp.

Disease.—Parasite of mammals.

Natural vectors.—*Blatta orientalis,* Somaliland (Mariani and Besta, 1936): 1 of 93 cockroaches examined contained ova of an undetermined species of *Ascaris.*

Order STRONGYLOIDEA

Family ANCYLOSTOMIDAE

Ancylostoma caninum (Ercolani, 1859) Hall, 1913

Disease.—Common hookworm of dogs and cats in temperate climates.

Experimental vectors.—*Periplaneta americana,* Netherlands (Akkerman, 1933): Cockroaches were fed dog feces containing eggs of *A. caninum* and *A. ceylanicum* or banana mixed with eggs of both worms. Five of ten cockroaches fed dog feces and four of eight cockroaches fed eggs in banana passed feces from which one to seven hookworm larvae were cultured. At least seven other cockroaches passed from 3 to 14 viable hookworm eggs within 24 hours after feeding; one of these passed 23 eggs in the feces 3 days after feeding. In conclusion, Akkerman doubted the conception of Chandler (1926) (see *Necator americanus*) concerning the destruction of hookworm eggs in the proventriculus of the cockroach.

Ancylostoma ceylanicum (Looss, 1911) Leiper, 1915

Diease.—Hookworm of dogs and, rarely, in man (Brumpt, 1949).

Experimental vectors.—*Periplaneta americana,* Gold Coast Colony (Macfie, 1922): The eggs passed unharmed through the gut and were recovered in the feces. Netherlands (Akkerman, 1933): See comments under *Ancylostoma caninum.*

Ancylostoma duodenale (Dubini, 1843) Creplin, 1845

Common name.—Old World hookworm.

Disease.—Human hookworm infection of temperate climates in Eastern Hemisphere.

Natural vectors.—*Periplaneta americana,* South Africa (Porter, 1929, 1930): The cockroach acted as a mechanical carrier in the gold mines. Ninety-seven cockroaches were examined from four mines; 8.2 percent of the insects contained viable hookworm eggs and larvae.

Experimental vectors.—*Periplaneta americana,* Gold Coast Colony (Macfie, 1922): The eggs passed unharmed through the gut and appeared in the feces for 1 to 3 days after the inoculative meal. Many eggs in the feces contained living embryos.

Necator americanus (Stiles, 1902) Stiles, 1906

Common name.—Tropical hookworm.

Disease.—Human hookworm infection of warm climates.

Natural vectors.—*Periplaneta americana,* India, western Bengal (Chandler, 1926): The American cockroach ingested the ova of *N. americanus* that were present in human feces in mines. Though a few eggs passed through the gut in a viable condition, most were destroyed in the proventriculus. Chandler concluded that the cockroach played an important role in *controlling* hookworm infection so long as other food was not available and the human stools were not concentrated too much in one area. However, in contrast to this conclusion, see Macfie (1922) below, Porter (1929, 1930) under *An-*

cylostoma duodenale, Akkerman (1933) under *Ancylostoma caninum,* and Morischita and Tsuchimochi (1926) under Hookworms.

Experimental vectors.—Periplaneta americana, Gold Coast Colony (Macfie, 1922): The eggs passed unharmed through the gut. See also comments after Macfie under *Ancylostoma duodenale.*

Hookworms

Disease.—Human hookworm infections.

Experimental vectors.—Periplaneta americana, Periplaneta australasiae, and *Neostylopyga rhombifolia,* Formosa (Morischita and Tsuchimochi, 1926): 9 of 21 *P. americana,* 3 of 7 *P. australasiae,* and 3 of 6 *N. rhombifolia,* when fed with hookworm eggs, excreted viable eggs for 1 to 3 days after feeding. In fresh cockroach feces that were not yet dry, the eggs showed good development and often contained larvae which soon hatched.

Family TRICHOSTRONGYLIDAE

Trichostrongylus sp.

Disease.—Intestinal parasites of birds, ruminants, and man.

Natural vectors.—Blatta orientalis, Somaliland (Mariani and Besta, 1936): 1 of 93 cockroaches examined contained ova of this parasite.

Order TRICHUROIDEA

Family TRICHURIDAE

Capillaria hepatica (Bancroft, 1893) Travassos, 1915

Common name.—The capillary liver worm.

Disease.—Tissue parasite in the liver of domestic and wild mammals and occasionally in man.

Experimental vectors.—Blatta orientalis. According to Giordano (1950), the eggs of *C. hepatica* can pass unchanged through the intestinal tract of the oriental cockroach, and therefore this insect could be a vector. Neveu-Lemaire (1933, 1938) considered *Periplaneta americana* as a probable vector of the eggs of this worm; there is no direct evidence to support this view, as far as we know.

Trichuris trichiura (Linnaeus, 1771) Stiles, 1901

Common name.—Human whipworm.

Disease.—Trichocephaliasis or trichuriasis.

Natural vectors.—Blatta orientalis, Somaliland (Mariani and Besta, 1936): Of 93 cockroaches examined, 4 contained ova of human whipworm. U.S.S.R. (Sondak, 1935): In the 412 cockroaches examined, one egg was isolated from the rectum of a specimen caught in a dining room.

Blattella germanica, U.S.S.R. (Sondak, 1935): In the 788 cockroaches examined, one egg was found in the rectum of a specimen caught in a buffet.

Periplaneta americana, Gold Coast Colony (Macfie, 1922): A single egg, indistinguishable from that of *T. trichiura,* was found in 1 of 30 cockroaches captured in the laboratory, where there was little or no opportunity for the insects to feed on human feces. Formosa (Morischita and Tsuchimochi, 1926): Eggs of this worm were often found in the feces and intestinal contents of cockroaches in the animal house of the Government Research Institute.

Experimental vectors.—Periplaneta americana, Gold Coast Colony (Macfie, 1922): Numerous eggs passed through the gut unharmed and appeared in the feces the next day; some of the eggs had developed slightly. India, western Bengal (Chandler, 1926): After having fed on human feces containing *Trichuris* eggs (species not mentioned but presumably *trichiura*), the cockroaches excreted small numbers of these eggs in their feces.

Periplaneta americana, Periplaneta australasiae, and *Neostylopyga rhombifolia,* Formosa (Morischita and Tsuchimochi, 1926): In feeding experiments, 8 of 11 *P. americana,* all 7 *P. australasiae,* and 4 *N. rhombifolia* passed viable eggs the following day and for 3 days thereafter.

PART II. PATHOGENIC HELMINTHS FOR WHICH COCKROACHES SERVE AS INTERMEDIATE HOSTS

Phylum ACANTHOCEPHALA

Order ARCHIACANTHOCEPHALA

Family OLIGACANTHORHYNCHIDAE

Prosthenorchis elegans (Diesing, 1851) Travassos, 1915

Disease.—Intestinal parasite of the definitive hosts.

Natural intermediate hosts.—Blattella germanica, France (Brumpt and Urbain, 1938, 1938a; Brumpt et al., 1939): 40 percent of *B. germanica* in the monkey house of the Museum of Natural History of Paris were infected with larvae of *P. elegans* and *P. spirula* (Brumpt and Urbain, 1938, 1938a). A similar heavy infestation was found in cockroaches in the menagerie of the Jardin des Plantes, where many parasitized lemurs and monkeys died. The epizootics were stopped only by exterminating the cockroaches (Brumpt and Urbain, 1938a; Brumpt et al., 1939).

Experimental intermediate hosts.—The following were apparently infected with both *P. elegans* and *P. spirula: Blaberus fuscus* and *Leucophaea maderae,* Netherlands (Brumpt and Desportes, 1938): Both species successfully infected.

Blatta orientalis and *Periplaneta americana,* Netherlands (Brumpt and Desportes, 1938): The worms did not develop in either species of cockroach.

Natural definitive hosts.—Monkeys (*Callithrix chrysolevea, Saimiri sciurea, Midas rosalia, Mystax rosalia, Mystax ursulus,* and *Oedipomidas aedipus*) (Brumpt and Urbain, 1938). Lemurs (*Lemur fulvus, L. fulvus albifrons, L. mongos, L. macao,* and *L. catta*), *Cebus apella,* and *Cheirogaleus major* (Brumpt et al., 1939).

Experimental definitive hosts.—The following were infected by feeding on *B. germanica* that contained larvae of both *P. elegans* and *P. spirula:* Baboon (*Papio papio*), cat, hedgehog (*Erinaceus europaeus*), macaque (*Macacus rhesus*), fox (*Vulpes vulpes*), and badger (*Meles meles*) (Brumpt and Urbain, 1938, 1938a).

Prosthenorchis spirula (Olfers in Rudolphi, 1819) Travassos, 1917

Disease.—Intestinal parasite of the definitive hosts.

Natural intermediate hosts.—*Blattella germanica,* France (Brumpt and Urbain, 1938, 1938a; Brumpt et al., 1939): See comments following these citations under *Prosthenorchis elegans.* Netherlands (van Thiel and Wiegand Bruss, 1946, 1948): 5 of 11 cockroaches were naturally infected in a monkey house.

Experimental intermediate hosts.—*Blattella germanica,* Netherlands (van Thiel and Wiegand Bruss, 1946, 1948): 13 of 17 insects were infected with from 1 to 3 or 6 to 12 larvae in different stages of development.

Periplaneta americana, Netherlands (van Thiel and Wiegand Bruss, 1946, 1948): The parasite did not develop in any of the 45 cockroaches of this species that were fed infective meals.

See also species experimentally infected with *Prosthenorchis elegans.*

Natural definitive hosts.—Monkeys (*Midas rosalia, Cebus apella, Callithrix jacchus*), coati (*Nasua narica*), lemurs (*Perodicticus potto, Lemur coronatus, Lemur fulvus*), and *Inuus sylvanus* (Brumpt and Urbain, 1938). Chimpanzee (van Thiel and Wiegand Bruss, 1946).

Experimental definitive hosts.—See under *Prosthenorchis elegans.*

Family MONILIFORMIDAE

Moniliformis moniliformis (Bremser in Rudolphi, 1819) Travassos, 1915, and/or Moniliformis dubius Meyer, 1932

Synonymy.—The nomenclature of the *Moniliformis* found in man is confusing. According to Chandler (1949), the only species found in man is *M. dubius.* Faust (1955) stated that the only species found in man is *M. moniliformis.* Both were apparently referring to the same organism. Meyer (1932) made *Gigantorhynchus moniliformis, in* Magalhães (1898), and *Moniliformis moniliformis* Bremser, *in* Travassos (1917), synonyms of *Moniliformis travassosi* Meyer, 1932. Chandler (1941) made *Moniliformis travassosi* Meyer, 1932, *Moniliformis* sp. of Chandler (1921), and *Moniliformis* sp. of Southwell (1922) synonyms of *Moniliformis dubius.* Hyman (1951a) stated that *M. moniliformis* is a variable form inhabiting many small mammals and that *M. dubius* is cosmopolitan in rats. According to Chandler (1949), the form of *Moniliformis* found in wild rodents in Europe is not identical with that found in rats in the United States and South America. The reader is referred to Van Cleave (1946) for a discussion of this problem.

Disease.—The worm is a cosmopolitan parasite in the small intestine of rodents; it occasionally infects man.

Natural intermediate hosts.—The following records apparently refer to *M. dubius:*

Periplaneta americana, Brazil (Magalhães, 1898): Only 3 to 4 percent of the insects examined were infected; one cockroach contained five encapsulated larvae in an advanced state of development. Brazil (Travassos, 1917): Larvae found in body cavity. Gold Coast Colony (Southwell, 1922): 30 cysts of the worm were collected from two cockroaches. India (Pujatti, 1950): 18 percent of 78 cockroaches contained acanthellas. U.S.A., Texas (Burlingame and Chandler, 1941; Moore, 1946): Naturally infected cockroaches were collected in the Houston Zoological Garden. These cockroaches were between 80 and 90 percent infected (Moore, 1946).

Periplaneta australasiae, India (Pujatti, 1950): 8 percent of 86 cockroaches were infected. (Pujatti did not find the parasite in 152 specimens of *Blattella germanica.*)

The following records apparently pertain to *M. moniliformis:*

Periplaneta americana, Argentina (Bacigalupo, 1927, 1927a, 1928): In these records, 8 percent of 38 cockroaches and 10 percent of 78 cockroaches were infected. Brazil (Pessoa and Correa, 1929): 1½ to 2 percent of the cockroaches examined were infected. Algiers (Seurat, 1912): From 1 to 30 worm larvae were found free in the abdomens of the cockroaches. Burma, Rangoon (Subramanian, 1927): Innumerable larvae were encysted in the body cavity. South Africa (Porter, 1930): The larvae were found in one cockroach. Madras (Sita, 1949).

Experimental intermediate hosts.—The following records apparently pertain to *M. moniliformis:*

Blaberus fuscus, Netherlands (Brumpt and Urbain, 1938a): This species was refractory to infestation. Brumpt (1949) apparently refers this record to *Blaberus atropos.*

Blatta orientalis and *Leucophaea maderae,* France (Brumpt and Urbain, 1938a): These cockroaches were easily infected. Argentina (Bacigalupo, 1928): Bacigalupo could not get the parasite to develop in *B. orientalis.*

Blattella germanica, France (Brumpt and Urbain, 1938a). Argentina (Bacigalupo, 1928): Bacigalupo could not get the parasite to develop in this host.

Periplaneta americana, Japan (Yamaguti and Miyata, 1942). France (Brumpt, 1949). Madras (Sita, 1949).

The following records apparently pertain to *M. dubius:*

Blattella germanica, Japan (Yamaguti and Miyata, 1942).

Periplaneta americana, Japan (Yamaguti and Miyata, 1942). U.S.A. (Chandler, 1941; Moore, 1946).

Development in intermediate host.—The eggs, when ingested by *P. americana,* hatched in the midgut within 24 to 48 hours. The larvae which were at first free in the lumen of the gut passed through the gut wall in the course of 10 to 12 days and dropped into the hemocoele or became embedded in fat tissue. The infective acanthella appeared about 7 to 8 weeks after infection. The encysted larvae remain dormant in the body cavity of the cockroach until it is eaten by a definitive host. (Moore, 1946.) Chandler (1949) found over 100 cystacanths of *M. dubius* in the body cavity of *P. americana.*

Natural definitive hosts.—Rodents such as rat, mouse, hamster, hedgehog, and squirrel; the parasite is sometimes found in man. (Burlingame and Chandler, 1941.)

Experimental definitive host.—Cotton rat (*Sigmodon hispidus*) (Moore, 1946).

Development in definitive host.—The cyst which contains the larva dissolves in the host's stomach. The freed larvae pass into the small intestine and attach themselves to the intestinal wall. (Burlingame and Chandler, 1941; Moore, 1946.)

Moniliformis kalahariensis Meyer, 1931

Disease.—Intestinal parasite of the definitive host.

Natural intermediate hosts.—Blattella germanica, India, Bombay (Meyer, 1931, 1932).

Definitive hosts.—Hedgehog (*Erinaceus frontalis*); bird (*Pterocles namaqua*), Africa (Meyer, 1931, 1932).

Phylum ASCHELMINTHES

Class NEMATODA

Order OXYURОIDEA

Family SUBULURIDAE

Subulura jacchi (Diesing, 1861) Railliet and Henry, 1914

Disease.—Intestinal parasite of primates.

Experimental intermediate hosts.—Blaberus fuscus (Thunberg) [sic], France (Chabaud and Larivière, 1955): Both encapsulated larvae and larvae free in the body cavity were found in the same cockroach. The free larvae grew more rapidly. At 25°C. infective larvae appeared in about 12 days. The infective third-stage larvae underwent a contraction that rendered them almost spherical. Attempts to infect *Periplaneta americana* were negative.

Definitive hosts.—Wistiti, *Hapale jacchus* (L.), in captivity. Other South American primates.

Order SPIRUROIDEA

Family THELAZIIDAE

Oxyspirura mansoni (Cobbold, 1879) Ransom, 1904

Synonymy.—Oxyspirura parvovum Sweet, 1910, the Australian eyeworm of poultry, may be the same as *O. mansoni,* as there is some question as to the validity of *O. parvovum* (Tryon, 1926).

Disease.—Eyeworm infection in poultry.

Common name.—Manson's eyeworm of poultry; chicken eyeworm, tropical eyeworm.

Natural intermediate hosts.—Pycnoscelus (=*Leucophaea*) *surinamensis,* Australia (Fielding, 1926, 1927, 1928, 1928a). U.S.A., Florida (Sanders, 1927, 1928, 1929; Shealy, 1927). Formosa (Kobayashi, 1927). Antigua (Hutson, 1938, 1943). Hawaii (Illingworth, 1931; Schwabe, 1950, 1950a, 1950b, 1951). The Japanese quail (*Coturnix coturnix japonica*) is commonly infected with eyeworms, but *Pycnoscelus* was not found to be a food for this bird in Hawaii;

either the bird eats this cockroach, or there is another unknown host for the eyeworm (Schwartz and Schwartz, 1949).

Experimental intermediate hosts.—*Periplaneta americana,* Antigua (Hutson, 1943): The eyeworms developed to the infective stage in *P. americana* when injected into the body cavity. However, these cockroaches could not be infected by eating fowl feces because the feces were toxic and killed all cockroaches tested within 2 weeks. The American cockroach undoubtedly is not a vector of the eyeworm in nature for this reason.

Pycnoscelus surinamensis, U.S.A., Florida (Sanders, 1929): The cockroaches became infected with the eyeworm after having had access for 72 hours to the freshly voided feces of a chicken severely infested with the eyeworm. Australia (Fielding, 1927, 1928a). Hawaii (Schwabe, 1951).

Development in intermediate host.—*Pycnoscelus* becomes infected by eating bird feces containing embryonated eggs or first-stage larvae of the eyeworm. First-stage larvae migrate through the wall of the midgut into the hemocoele where they burrow into the fat body. Second-stage larvae encyst on the alimentary tract, particularly around the rectum and entangled in the malpighian tubules. The tracheated cyst wall is secreted by the cockroach; the cyst is filled with fluid and the enclosed larva is able to move about in it. The encysted larva molts again between the forty-fifth and fiftieth days. During the period of ecdysis, most of the parasites free themselves from the cysts and wander in the body cavity of the host. The complete developmental period requires about 51 days, and the third-stage larvae are infective to birds. (Schwabe, 1951.)

The eyeworm may remain alive for some time in dead cockroaches (Sanders, 1928), and may live up to 72 hours in cockroaches killed by insecticides (Schwabe, 1950b); Schwabe (1950) emphasized the importance of preventing birds from eating dead cockroaches.

Effect of worm on intermediate host.—Sanders (1929) believed that penetration of the intestine by large numbers of migrating larvae at one time is sufficient to kill the insect in some cases.

Natural definitive hosts.—Chicken, turkey, peafowl (*Pavo cristatus*), English sparrow (*Passer domesticus*), mynah bird (*Acridotheris tristis*), Chinese dove (*Streptopelia chinensis*), Japanese quail (*Coturnix coturnix japonica*), pheasant (*Phasianus torquatus torquatus* and *P. vesicolor vesicolor*), Argus pheasant (*Argusianus argus argus*), and Siamese fireback pheasant (*Diardigallus diardi*) (Schwabe, 1951). Ducks (Fielding, 1926).

Infected wild birds are not important reservoir hosts in dissemination of the eyeworm because their feces are too scattered to be eaten to any great extent by vector cockroaches (Schwabe, 1951).

Experimental definitive hosts.—In Florida the following wild birds were experimentally infected: Blackbird (*Agelaius phoeniceus phoeniceus*), bobolink (*Dolichonyx oryzivorus*), loggerhead shrike (*Lanius ludovicianus ludovicianus*), Florida jay (*Aphelecoma cyanea*), and the pigeon (Sanders, 1928, 1929).

The eyeworms will develop to maturity in the eyes of guinea pigs (Fielding, 1927) and white rats (Schwabe, 1951); but when placed in the mouths of these rodents, the larvae were unable to reach the eyes.

Development in the definitive host.—Host birds eat the cockroach containing infective third-stage larvae. The larvae (pl. 6) leave the cockroach host in the bird's crop and migrate up the esophagus to the roof of the mouth, then through the nasolacrimal ducts into the eyes. Infestation of the eyes of chickens has been produced within 20 minutes after they had eaten infected cockroaches (Sanders, 1928, 1929). Larvae placed in the mouths of 4-week-old chicks were observed to enter the eyes several minutes later (Schwabe, 1951). The worms molt within a few days to fourth-stage larvae, and after about 3 weeks they molt into adult worms. The sexually mature worms are found beneath the nictitating membranes, in the conjunctival sacs, and nasolacrimal ducts of the bird. The adult females begin to lay eggs in the host's eyes about 11 days after becoming mature. The eggs are washed down the nasolacrimal ducts with the eye fluid into the mouth, swallowed, and passed out with the feces. (Schwabe, 1951.)

Illingworth (1931) found as many as 205 worms in the eyes of a single chick, and Schwabe (1950a) states that the approximate maximum number of worms found in the eyes of a single bird is 200.

Effect of worm on definitive host.—In heavy infestations (60 worms per eye), the eye shows signs of irritation; there is continuous winking and the bird rubs its head on its wing feathers. Other symptoms include lacrimation, nasal discharge, white corneal opacity, and inflammation of the nictitating membrane. The bird may scratch its eye with its foot, lacerating the outer surface of the eyelids, and finally become blind. Less marked disturbances occur in mild infestations. (Sanders, 1929.)

Blindness and advanced pathologic changes found in the eyes of heavily infected birds are possibly the result of secondary viral or bacterial infections which may be further complicated by the death and decomposition of the worms in the eyes (Schwabe, 1950a).

Distribution.—China, Mauritius, Brazil, Hawaii, Jamaica, Florida

(Sanders, 1929). Australia, Indo-China, Guam, Rabaul, Reunion (Fielding, 1928). British West Indies (Hutson, 1938, 1943). Formosa (Kobayashi, 1927). Samoa (Alicata *in* Schwabe, 1951). The geographical distribution of *O. mansoni* closely agrees with the distribution of its intermediate host, *P. surinamensis* (Fielding, 1928; Sanders, 1929; Schwabe, 1951).

It is interesting that Ransom (1904), over 20 years before the intermediate host was independently discovered by Fielding (1926), Sanders (1927), and Kobayashi (1927), observed that the eyeworm had been reported only from localities on or near the seacoast. He predicted that this restricted distribution indicated ". . . that certain conditions, peculiar to the seashore but yet unknown, are necessary to enable the parasite to complete the cycle of its development." The distribution of the intermediate host is circumtropical on islands or in coastal countries (Schwabe, 1949), thus effectively limiting the spread of the parasite to the localities noted by Ransom.

Family SPIRURIDAE

Agamospirura parahormeticae Pessoa and Correa, 1929

Disease.—Pessoa and Correa (1929) were unable to obtain development of encysted larvae that were fed to white rats. They suggested that the worm may be parasitic in birds.

Natural intermediate hosts.—*Parahormetica bilobata* Saussure, Brazil, São Paulo (Pessoa and Correa, 1929): Encysted larvae were found in the visceral cavity.

Definitive host.—Unknown.

Gongylonema ingluvicola Ransom, 1904

Disease.—Parasite in esophagus of birds.

Experimental intermediate hosts.—*Blattella germanica,* U.S.A. (Cram, 1935): Larvae of the parasite encysted in the cockroach's body cavity.

Definitive host.—Mountain quail (*Oreortyx picta*).

Gongylonema neoplasticum (Fibiger and Ditlevsen, 1914) Ransom and Hall, 1916

Synonymy.—*Spiroptera* sp. Fibiger, 1913; *Spiroptera neoplastica* Fibiger and Ditlevsen, 1914; *Spiroptera* (*Gongylonema*) *neoplastica* Fibiger and Ditlevsen, 1914 (Hall, 1916). *Gongylonema orientale* Yokagawa (Brumpt, 1949).

Disease.—Parasites in the walls of the esophagus, tongue, and forestomach of the definitive hosts.

Natural intermediate hosts.—Blatta orientalis, Netherlands, Amsterdam (Baylis, 1925): About one in seven cockroaches (*Periplaneta americana* and *B. orientalis*) contained larvae.

Blattella germanica, U.S.A., Minnesota (Hitchcock and Bell, 1952).

Periplaneta americana, Denmark and Saint Croix (Fibiger, 1913, 1913a; Fibiger and Ditlevsen, 1914). Netherlands, Amsterdam (Baylis, 1925). About one in seven cockroaches (*P. americana* and *Blatta orientalis*) was found to contain the parasite larvae. Surinam (Baylis, 1925). Argentina (Bacigalupo, 1930). England (Leiper, 1926). South Africa (Porter, 1930). U.S.A., Minnesota (Hitchcock and Bell, 1952): Several hundred cockroaches (*P. americana* and *Blattella germanica*) were caught at a rendering plant; 90 percent of these contained encysted larvae. Formosa (Yokagawa, 1924, 1925, 1925a): Cockroaches (*P. americana* and *P. australasiae*) in the vicinity of Taihoku were about 30 percent parasitized.

Periplaneta australasiae, Formosa (Yokagawa, 1924, 1925, 1925a).

Experimental intermediate hosts.—Blattella germanica, Denmark (Fibiger and Ditlevsen, 1914). U.S.A., Minnesota (Hitchcock and Bell, 1952). France (Brumpt, 1949).

Blatta orientalis, Denmark (Fibiger and Ditlevsen, 1914).

Periplaneta americana, Denmark and St. Croix (Fibiger, 1913; Fibiger and Ditlevsen, 1914). U.S.A., Minnesota (Hitchcock and Bell, 1952).

Development in intermediate host.—The cockroach becomes infected by feeding on rat feces containing embryonated eggs (pl. 7, right) of the worm. The hatched larvae migrate through the digestive tract and encyst in the muscles of the thorax and legs. The infected cockroaches are then capable of infecting rats (Fibiger and Ditlevsen, 1914).

Definitive hosts.—Wild rats (*Rattus norvegicus* and *Rattus rattus*), and in laboratory rats, white mice, rabbits, and guinea pigs (Fibiger and Ditlevsen, 1914).

Development in definitive host.—The rat becomes infected by eating cockroaches containing encysted nematode larvae (pl. 7, left). The nematode larvae leave the cyst and enter the squamous-celled epithelium of the fundus of the stomach and also the epithelium of the esophagus, tongue, and mouth. After about 2 months, the female worms lay eggs which are voided with the rat feces (Fibiger and Ditlevsen, 1914).

Gongylonema pulchrum Molin, 1857

Common name.—Gullet worm.

Synonymy.—*Gongylonema scutatum* (Müller, 1869) Railliet, 1892 (Baylis et al., 1926; Lucker, 1932; Alicata, 1937; Brumpt, 1949). *Gongylonema hominis* Stiles, 1921 (Faust, 1939; Chandler, 1949). The taxonomic status of the *Gongylonema* species obtained from various definitive hosts is uncertain because authors disagree as to the characters used for species determination (Faust, 1939).

Disease.—Parasite of esophagus and mouth cavity of vertebrate hosts including man.

Experimental intermediate hosts.—*Blattella germanica,* U.S.A. (Ransom and Hall, 1915, 1916, 1917; Stiles and Baker, 1927; Schwartz and Lucker, 1931; Lucker, 1932; Alicata, 1934a, 1935). Europe (Baylis et al., 1925, 1926, 1926a; Sambon, 1926).

Parcoblatta sp. (Alicata, 1934, 1935).

Attempts to infect *Blatta orientalis* were negative (Sambon, 1926; Baylis et al., 1925).

Development in intermediate host.—Eggs eaten by *B. germanica* hatched within 24 hours and the larvae developed to the infective third stage in about 32 days. The third-stage larvae encysted in the muscles of the cockroach (Alicata, 1935). The infective larvae of the *Gongylonema* of ruminants can emerge spontaneously from the cockroach if the insect is killed and placed in water. The larvae are capable of living for 4 to 11 days in water and are a possible source of infection for the definitive host. If an infected cockroach drowns in shallow water, the worms will be liberated as the insect begins to decompose. Although the worms sink to the bottom, in shallow water they may be ingested by humans or other animals while drinking. (Baylis et al., 1926a.)

Natural and experimental definitive hosts.—White rat, rabbit, rats, swine, sheep, goat, ox, camel, fallow deer, buffalo, zebu, chevrotain, guinea pig, wild boar, horse, donkey, macaque, *Ateles* sp., *Pithecus entellus,* man; some human records in Ward (1916), Stiles (Anonymous, 1921), Sambon (1925), and Chandler (1949). Records of the occurrence of this parasite in man are reviewed by Waite and Gorrie (1935) and Johnston (1936).

Development in definitive host.—Cockroaches containing infective larvae are eaten by the primary host. In the guinea pig, the third-stage larvae penetrate the tissue at the junction of the stomach and esophagus; the larvae usually enter the esophageal wall where they migrate under the linings of the esophagus and the oral cavity. (Alicata, 1935.)

Distribution.—Africa, Asia, Australia, Europe, United States (Alicata, 1935).

Gongylonema sp. (?)

Synonymy.—The larvae found by Magalhães (1900) to be similar to *Filaria rytipleurites* probably belong here (Seurat, 1916).

Disease.—Parasites of esophagus and mouth cavity of vertebrates including man.

Natural intermediate hosts.—*Periplaneta americana,* Brazil (Magalhães, 1900): Encysted larvae of the parasite were found in the insect's body cavity.

Microtetrameres helix Cram, 1927

Disease.—Stomach parasite of birds.

Experimental intermediate hosts.—*Blattella germanica,* U.S.A. (Cram, 1934).

Development in intermediate host.—Eggs fed to the cockroaches developed to third-stage larvae in 26 to 68 days.

Definitive hosts.—Crow, pigeon.

Protospirura bonnei Ortlepp, 1924

Disease.—Parasite of rats.

Natural intermediate hosts.—*Leucophaea maderae,* Venezuela, Caracas (Brumpt, 1931): The larval nematode is sometimes very abundant in this cockroach.

Experimental intermediate hosts.—*Blatta orientalis, Blattella germanica,* and *Leucophaea maderae* (nymphs), France, Paris (Brumpt, 1931).

The parasite does not seem to develop in *Blaberus giganteus, Periplaneta americana,* and *P. australasiae* (Brumpt, 1931).

Definitive host.—Norway rat (*Rattus norvegicus*).

Effect of worm on definitive host.—The worm apparently does not alter the histology of the stomach mucosa of the rat which does not seem to show any clinical signs of infection.

Protospirura columbiana Cram, 1926

Disease.—Parasite of esophagus, stomach, and upper intestine of rats.

Experimental intermediate host.—*Blattella germanica,* U.S.A. (Cram, 1926).

Definitive host.—Norway rat (*Rattus norvegicus*).

Protospirura muricola Gedoelst, 1916

Disease.—Stomach parasite of rats and primates.

Natural intermediate hosts.—*Leucophaea maderae,* Panama (Foster and Johnson, 1938, 1939): 96 percent of 135 cockroaches were infected. Only cockroaches caught in the vicinity of the monkey cages contained spiruroid larvae; cockroaches caught elsewhere were not infected. Five other species of cockroaches that were examined were not infected.

Development in intermediate host.—The cockroaches acquired the parasite by ingesting eggs in the feces of the definitive host. Infective larvae were found in discoidal cysts mainly in the thorax, around the crop, and at the bases of the large muscles of the first pair of legs. An average of over 100 cysts per dissection per day's catch was not unusual.

Definitive hosts.—Rats are the normal hosts for this nematode, but the worm apparently can adapt to the following primate hosts: White-faced monkey (*Cebus capucinus*), Darien black spider monkey (*Ateles dariensis* Goldman), and Canal Zone night monkey (*Aotus zonalis* Goldman).

Development in definitive host.—The monkeys become infected by eating Madeira cockroaches that contain encysted larvae. The worms live in the esophagus and stomach and cause injury by obstruction, tissue invasion, and secondary infection. Infections may be fatal, particularly to white-face monkeys; 20 deaths of experimental monkeys have been ascribed to protospiruriasis.

Seurocyrnea colini (Cram, 1927) Cram, 1931

Synonymy.—*Cyrnea colini* Cram, 1927.

Disease.—Parasite in proventriculus of birds.

Experimental intermediate hosts.—*Blattella germanica,* U.S.A. (Cram, 1931, 1931a, 1933a). It is possible that cockroaches found in fields and woods serve as normal hosts (Cram, 1931, 1931a).

Development in intermediate host.—The eggs ingested by the cockroach hatch and the larvae leave the digestive tract and develop in the body cavity. The larvae do not appear to encyst but develop to the third stage in the tissues and apparently mature after 18 days in the insect.

Definitive hosts.—Bobwhite quail (*Colinus virginianus virginianus* and *Colinus virginianus texanus*), turkey, prairie chicken (*Tympanuchus americanus americanus*), sharp-tailed grouse (*Pedioecetes phasianellus compestris*). (Cram, 1931.)

Spirura gastrophila (Müller, 1894) Seurat, 1913

Synonymy.—Filaria rytipleurites Deslongchamps, 1824; *F. rytipleurites* as used also by Galeb (1878); *Spirura talpae* as used by Seurat (1911); and *Spiroptera sanguinolenta* as used by Grassi (1888) and Roger (1906, 1907) (Seurat, 1911, 1916). See discussion under *Spirocerca sanguinolenta,* p. 109.

Disease.—Parasite in alimentary canal of vertebrate animals.

Natural intermediate hosts.—Blatta orientalis, Europe (?) (Deslongchamps, 1824, *in* Seurat, 1911): The larval worm was found encysted in the abdomen of the insect. Italy (Grassi, 1888). Algeria (Seurat, 1911, 1916): 4 of 17 cockroaches harbored fourth-stage larvae of this parasite; there were 15 cysts in one insect.

Periplaneta americana, Brazil (Pessoa and Correa, 1929): Four cysts were found in one cockroach and one cyst in another.

Experimental intermediate hosts.—Blatta orientalis, France (Galeb, 1878): The cockroaches fed on feces from infected rats; embryos of the nematode hatched in the digestive tract of the insect, pierced the intestinal wall, and became encysted in the fat body. Infected cockroaches were fed to white rats; nematodes were recovered in the rat after 8 days.

Cockroaches ("cafards"), Algeria (Roger, 1906, 1907): Cysts were obtained from the abdominal cavities after the cockroaches had ingested the parasites. Roger did not complete the experiment by feeding the infected cockroaches to dogs.

Definitive hosts.—Hedgehog (*Erinaceus algirus* Duv.), fox, lizard, chameleon (Seurat, 1916). Dog, cat, mongoose (Hall, 1929).

Tetrameres americana Cram, 1927

Disease.—Parasite in proventriculus of poultry.

Natural intermediate hosts.—Blattella germanica, U.S.A. (Cram, 1931b; Dr. Eloise B. Cram, p. c.): Control chickens in experiments with this worm became infested with immature, therefore recently acquired, nematodes. As *B. germanica* was the only arthropod in evidence, it was presumed to be the vector. Hawaii (Alicata, 1938, 1947).

Experimental intermediate hosts.—Blattella germanica, U.S.A. (Cram, 1931b): Eggs of the nematode developed in the cockroach to third-stage larvae and were recovered in 40 days. Attempts to infect *Periplaneta australasiae* were unsuccessful (Cram, 1937).

Natural definitive hosts.—Chicken, bobwhite quail (*Colinus virginianus*) (Cram, 1931a).

Experimental definitive hosts.—Duckling of domestic duck, ruffed grouse (*Bonasa umbellus*), pigeon (Cram, 1931a).

Tetrameres pattersoni Cram, 1933

Disease.—Parasite in glandular stomach of bobwhite quail.

Experimental intermediate hosts.—*Blattella germanica,* U.S.A. (Cram, 1933): Third-stage larvae had encysted in the muscles of the legs and head and in the body cavity within 24 days after an infective meal.

Definitive host.—Bobwhite quail (*Colinus virginianus*).

Family PHYSALOPTERIDAE

Physaloptera hispida Schell, 1950

Disease.—Stomach parasite in the definitive hosts; it causes chronic ulcers.

Experimental intermediate hosts.—*Blattella germanica,* U.S.A. (Schell, 1952, 1952a). Attempts to infect *Periplaneta americana, Periplaneta australasiae,* and *Parcoblatta pensylvanica* failed (Schell, 1952).

Development in intermediate host.—Eggs ingested by the cockroach hatch in the midgut and the larvae pass on to the colon where they penetrate the peritrophic membrane and invade the epithelium. The invaded epithelial cells are destroyed. The larva undergoes two molts and encysts within the tissues of the colon or rectum. The infective stage was reached in 30 to 35 days, and the larva was infective for the definitive host even after 4-months' encystment in the cockroach. (Schell, 1952, 1952a.)

Natural definitive hosts.—Cotton rat (*Sigmodon hispidus littoralis* Chapman).

Experimental definitive hosts.—Norway rat (*Rattus norvegicus*) and albino rat (Schell, 1952).

Development in definitive host.—Infective larvae which were fed to cotton rats grew rapidly and developed in the pyloric region of the stomach. The worms reached sexual maturity within 73 to 90 days, after which embryonated eggs were detected in the rats' feces. The parasites caused formation of chronic ulcers although infected animals exhibited no noticeable external symptoms. (Schell, 1952.)

Physaloptera maxillaris Molin, 1860

Disease.—Parasite in alimentary tract.

Experimental intermediate hosts.—*Blattella germanica,* U.S.A. (Hobmaier, 1941).

Development in intermediate host.—Eggs eaten by cockroaches reached the infective larval stage in 4 to 6 weeks.

Definitive hosts.—Skunk, badger, mink, raccoon (Schell, 1952).

Physaloptera praeputialis v. Linstow, 1889

Disease.—Parasite in alimentary tract of definitive host.

Experimental intermediate hosts.—*Blattella germanica,* U.S.A. (Petri and Ameel, 1950).

Definitive hosts.—Various species of *Felis, Canis, Lynx, Urocyon, Vulpes,* and *Genetta* (Mildred A. Doss, p. c.).

Physaloptera rara Hall and Wigdor, 1918

Disease.—Parasite in alimentary tract of definitive hosts.

Experimental intermediate hosts.—*Blattella germanica,* U.S.A., Kansas (Petri and Ameel, 1950; Petri, 1950): Petri suggests that wood roaches might be intermediate hosts in nature.

Development in intermediate host.—Eggs ingested by the cockroach developed to encysted third-stage larvae, attached to the hind gut, primarily the rectum. The larvae migrated to the outside layers of the gut but did not pass into the hemocoele.

Definitive hosts.—Cat, dog, coyote.

Physaloptera turgida Rudolphi, 1819

Disease.—Parasite in alimentary tract of definitive host.

Experimental intermediate hosts.—*Blattella germanica,* U.S.A. (Alicata, 1937; Schell, 1952).

Development in intermediate host.—First- and second-stage larvae are encysted in the tissue surrounding the body cavity (Alicata, 1937). Schell (1952), however, stated that the larva did not penetrate the digestive tract of the cockroach and never entered the hemocoele.

Definitive host.—Opossum (*Didelphis virginiana*) (Alicata, 1937).

PART III. DOUBTFUL RECORDS OF THE TRANSMISSION OF HELMINTHS BY COCKROACHES

Hymenolepis diminuta (Rudolphi, 1819) Blanchard, 1891

Stiles and Hassall (1926) and Tubangui (1931) cite *Blatta orientalis* and *Blattella germanica* as intermediate hosts for this rat tapeworm which is not uncommon in man. Faust (1939), Blakiston's new Gould medical dictionary (Jones et al., 1949), and Giordano (1950) list *Periplaneta americana* as well as the above two species of cockroaches as intermediate hosts of this tapeworm. Faust (1955) states that cockroaches, among other insects, may serve as the intermediate hosts and cites Oldham (1931) as the source of this information. However, Oldham (1931) pointed out the lack of experimental evidence for claims that cockroaches serve as host for this cestode. Joyeux (1920) and Riley and Johannsen (1938), using *B. orientalis* and *B. germanica,* and Chandler (1922), using *B. germanica* and *P. americana,* could not infect these cockroaches with *H. diminuta.* Zmeev (1936) in Tadzikhistan found two specimens of *Polyphaga saussurei,* each of which contained an egg of *Hymenolepis* sp.; these insects were found where there were numerous rats that were infected with *Hymenolepis diminuta.*

Inermicapsifer madagascariensis (Davaine in Grenet, 1870) Baer, 1956

Synonymy.—Raillietina madagascariensis. Davainea madagascariensis.

Blanchard (1899, footnote p. 214) stated that it seemed to him that cockroaches (*Periplaneta americana* and *Blatta orientalis*) could be looked upon with suspicion as vectors of this cestode. The following statements probably trace back to Blanchard. Wellman (1910) stated that the tapeworm *Davainea* was thought to be disseminated by cockroaches. Castellani and Chalmers (1919) suggested that the cysticercus may be found in *Blatta orientalis* or *Periplaneta americana.* Fox (1925), Faust (1939), and Mackie et al. (1945) stated that species of *Periplaneta* are believed to be intermediate hosts of this tapeworm. However, we have been unable to locate direct evidence that supports these suggestions. Joyeux and Baer (1936), Chandler (1949), Faust (1955), and Baer (1956) did not mention cockroaches as possible intermediate hosts for this cestode.

Spirocerca sanguinolenta (Rudolphi, 1819) Seurat, 1913

Synonymy.—Spiroptera sanguinolenta Rudolphi, 1819.

Grassi (1888) believed that he showed that *Blatta orientalis* served in Sicily as the intermediate host of this spiruroid parasite of dogs. (See also Railliet, 1889; Nuttall, 1899; Roger, 1906, 1907.) However, Faust (1928), working in China, could not infect *B. orientalis, Periplanta americana,* or *Periplaneta australasiae* by feeding them the eggs of this nematode, and he found a dung beetle to be the insect host. Dung beetles are listed as intermediate hosts of *S. sanguinolenta* by Chandler (1949). Faust believed that Grassi was probably dealing with another spiruroid parasite of which the dog is an abnormal host. This conclusion probably applies equally well to the work of Roger

(1906, 1907). See also Seurat (1911, 1916) and the section on *Spirura gastrophila,* p. 106.

Gordius aquaticus Linnaeus, 1758

Leidy (1879) identified a 9-inch-long nematode found in a cockroach (*Blatta orientalis*?) as probably being *Gordius aquaticus.* Stiles and Hassel (1894) list *Blatta* sp. as a host for this worm. Ransom (*in* Pierce, 1921) stated that *G. aquaticus* may be an accidental parasite of man. However, the Gordiaceae, or horsehair worms, live as parasites in *insects* until almost mature and emerge from the insects to become free-living adults, reproducing in water or soil (Chandler, 1949). Although this worm may accidentally be swallowed with drinking water, it should not be considered a parasite of man.

PART IV. NEGATIVE FINDINGS

The helminths listed below are only those for which cockroaches have been shown experimentally not to be intermediate hosts. Negative findings with helminths for which other cockroaches have been shown to be intermediate hosts are cited above.

Cockroaches were unsuitable intermediate hosts for the following cestodes, or were found uninfected in nature:

Diphyllobothrium latum (Linnaeus, 1758) Lühe, 1910

Definitive host.—Fish.

Cockroach.—Blattella germanica. Degenerated eggs of the tapeworm were isolated from the insect's rectum (Sondak, 1935).

Hymenolepis exigua Yoshida, 1908

Definitive host.—Poultry.

Cockroach.—Pycnoscelus surinamensis. Ten cockroaches collected in a poultry yard were dissected and examined for cysticercoid stages (Alicata and Chang, 1939).

Hymenolepis nana (v. Siebold, 1852) Blanchard, 1891

Definitive host.—Man.

Cockroaches.—Neostylopyga rhombifolia, Periplaneta americana, and/or *Periplaneta australasiae.* (Morischita and Tsuchimochi, 1926.)

Cockroaches were unsuitable intermediate hosts for the following nematodes:

Angiostrongylus cantonensis (Chen)

Definitive hosts.—Wild and laboratory rats.

Cockroaches.—Blattella germanica, Pycnoscelus surinamensis, Periplaneta ignota. (Mackerras and Sandars, 1955.)

Cheilospirura hamulosa (Diesing, 1851) Diesing, 1861

Definitive hosts.—Chicken, turkey.

Cockroaches.—Blattella germanica (?). (Cram, 1931a, 1931b.) *Pycnoscelus surinamensis.* (Alicata, 1938a.)

Cheilospirura spinosa Cram, 1927

Definitive hosts.—Ruffed grouse, bobwhite quail.

Cockroach.—Blattella germanica (?). (Cram, 1929, 1931a.)

Dispharynx spiralis (Molin, 1858) Gedoelst, 1916

Definitive hosts.—Hungarian partridge, ruffed grouse, bobwhite quail, turkey, chicken, pigeon, guinea fowl.

Cockroach.—Blattella germanica (?). (Cram, 1931a.)

Skrjabinoptera phrynosoma (Ortlepp, 1922) Schulz, 1927

Definitive host.—Texas horned toad.

Cockroach.—Blattella germanica. (Lee, 1955, 1957.)

Spirocerca sanguinolenta (Rudolphi, 1819) Seurat, 1913

Definitive host.—Dogs.

Cockroaches.—Blatta orientalis, Periplaneta americana, Periplaneta australasiae. (Faust, 1928.)

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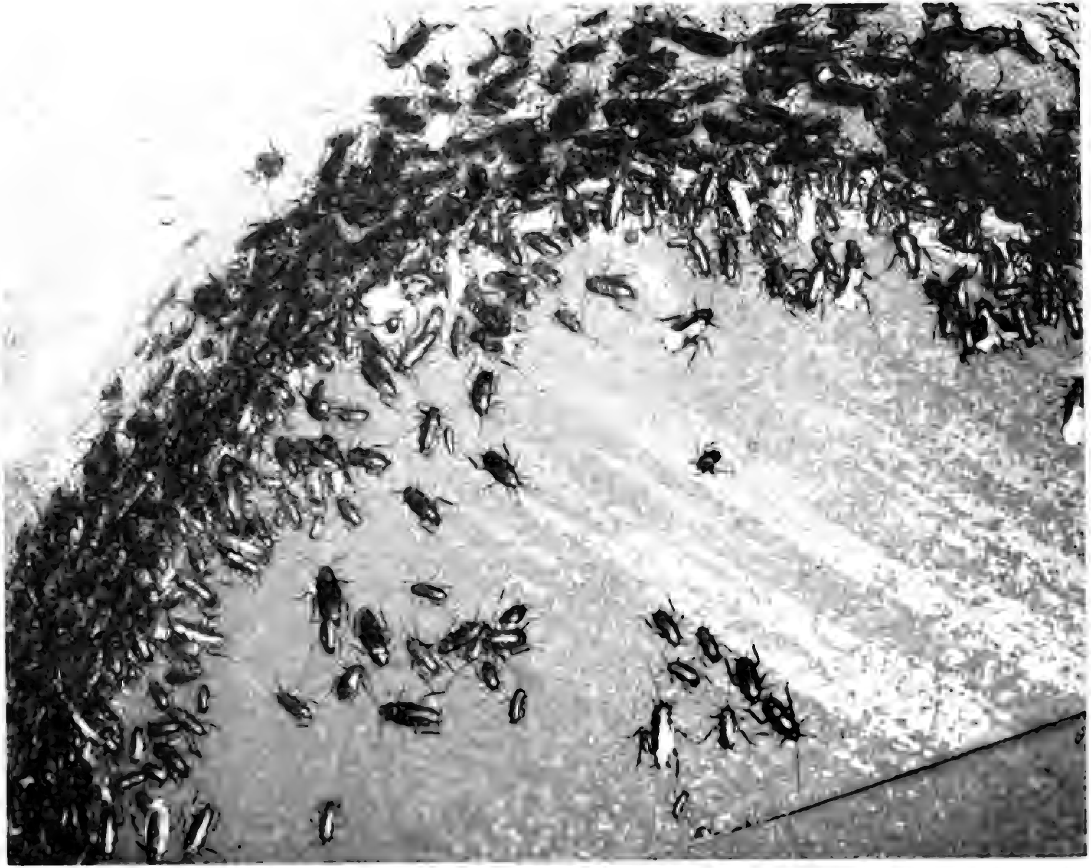
Periplaneta sp. in a sewer manhole in Houma, La. (From Gary, 1950. Courtesy of Public Works Journal Corporation.)



Periplaneta americana congregated on the arched roof and walls of a large sewer in Minneapolis, Minn. Approximately 3,000 cockroaches were present in a space of 12 square feet at the time the picture was taken. (See p. 11 for other details. Photograph by Jess Diggs and Alton Hollenbeck.)

Periplaneta americana (identified by Dr. R. B. Eads) apparently feeding on feces in a sewer manhole in Tyler, Tex. (From Anonymous, 1953. Courtesy of Texas State Department of Health.)

Periplaneta americana crawling through opening in sewer manhole cover in Texas. (See p. 16 for details. Courtesy of Texas State Department of Health.)

Oxyspirura mansoni protruding from a leg of *Pycnoscelus surinamensis.* Part of the nematode still extends into the femur. X 16.
(Preparation stained with Delafield's haematoxylin and mounted in balsam.)

Left, Larvae of *Gongylonema neoplasticum* encysted in the prothoracic muscles of *Periplaneta americana*. *Right*, Egg of *Gongylonema neoplasticum*. X 950. (Photomicrographs by Dr. Claude R. Hitchcock.)

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ANATOMY AND TAXONOMY OF THE MATURE NAIADS OF THE DRAGONFLY GENUS PLATHEMIS (FAMILY LIBELLULIDAE)

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ANATOMY AND TAXONOMY OF THE MATURE NAIADS OF THE DRAGONFLY GENUS PLATHEMIS (FAMILY LIBELLULIDAE)[1]

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The interrelationships of a particular group of insects cannot be fixed conclusively until a complete comparative study has been made. Studies of external morphology of various portions of widely differing species of insects have been published, but detailed comparative studies, particularly on the generic and specific levels, are few. Not until one compares all the structures of any given species with all the structures of other species do we begin to understand fully the phylogenetic and taxonomic relationships of the insects in question.

The difficulty with which the immature stages of dragonflies are identified to species is concurrent with a sparsity of morphological work done on these naiads. This paper is intended to provide a detailed morphological study of the last instar naiad of a common dragonfly, *Plathemis lydia* (Drury), that may serve as a foundation for comparative morphological studies, which in turn may reveal some taxonomic characters.

About 25 specimens were used in this study, and most of the features described were checked on the entire series.

Figures of nearly all the external anatomical features of *Plathemis lydia* are included to supplement the discussion. The presentation of the comparative morphology of the mature naiad of the only other known species of this genus, *Plathemis subornata* Hagen, is supplemented by figures wherever characters of taxonomic significance occur.

EXTERNAL ANATOMY OF PLATHEMIS LYDIA (DRURY)

The naiad of *Plathemis lydia* is rather large, robust, and elongate, approximately 23 to 24 mm. in length. Its surface is smooth and

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[2] The author wishes to express his sincere thanks and appreciation for the advice and criticism received from Dr. John F. Hanson and other staff members at the University of Massachusetts. He is also particularly indebted to Dr. R. E. Snodgrass for his valuable criticism of the manuscript.

covered with long light-colored setae, most densely on the legs and lateral margins of the body.

The genus *Plathemis* differs from its closest relative, *Libellula,* in having the head widest behind the eyes and the front margin of the median lobe of the labium crenulate (Needham and Betten, 1901).

THE HEAD

The head of *Plathemis lydia* (figs. 1-13) is essentially hypognathous but is slightly inclined to the horizontal so that the ventral portions are anteriormost. The head is approximately 4.5 mm. in width, widest behind the compound eyes, and somewhat wider than long. The antennae are located on the median portion of the face, above a protuberant transverse ridge, which is provided with numerous long scurfy hairs. The enormous eyes cap the prominent anterolateral angles of the head, while the mandibles and maxillae are lateroventral in position. The prehensile spoon-shaped labium, characteristic of all libelluloid naiads, forms, in its natural position, a mask that completely covers the other mouthparts and the face up to the antennal bases.

SUTURES OF THE CRANIUM

The principal cranial sutures of *Plathemis lydia* are the epicranial, postoccipital, pleurostomal, epistomal, clypeolabral, clypeal, ocular, and antennal sutures.

The EPICRANIAL "SUTURE" or ecdysial sulcus is completely developed and consists of *postfrontal* arms and a *coronal* stem. This "suture" is more or less T-shaped, with the postfrontal arms diverging laterally, a condition that is typical of odonate naiads (Snodgrass, 1947). The *postfrontal sutures* (pfs) or arms of the cleavage line are well developed but extremely short and merge with the ocular sutures at the posteromedial corners of the compound eyes. The *coronal suture* (cos) or stem of the cleavage line is of greater extent and proceeds across the top of the head almost to the cervical margin where it meets the postoccipital suture.

The POSTOCCIPITAL SUTURE (pocs) is not strongly developed and lies very close to and somewhat parallel with the dorsal and lateral margins of the foramen magnum. The greatly elongated exterior edges of the posterior tentorial pits are partially coincident with this suture. There is no *occipital suture.*

The PLEUROSTOMAL SUTURES (pms) are only faintly indicated where they are identical with the exterior edges of the anterior tentorial pits formed by the fan-shaped ends of the anterior tentorial

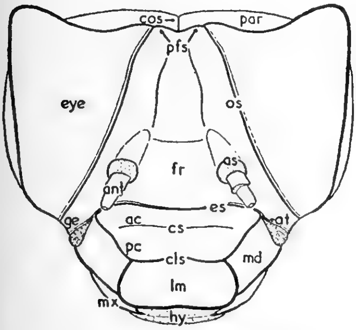

FIG. 1 HEAD, ANTERIOR

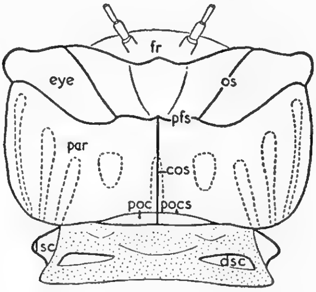

FIG. 2 HEAD and CERVIX, DORSAL

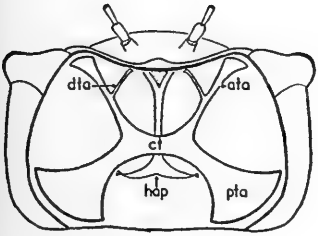

FIG. 3 TENTORIUM, DORSAL

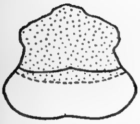

FIG. 4 LABRUM, ANTERIOR

FIG. 5 ANTENNA

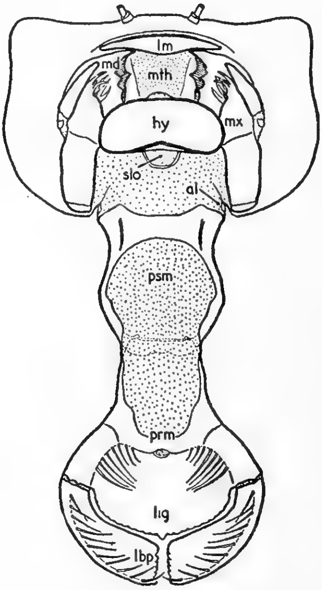

FIG. 6 HEAD, VENTRAL LABIUM, DORSAL

Figs. 1-6.—Head capsule of *Plathemis lydia*.

arms. Their posterior counterparts, the *hypostomal sutures,* are absent.

The EPISTOMAL SUTURE (es) is a very distinct suture connecting the two anterior tentorial pits across the face. This suture is the external indication of a deep inflection, which results internally in a strong *epistomal ridge* that forms a brace between the anterior mandibular articulations.

The CLYPEOLABRAL SUTURE (cls) separates the anteclypeus and the labrum. It is well developed and is regarded by Ferris (1942, 1943) as a primary segmental line.

The CLYPEAL SUTURE (cs) is a very shallow fold on the dorsal surface of the clypeus. It divides the clypeus into a ventral anteclypeus (ac) and a dorsal postclypeus (pc). It is often only faintly indicated.

OCULAR SUTURES (os) are present and surround the compound eyes at their bases.

An ANTENNAL SUTURE (as) entirely surrounds each antennal socket.

AREAS OF THE HEAD CAPSULE

The demarked areas of the cranium are the clypeus, frons, antennal and ocular sclerites, parietals, postocciput, genae, subgenae, and postgenae.

The CLYPEUS (cl) is a broad sclerite typically supporting the anterior mandibular articulations at its basal angles and the labrum at its distal margin. A clypeal suture (cs) transversely divides the clypeus into a ventral *anteclypeus* (ac) and a dorsal *postclypeus* (pc). The clypeus bears numerous long inconspicuous setae which are closely appressed to its surface.

The FRONS (fr) is a large area bounded dorsally, laterally, and ventrally by the postfrontal, ocular, and epistomal sutures, respectively. The frons bears the antennal sockets. The facial portion is provided with long setae which lie between the antennal sockets and in two lines on either side of an imaginary vertical midline. There are no ocelli.

The ANTENNAL SCLERITES (asc) are extremely narrow rings surrounding the antennal sockets. They are too faintly indicated to be included in a drawing of this scale.

The OCULAR SCLERITES (osc) are very faintly indicated narrow rings, which surround the enormous compound eyes.

The PARIETALS (par) are a pair of sclerites that encompass most of the dorsal and dorsolateral areas of the cranium, extending laterally to the genae and posterolaterally to the postgenae. The two sclerites are separated on the dorsal surface of the cranium by the median coronal suture.

Seven elongate and two ovoid areas are present on the dorsal surface and are surrounded by numerous medium to long setae and short dark-colored spines. These glabrous spots are the areas of insertion of the gnathal muscles (Asahina, 1954).

The COMPOUND EYES (eye) are situated on the prominent anterolateral angles of the head. They are irregular in shape and, according to Lew (1933), composed of "three sets of distinctly distinguishable tissues." Lew also notes that only the pigmented tissue on the protuberant portion of the eye is functional.

The POSTOCCIPUT (poc) forms the posterior rim of the cranium. It is a narrow U-shaped sclerite, with its ends terminating at the posterior tentorial pits.

Of the SUBGENAE, only the *pleurostomae* (pm) are present. Each pleurostoma is an extremely small, elongate sclerite arising at the base of the mandible and extending to the ventral exterior edge of the anterior tentorial pit.

The GENAE (ge) are a pair of undifferentiated sclerites between the compound eyes and the antennal bases.

The POSTGENAE (pge) are a pair of undifferentiated areas posterolateral to the compound eyes.

THE TENTORIUM

The tentorium consists of a corporotentorium in the center of the head and three pairs of arms supporting it from different parts of the cranium. The anterior and posterior tentorial arms arise as invaginations of the cranial wall, while the small dorsal tentorial arms are outgrowths of the anterior tentorial arms.

The ANTERIOR TENTORIAL ARMS (ata) arise from slits (at) between the compound eyes and the bases of the mandibles. From these points of attachment the anterior arms converge posteriorly to fuse with the corporotentorium in the center of the head.

The POSTERIOR TENTORIAL ARMS (pta) arise from the posterior tentorial pits which are partially coincident with the anterior portions of the postoccipital suture. They are much stouter than the anterior arms.

The DORSAL TENTORIAL ARMS (dta) are shorter and narrower than those described above. Each dorsal arm arises from the mesal margin of the anterior tentorial arm midway between the anterior tentorial pit and the region of fusion of the anterior arm with the corporotentorium. The dorsal tentorial arms are weakly attached to the cranial wall and are easily dislodged.

The CORPOROTENTORIUM (ct) is located in the center of the head and is transverse in shape.

HEAD APPENDAGES

The movable parts of the head are the antennae, labrum, mandibles, maxillae, hypopharynx, and labium.

The ANTENNAE (ant) are setiform and about equal in length to the length of the head. Each antenna is composed of seven segments. The basal segment or *scape* (s) is short and thick and located in the medioventral portion of a circular membrane that is bounded by the antennal sclerite. The second segment or *pedicel* (p) is longer than and about two-thirds the diameter of the scape. It narrows abruptly distally to meet the *flagellum* (f), which is about one-half the diameter of the pedicel. The first, third, fourth, and fifth flagellar segments are subequal in length and each is approximately one and one-half times the length of the second segment. The terminal or fifth flagellar segment tapers apically to a fine point. Each segment of the antenna bears several long light-colored setae.

The LABRUM (lm) or upper lip is movable and, though not a true appendage, complements the other mouthparts. It is a transverse, reniform sclerite suspended from the clypeus by a narrow strip of membrane. The dorsal and ventral margins are parallel, the dorsal margin being produced while the ventral margin is emarginate. The anterolateral *tormae* extend into the membranous region at the base of the labrum but do not articulate with the clypeus. With the exception of a small bare subtriangular dorsomedial area, the anterior surface bears numerous short spiniform setae. In addition, many long setae are present on the distal margin.

The MANDIBLES (md) are well developed and lie horizontally in the space between the labrum and the hypopharynx. Each mandible has its mesal surface differentiated into a distal toothed *incisor area* (in) and a proximal *molar surface* (mo). The right mandible bears three sharp apical teeth on the incisor lobe, apparently for tearing the food, and three heavily sclerotized, blunt teeth on the molar surface. The left mandible is identical in size to the right mandible but differs slightly in dentition. The former has the ventral incisor tooth apically bicuspidate and the proximal molar tooth lacking.

The base of the mandible is triangular in outline. Each mandible articulates dorsally on the base of the clypeus and ventrally, by means of a conspicuous *condyle* (co), on the lower margin of the cranium. A strong *adductor tendon* (adt) is attached to the inner angle of the

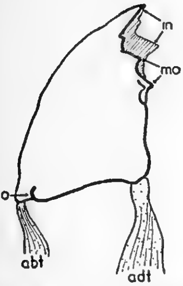

FIG. 7 RIGHT MANDIBLE, VENTRAL

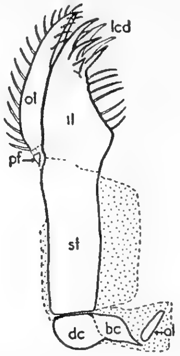

FIG. 8 RIGHT MAXILLA, VENTRAL

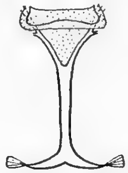

FIG. 9. HYPOPHARYNGEAL APODEME, VENTRAL

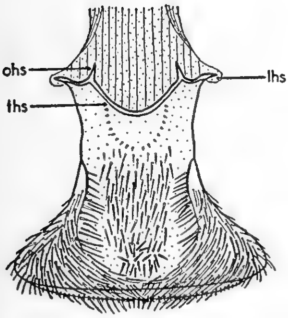

FIG. 10 HYPOPHARYNX, ANTERIOR

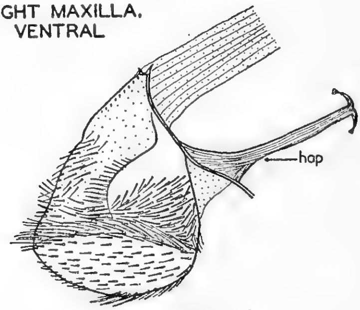

FIG. 11 HYPOPHARYNX, LATERAL

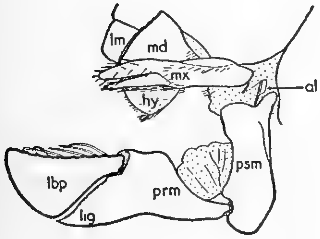

FIG. 12 GNATHAL APPENDAGES, LATERAL

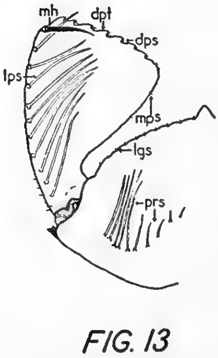

FIG. 13 RIGHT LABIAL PALPUS and LIGULA, DORSAL

FIGS. 7-13.—Gnathal appendages of *Plathemis lydia.*

base of each mandible. In addition, a weaker *abductor tendon* (abt) is attached to the lateral margin of the base, close to the ventral condyle. The muscles inserted on these tendons have their origins on the cranium.

The MAXILLAE (mx) are composed of two distinct portions; a basal part consisting of cardo and stipes, and an apical portion divided into two freely movable processes, here called the inner lobe and the outer lobe. The maxillae assume a position beneath the mandibles and lateral to the hypopharynx and are suspended from the head by a single point of articulation.

The *cardo* is divided by an arcuate suture into two sclerites, the *basicardo* (bc) and the *disticardo* (dc). The dividing suture almost encloses the more proximal and convex disticardo close to the margin of the stipes. In the retracted position the cardo is folded dorsally above the stipes, where it articulates on the anterior margin of the posterior tentorial pit.

The *stipes* (st) is the largest sclerite of the maxilla. The parastipital region is undemarked from the remainder of the stipes.

The *inner lobe* (il) has been generally regarded as representing the fused *lacinia* and *galea* of more typical mandibulate insects (Tillyard, 1917; Chao, 1953; Asahina, 1954), but Snodgrass (1954) has theorized that the galea has been lost and that the inner lobe represents only the lacinia. In *Plathemis lydia* this lobe typically bears, on its mesal margin, a subapical fringe of long setae and several long, sharp apical teeth, called *laciniadentes* (lcd) by Crampton (1923). In protraction of the maxillae the inner lobes are thrust forward beyond the mandibles to grasp the prey and pass it from the labium to the mandibles.

The slender *outer lobe* (ol), arising at the distolateral angle of the stipes, has been interpreted as the galea by Crampton (1923), but numerous other workers regard it as the *palpus* of the maxilla. In the adult dragonfly the outer lobe is provided with two muscles, as shown by Snodgrass (1954). This, according to Snodgrass, identifies it as the maxillary palpus; a galea has but one muscle. The outer margin of this lobe bears many well-developed inwardly curving setae.

A small sclerite, the *palpifer* (pf), is the actual area upon which the outer lobe takes its origin.

The HYPOPHARYNX (hy) of *Plathemis lydia* is a large cushionlike lobe that projects downward between the anterior portions of the maxillae and is separated from the base of the labium by a wide membranous area between the maxillary stipites. It apparently consists only of the lingua; superlinguae are not present. The adoral surface is mostly unsclerotized. It bears a curious group of eighteen short spines arranged in a semicircle just ventrad of the transverse bar of the hypopharyngeal suspensorium as well as numerous other setae and spinulae scattered over the surface. The lateral, distal, and aboral surfaces are sclerotized. The former two bear many long, curved setae and spines, while the latter is glabrous.

The *hypopharyngeal apodeme* (hap) is a characteristic feature of the dragonfly naiad. Its shaft extends posteriorly through the head below the tentorium and the crossbar is embedded in the posterior edge of the base of the postmentum of the labium where it is held in place by "small apical brushes of fine fibers" (Snodgrass, 1954).

The *suspensorium of the hypopharynx* consists of a transverse bow-shaped bar (ths) on the dorsal margin of the base of the hypopharynx and two pairs of arms, oral (ohs) and lateral (lhs), which are continuous with the former.

The nymphal LABIUM consists of two major parts hinged on each other by an elbowlike joint. Numerous inconsistencies in the terminology of these parts are present in the literature. The present writer has followed the labial nomenclature of Corbet (1953) and Snodgrass (1954) in calling the proximal part the *postmentum* and the distal portions the *prementum* and its distal lobes the *labial palpi* and the *ligula*. In the retracted position the labium is folded so that the aboral surface of the postmentum is pressed against the ventral surface of the head and thorax, and the distal adoral surface, formed by the prementum, the palpi, and the ligula, forms a deep spoonlike mask that covers the face and other mouthparts up to the antennal bases. In protraction, the prementum is thrust out beyond the head by a forward swing of the postmentum. At the same time the distolateral lobes are thrown wide apart with their movable hooks erect (Amans, 1881—from Snodgrass, 1954).

The *labial palpi* (lbp) are curved lamellar structures forming part of the spoonlike mask. In broadest perspective, as in figure 13, each palpus appears more or less triangular in outline because of its greatly expanded distal portion. Each palpus possesses a prominent *movable hook* (mh) on its distolateral angle and 10 long, slender *lateral palpal setae* (lps) lying nearly parallel to its outer margin. In addition, the distal margin of the palpus bears seven or eight teeth (dpt), which are mesally directed and about as broad as long. Each tooth is provided with one to three short, spiniform setae (dps). The mesal margin of each palpus also bears several minute setae (mps).

The *ligula* (lig) lies between the bases of the palpi and is fused with the prementum. The median portion of its distal margin is anteriorly produced, forming a small triangular lobe. The remainder of the distal margin is evenly crenulate and possesses 10 or 11 short, spiniform setae (lgs) on each side of the central lobe.

The *prementum* (prm) bears, on each side, eight long, slender setae (prs), of which the five outermost ones are distinctly the longer. In addition, a pair of small secondary setae is present on each side just mesad of the premental setae with which they are often included by many authors.

Of the numerous setae mentioned above, the *lateral palpal setae* (lps) and the *premental setae* (prs) are of the greatest importance in the current taxonomy of immature Odonata.

The *postmentum* (psm) is a hollow stalk that supports the prementum, and the entire labium swings on its base. The lateral margins of the base of the postmentum are thickened and extend laterally in the head membrane as a pair of folding *articular rods* (al) the ends of which lie adjacent to the maxillary cardines. "The true hinge points of the labium on the head are thus at the mesal ends of these rods where the rods join the basal lobes of the postmentum" (Snodgrass, 1954).

CERVIX OR NECK

Since the origin of the cervix (figs. 2, 16) has not been definitely established, it is discussed briefly and separately from both head and thorax. In *Plathemis lydia* this membranous region bears two pairs of sclerites, the lateral cervical sclerites and the dorsal cervical sclerites.

The LATERAL CERVICAL SCLERITES (lsc) are large, laterally protuberant pyramidal sclerites on the anterolateral margin of the neck membrane.

The DORSAL CERVICAL SCLERITES (dsc) lie free in the neck membrane. They are transversely elongate and much smaller than the above.

THORAX

The thorax of *Plathemis lydia* (figs. 14-19) is "characterized by three special features. First is the obliquity of the mesothoracic and metathoracic pleura as indicated by the posterior slant of the pleural sulci from the leg bases to the wings. Second is the almost complete union of the adjoining pleural plates of the wing-bearing segments, resulting in the suppression of an intersegmental groove between the epimeron of the mesothorax and the episternum of the metathorax. Third is the dorsal extension of the upper plates of the mesothoracic

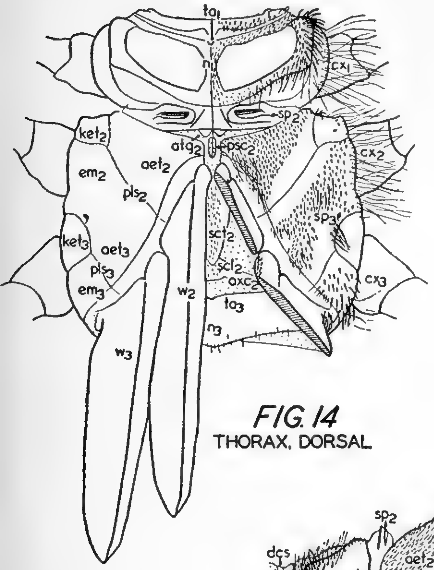

FIG. 14 THORAX, DORSAL

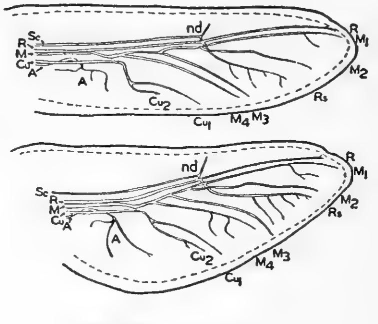

FIG. 15 WING PADS

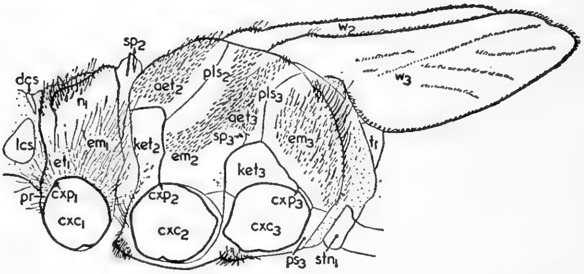

FIG. 16 THORAX, LATERAL

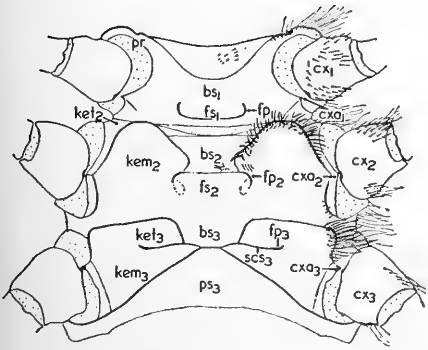

FIG. 17 THORAX, VENTRAL

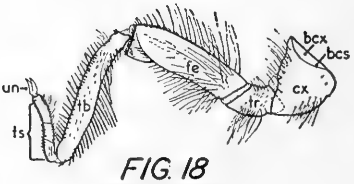

FIG. 18 LEFT MESOTHORACIC LEG

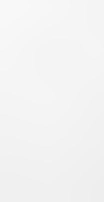

FIG. 19 MESOTHORACIC PRETARSUS

FIGS. 14-19.—Thorax of *Plathemis lydia.*

episterna until they meet along the midline of the back in front of the wings, and the corresponding downward extension of the metathoracic epimera on the ventral surface behind the legs. These features of the thorax evidently have no particular functional significance for the larva, since the larva uses its legs in the ordinary manner for locomotion, and its wings are entirely passive rudiments of the future organs of flight. On the other hand, the thoracic structure is clearly a functional adaptation for the benefit of the adult; it must have been early impressed upon the larva, and retained by the larva because it had no disadvantage for the larval activities" (Snodgrass, 1954). Sargent (1937), by puncture-scarring the larval cuticle, has shown that the dorsal extension of the mesothoracic episterna takes place by marginal growth, while the metathoracic epimera increase both by general expansion and by growth of the ventral margins. The postcoxal plate of the metasternum, according to Sargent, moves bodily backward from the legs as the epimeral plates intervene.

THORACIC TERGA

PRONOTUM: The prothoracic tergum (fig. 14) consists of a single large sclerite, the *pronotum* (n_1), which is roughly transversely rectangular in shape. The anterodorsal angles are produced as hemispherical lobes each of which bears numerous long setae and short spines. The *disc* or dorsal surface of the pronotum consists of two oblong glabrous areas which are bounded anteriorly and posteriorly by bands of minute inconspicuous setae and separated by a median longitudinal spiniferous band which is enlarged at either end. A conspicuous pit close to the spiniferous anterior margin marks the position of the *prothoracic tergal apophysis* (ta_1) which gives attachment to the dorsal longitudinal muscles (Asahina, 1954).

MESONOTUM: The mesothoracic tergum (fig. 14) is transversely compressed as a result of the upward extension of the pleural sclerites. The mesonotum proper is demarked into four main regions: acrotergite, prescutum, scutum, and scutellum. A portion of the dorsal surface of the intersegmental membrane, lying between the mesothoracic spiracles, has become secondarily sclerotized forming a plate which narrows anteriorly and is roughly trapezoidal in shape.

The *acrotergite* (atg) is the anteriormost mesotergal sclerite. It is secondarily divided into two triangular plates with posteriorly directed apices. It is extremely reduced and separated from the prescutum by membrane.

The *prescutum* (psc_2) is a much-reduced, longitudinally elongate, protuberant sclerite between the dorsally extended portions of the mesothoracic anepisterna. It is separated from the latter, and also from the wing bases and the scutum, by a membranous area.

The *scutum* (sct_2), the largest sclerite of the tergum, is a longitudinally elongate, posteriorly convergent, weakly sclerotized lobe in the membranous region between the anterior wing bases. Its posterior margin is fused with the scutellum. Numerous tiny posteriorly-directed spines are present on the dorsal surface.

The *scutellum* (scl_2) is a small hemispherical lobe just posterior to the scutum. Its anterior end is undemarked, but its posterior margin is arcuate and continuous laterally with the *axillary cords* (axc_2) of the basal wing membrane. Setae of various sizes are scattered over the scutellar surface.

METANOTUM: The metathoracic tergum (fig. 14) consists of a single transversely elongate sclerite, the *metanotum* (n_3), which is situated between the posterior wing bases. The *metathoracic tergal apophysis* is represented by a shallow pit (ta_3) on its anterior margin. Numerous short setae are borne on the median dorsal surface.

THORACIC PLEURA

The thoracic pleura (figs. 14, 16, 17) are relatively large and greatly modified and consist of propleuron, mesopleuron, and metapleuron.

PROPLEURON: The prothoracic pleuron is composed of two regions, the episternum and the epimeron, which are somewhat separated by a shallow vertical depression lying above the pleural coxal process (cxp_1). The pleural suture is lacking.

The *episternum* (et_1) is a relatively very small area bounded anteroventrally by the precoxal bridge and posteriorly by the epimeron. Neither of the delimiting sutures is entire. The marginally setiferous *precoxal bridge* (pr) is well sclerotized and united ventrally with the basisternum.

The *epimeron* (em_1), the largest portion of the propleuron, is fused with the pronotum. It is posteriorly separated from the mesothoracic katepisternum by the peritremal plate of the mesothoracic spiracle above and a flexible, folded, partially sclerotized area below.

MESOPLEURON: The mesothoracic pleura are much more highly developed than the prothoracic pleura. Each pleuron is divided into two main regions, the episternum and the epimeron, by the *pleural suture* (pls_2), which extends obliquely posterodorsad from the pleural coxal process to the wing base. The episternum is further divided by a well-demarked transverse suture into two secondary regions known as anepisternum and katepisternum.

The *anepisternum* (aet_2) is a large sclerite which is bounded anteriorly by the spiracular peritreme, anterodorsally by a small membranous area which bears the metanotal prescutum, and posterodorsally by the base of the fore wing. This dorsal extension is typical of odonate naiads.

The *katepisternum* (ket_2) extends ventrally in front of the coxal cavity and meets the basisternum on the anterior margin of the mesosternal surface. The katepisternum is bounded anteriorly by a flexible, vertically folded, partially sclerotized area beyond which lies the prothoracic epimeron.

The *epimeron* (em_2) has become fused with the posteriorly adjacent metathoracic anepisternum. This fusion has resulted in the suppression of the mesopleural-metapleural intersegmental suture but the posterior portion is obviously the metanepisternum since it bears the metathoracic spiracle. The resultant large composite sclerite is reflected ventrally and passes behind the coxal cavity to the sternal surface, where it is produced into a large forwardly directed lobe which bears numerous long curved spines and setae.

The *mesothoracic spiracle* (sp_2) lies in the upper part of a long sclerotized peritermal plate between the pronotum and the mesothoracic anepisternum. This is the only spiracle that becomes immediately functional for respiration upon emergence of the naiad from the water prior to transformation. The remaining thoracic and abdominal spiracles are functional in the adult only (Snodgrass, 1954).

METAPLEURON: The metathoracic pleuron is somewhat similar to, but smaller than, that of the mesothorax described above. It is divided into two portions, the episternum and the epimeron, by the *pleural suture* (pls_3), which proceeds obliquely dorsocephalad from the *coxal process* (cxp_3) to the center of the pleuron and then swings posteriorly to the wing base. The episternum is further divided by a distinct arcuate suture into an anepisternum and a katepisternum.

The *anepisternum* (aet_3), which bears the *metathoracic spiracle* (sp_3), is fused with the mesothoracic epimeron, i.e., it is not anteriorly delimited by an intersegmental suture. It extends dorsally to the base of the hind wing.

The *katepisternum* (ket_3) or lower region of the episternum is smaller than the anepisternum. In addition to its normal pleural position, the katepisternum narrows abruptly to pass in front of the coxal cavity and is reflected ventrally where it expands and extends to the basisternum. This sternal portion is fused with the posteriorly adjacent, ventrally isolated katepimeron, from which it is partially demarked by the lateral portions of the *sternacostal suture* (scs_3). The resultant composite sclerite is anterolaterally produced into a distinct, large, setiferous lobe close to the anterior margin of the coxal cavity.

The *epimeron* (em_3) is the posteriormost sclerite of the pleuron. It extends from behind the coxal cavity to the posterior portion of the base of the hind wing. The *katepimeron* (kem_3), or ventral portion of the epimeron, has become completely isolated on the sternal surface owing to the intervention of the large poststernum posterior to the coxal cavity. This ventral prolongation of the epimeron extends almost to the midline of the venter.

PLEURAL CHAETOTAXY: The entire pleural surface, with the exception of the portions adjacent to the pleural sutures, is clothed with short setae and spines, whose average length increases slightly posteriorly. In addition, the prothoracic pleura and the areas adjacent to the coxal cavities are provided with numerous light-colored setae, which are unusual in their extreme length.

THORACIC STERNA

PROSTERNUM: The prothoracic sternum (fig. 17) consists of a single broad sclerite which represents the fused basisternum and furcasternum. A large partially sclerotized, spiniferous, hemispherical area anterior to the prosternum is of secondary origin and not part of the definitive prosternum.

The *basisternum* (bs_1), the largest prosternal area, is fused anterolaterally with the *precoxalia* (pr) of the episternum and posteriorly with the small furcasternum. Its lateral margins form the *sternal coxal articulations* (cxa_1).

The *furcasternum* (fs_1) is a small transverse area located between the prosternal *furcal pits* (fp_1), which are the external manifestations of the endoskeletal furcal apophyses.

MESOSTERNUM: The mesothoracic sternal sclerites (fig. 17) are also two in number.

The *basisternum* (bs_2) is a medium-sized roughly anvil-shaped sclerite in the anteromedian portion of the mesosternum. It is bounded anteriorly and laterally by the ventrally prolonged mesothoracic pleura.

The *furcasternum* (fs_2) is a small transverse sclerite situated at the posterior end of the basisternum and demarked from it by a spiniferous ridge that extends between the *furcal pits* (fp_2).

METASTERNUM: The metathoracic sternum (fig. 17) is composed of two sclerites, the basisternum and the poststernum (Asahina, 1954), which are completely separated by the medioventrally convergent metapleura. The anterior margin of the metasternum is undemarked from the posterior portion of the mesosternum.

The *basisternum* (bs_3) is a small transversely elongate area in the anterior portion of the metasternum situated between the ventrally extended portions of the metapleural katepisterna.

The *poststernum* (ps_3), the largest sternal sclerite, is the posteriormost portion of the metasternum. It is roughly triangular in outline, with the blunt apex directed forward and the basal angles reflected upward on the pleuron behind the coxal cavities. The poststernum intervenes between the pleural and ventral portions of the metepimeron.

The *furcal pits* (fp_3) have become isolated and lie in the lateral ends of a deep inflection that partially separates the ventrally reflected episternal and epimeral plates.

WINGS

The wing pads (fig. 15) of a dragonfly naiad are held inverted on the back with the spiniferous costal margin uppermost. One distinct axillary sclerite is present at the base of the adult wing (Snodgrass, 1909) but this sclerite is not demarked in the naiad.

WING TRACHEATION: The veins of the adult wings are preceded by tracheae in the nymphal wing pads. "Springing from a basal tracheal trunk that lies just inside the thorax, there are six tracheae extending out into the wing sac" (Needham, 1951). These tracheae are indicated externally on the wing pad surface by rows of well-developed setae. The tracheae themselves are best observed in freshly killed specimens in which the tracheae are filled with air (Needham, 1903), but the present writer observed the tracheae through the morphologically ventral surface of the left wing pad by rendering dried specimens translucent with the addition of either alcohol or xylene.

In describing the position of these tracheae, the Comstock-Needham system of wing-venation terminology has been used.

The *fore wing* (w_2) of *Plathemis lydia* is rather narrow and elongate. Six tracheae extend out into the wing sac: costa, subcosta, radius, media, cubitus, and anal.

The *costa* or *costal trachea* is almost completely atrophied. The remaining portion is fused into the thickened leading edge of the wing.

The *subcosta* (Sc) is shallowly forked at its terminus, which is approximately two-thirds the distance from the wing base to the apex. It sends a short branch obliquely forward to the nodal region (nd) of the costal margin and a very minute branch posteriorly to connect with the radius.

The *radius* (R) is of greater extent than the subcosta. It is deeply forked in the region of the nodus (nd) just posterior to the subcostal fork. The main portion of the radial trachea proceeds unbranched to the apex of the wing where it sends a minute branch forward. The *radial sector* (Rs), or posterior branch of the radius, lies across the base of the terminal fork of the median trachea and extends out to occupy the field between M_2 and M_3.

The *media* (M) is 4-branched. At approximately one-third of the distance from base to apex it bends slightly posteriorly and gives off a narrow trachea, M_4, which proceeds almost to the wing margin. Farther along its extent it gives off a second posterior branch, M_3, which lies just above and parallel to M_4 and extends almost to the wing margin. At a point just posterior to the radial fork the median trachea again forks, this time sending one branch, M_2, nearly to the wing margin to occupy the field just above the radial sector and a second branch, M_1, to the wing apex posterior and parallel to the radius.

The *cubitus* (Cu) bends abruptly posteriorly just below the first forking of the median trachea and forks once into Cu_1 and Cu_2, the first of which almost reaches the hind margin of the wing.

The *anal trunk* (A) is crowded forward against the base of the cubital trachea. It loops forward under the cubitus and then returns to its original level via the anal crossing. The anal trachea then descends slightly and forks twice.

In the *hind wing* (w_3) the tracheation is almost identical with that of the fore wing and differs only in the extent of certain tracheae. The hind-wing pad is expanded posteriorly and subsequently the cubital and anal tracheae are of greater extent than in the fore wing, which has not undergone such an expansion.

LEGS

The legs of *Plathemis lydia* (figs. 18, 19) are long and slender. The forelegs are subequal in length to the mesothoracic legs, which in turn are considerably smaller than the metathoracic legs. The differences in sizes of the legs is accounted for primarily by differences in length of the femur, tibia, and tarsus since the coxa and trochanter are almost identical in size in all three pairs of legs.

The COXA (cx) or basal leg segment is of moderate size and more or less conical in shape. It articulates with the pleural coxal process and with the sternal coxal articulation of the thorax at the basal portion of the outer and inner surfaces, respectively. The basal end of the coxa is girdled by a submarginal *basicostal suture* (bcs), which forms internally a submarginal basicostal ridge and sets off a narrow marginal flange, the *basicoxite* (bcx), which is enlarged on the outer surface posterior to the pleural articulation.

The TROCHANTER (tr) is a rather small segment that is proximally constricted. This gives it a superficially 2-segmented appearance. Its distal end is obliquely truncate with the concave dorsal surface shorter than the convex ventral surface. It is attached proximally to the coxa by a membrane and articulates with the coxa by an anterior and a posterior condyle. The deeply emarginate dorsal margin of the coxa allows for a wide range of motion of the leg on this dicondylic hinge. A dicondylic hinge is present at the distal end of the trochanter also. This operates at a right angle to the coxotrochanteral hinge but permits of much less freedom than the latter since nearly the entire distal rim of the trochanter is closely adjacent to the end of the femur.

The FEMUR (fe) is the second longest segment of the leg. It is nearly cylindrical and armed with numerous spines and setae, especially on its dorsal and ventral surfaces. In addition, the posterior surface of the prothoracic femur, the anterior and posterior surfaces of the mesothoracic femur, and the anterior surface of the hind femur are also provided with numerous setae and spines. This is evidently correlated with the natural position of the legs; forelegs held anteriorly, middle legs held posterolaterally, and hind legs held posteriorly. The distal margin of the femur is crowned with several short spines.

The TIBIA (tb) is the longest segment of the leg, nearly cylindrical, and rather slender. Its proximal end is bent toward the femur, allowing the tibia to be flexed close against the undersurface of the femur. The tibia articulates with the femur by a dicondylic hinge. Numerous medium to long spines and setae are borne on both the dorsal and ventral tibial surfaces, the heaviest spines being present on the ventral surface close to the distal margin. In addition, there are many short spines scattered generally over the entire surface.

The TARSUS (ts) is 3-segmented. The basal segment or *basitarsus* is the second longest tarsal segment. It is slightly bent near its distal end and can be flexed against the tibia. The *second tarsomere* is only slightly shorter than the basitarsus. It is obliquely truncate distally so that its dorsal surface is shorter than the ventral surface. The third tarsomere, or *distitarsus* (dts), is the longest of the three tarsal segments. It bears a ventrodistal projection, the *plantella* (pt), which is well developed. All three segments of the tarsus bear on their ventral surfaces several heavy spurs which decrease in size distally.

The PRETARSUS (fig. 19) or terminal region of the leg consists of claws, empodium, and unguitractor. The *claws* or *ungues* (un) are the largest parts of the pretarsus, and they articulate with a small dorsal process of the distitarsus. Ventrally, the bases of the claws are connected with membrane which is also closely attached to the mesally located *unguitractor* (ut). The unguitractor is a sclerite that can be retracted into the distitarsus by the action of muscles in the tibia which are attached to the unguitractoral tendon which is in turn attached to the unguitractor. The unguitractor is partially hidden by the plantella. An *empodium* (emp) is attached to the distal end of the unguitractor by a narrow stalk. The remainder of the empodium is more or less paddle-shaped.

ABDOMEN

The abdomen of *Plathemis lydia* (figs. 20-24) is elongate and slightly longer than the head and thorax combined. It is broadest at the fifth segment and tapers gradually posteriorly to the tips of three horny processes enclosing the anus. The abdomen consists of ten complete annular segments and probably rudiments of the eleventh and twelfth segments (Heymons, 1904).

ABDOMINAL TERGA

The abdominal terga (figs. 20, 24) are distinctly transversely elongate in shape. They increase slightly in the transverse dimension from the first to the fifth segment and then shorten to give a markedly tapered appearance to the abdomen. The middorsal line and lateral margins are produced in the form of keels, giving the abdomen a triquetral appearance. Sharp, posteriorly curved *dorsal hooks* (dh) are present on the dorsal midline of segments three to six, but absent on the remaining segments. The dorsal hook on segment five is the longest of the four hooks, all of which are densely covered with sharp, spiniform setae. Long, sharp *lateral spines* (lsp) are present on the posterolateral angles of segments eight and nine, one pair per segment. The spines are approximately one-sixth as long as the segments bearing them. Smaller spines are present in rows on the lateral and posterior tergal margins and scattered generally over the dorsal surface. The spines gradually increase in size and density as they progress posteriorly. The terga are also adorned with a few scattered setae and long lateral hairs.

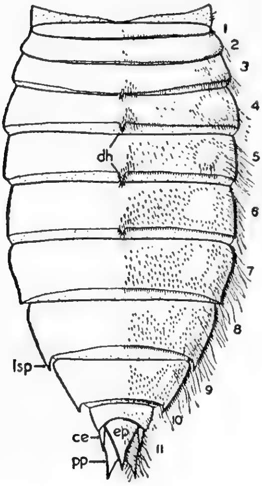

FIG. 20
ABDOMEN, DORSAL

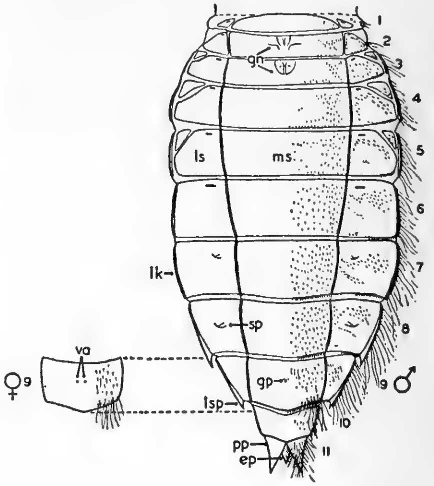

FIG. 21
ABDOMEN, VENTRAL

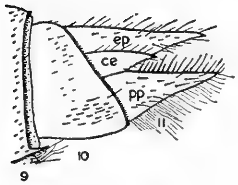

FIG. 22
ANAL APPENDAGES,
LATERAL

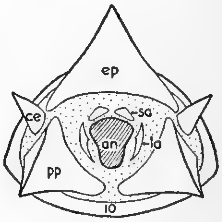

FIG. 23
ANAL APPENDAGES,
POSTERIOR

FIG. 24
DORSAL HOOKS – P. LYDIA

FIG. 25
DORSAL HOOKS – P. SUBORNATA

FIGS. 20-25.—Abdomen of *Plathemis lydia* and *P. subornata* (fig. 25).

ABDOMINAL STERNA

The sterna (fig. 21) are slightly convex and each of the first nine is divided by two longitudinal sutures into "a broad median plate (ms) and two small lateral plates (ls), which latter are movably hinged on the edges of the tergum and on the median sternal plate" (Snodgrass, 1954). The sternum of segment 10 is undivided and unseparated from the tergal surface.

The MEDIAN PLATES (ms) or *median sternites* (Snodgrass, 1954) of abdominal segments 1 and 4-8 of the male and of segments 1-8 in the female are unmodified and devoid of genital processes. The second and third median sternites of the male bear rudiments of the *accessory genitalia* (gn) of the adult, and the ninth median sternite bears the centrally located rudimentary *genital pore* (gp). On the ninth median sternite of the female there are two small, centrally located tubercles (va), which are most probably the rudiments of the *valvulae* of the ovipositor.

The LATERAL PLATES (ls) of the first eight segments bear the abdominal *spiracles* (sp), the largest of which is on segment eight. Numerous authors, including Calvert (1893), Wallengren (1914), Tillyard (1917), and Whedon (1918), have referred to the lateral plates as "pleurites," but Snodgrass (1954) states that the term "pleuron" "has no very definite meaning as applied to the abdomen." He substitutes instead the term *"laterosternites"* for the lateral sternal plates. In *Plathemis lydia* each laterosternite of segments 3, 4, and 5 is secondarily divided into a small anterolateral sclerite (episternite—Wallengren, 1914; triangular sclerite—Schmidt, 1951) and a larger posterior sclerite (epimerite—Wallengren; spiracular sclerite—Schmidt) which bears the spiracle.

Numerous posteriorly directed, short, spiniform setae are borne on the lateral keels, the lateroposterior margins of laterosternites 2-9, and the posterior margins of median sternites 7-9. Numerous other minute spines and setae are present on the entire ventral surface and are generally larger on the laterosternites than on the median sternites.

ANAL APPENDAGES

The anal appendages (figs. 22, 23) of the nymphal abdomen are of interest because of the different interpretations of their homologies. These terminal structures may be divided into two groups on the basis of their segmental relationships. The first group consists of epiproct, paraprocts, and cerci, of which the first two are thought to comprise the modified eleventh abdominal segment (Heymons, 1904) or anal pyramid (Tillyard, 1917). The cerci are considered to be the appendages of the eleventh segment. The second group is believed by Heymons (1904) to be the remnant of the twelfth abdominal segment. It is composed of the laminae supra-anales and the laminae sub-anales.

The EPIPROCT (ep) is the tergum of the eleventh segment (Heymons, 1904; Crampton, 1918). In *Plathemis lydia* the epiproct is a wide, triangular, horny process that emerges from beneath the posterodorsal margin of the tenth tergum to surround the anus from above.

The PARAPROCTS (pp) complement the epiproct by surrounding the anus laterally and ventrally. Each of these two triangular horny processes resembles the epiproct in appearance but is slightly smaller in size. The paraprocts, according to Heymons (1904), are actually the true cerci. Crampton (1918) contended that the paraprocts and cerci were distinct structures but that they belonged to the tenth segment. The most current theory is that of Snodgrass (1931), who maintains that the paraprocts pertain to the eleventh segment and probably represent the sternal sclerites of that segment.

The CERCI (ce) are paired appendages that arise from the dorsolateral posterior margin of the tenth tergum, immediately laterad of the epiproct. These appendages were termed "cercoids" by Heymons (1904) and Tillyard (1917), both of whom maintained that the true cerci were the lateral anal appendages or paraprocts. In recent papers, both Snodgrass (1954) and Asahina (1954) agree that the "cercoids" of Heymons are the true cerci, as previously maintained by Crampton (1918). Crampton, however, theorized that the cerci arose from the tenth abdominal segment, but more recent authors (Snodgrass; Asahina) place them with the epiproct and paraprocts on the eleventh segment.

If the epiproct and paraprocts are spread apart, as in figure 23, four small sclerites can be seen surrounding the anus (an). According to Heymons (1904), the middorsal pair or *laminae supra-anales* (sa) is the reduced twelfth tergite, while the two lateral ones or *laminae sub-anales* (la) represent the bipartite sternite. The membranous circumanal fold containing these sclerites has been termed the *periproct* by Snodgrass (1931).

COMPARATIVE ANATOMY OF THE GENUS PLATHEMIS

The present writer has found that the mature naiads of the two known species of the genus *Plathemis* are practically identical as regards external morphology. However, they have been shown by Needham and Westfall (1955) to differ in the relative size and shape of the dorsal abdominal hooks. Needham states that the dorsal hooks in both species are present on abdominal segments 2–6. Garman (1927), in his description of *Plathemis lydia,* states that the dorsal hooks are present on segments 3 to 5 or 6. The present writer's observations on 25 naiads of *P. lydia* from Amherst, Mass., and 6 exuviae of *P. subornata* from Ana Springs, Oreg., are not in conformity with those of either Needham or Garman. The writer has found that in both species the dorsal hooks occur always and only on segments 3–6.

In *Plathemis lydia* the dorsal hooks are present on abdominal segments 3 to 6, the longest being on segment 5. They are all posteriorly curved, sharp and thornlike, and covered with spiniform setae (fig. 24).

In *P. subornata* the dorsal hooks are also present on abdominal segments 3 to 6, the longest also being on segment 5. In this species, however, the dorsal hooks differ from those of *P. lydia* in being blunt and hairy (fig. 25).

TAXONOMY AND DISTRIBUTION

GENERIC CHARACTERS: The naiads of the genus *Plathemis* Hagen (1861) can be separated from all other odonate naiads by the following characters:

1. Naiads without caudal gills, with small spinose appendages at apex of abdomen ....Suborder Anisoptera—DRAGONFLIES
2. Labium forming a deep spoonlike mask covering face up to antennae; distal edge of labial palpus evenly and regularly toothed; ligula never with two large teeth at middle of distal margin...............Family LIBELLULIDAE
3. Head without frontal horn; lateral spines of abdominal segment 8 shorter than length (along sagittal line) of segment 9; no dorsal hook on abdominal segment 9..................................Subfamily LIBELLULINAE
4. Eyes capping anterolateral angles of head, more frontal than lateral; abdomen lanceolate in outline, gradually narrowed to apex......Tribe LIBELLULINI
5. Ligula of labium crenulate on distal margin; labial palpi each with 10 lateral setae; prementum with 8 setae. Abdomen with dorsal hooks on segments 3–6, and small lateral spines on segments 8 and 9; paraprocts twice as long as cerci..Genus *Plathemis*

SPECIFIC CHARACTERS: The mature naiads of the two known species of the genus *Plathemis* can be separated as follows:

Dorsal abdominal hooks on segments 3–6, all sharp and thornlike and bearing spiniform setae..*P. lydia*
Dorsal abdominal hooks on segments 3–6, all blunt and hairy......*P. subornata*

PREVIOUS SPECIFIC DESCRIPTIONS

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DISTRIBUTION AND DATES

Plathemis lydia: A very common and widely distributed species, inhabiting mucky ponds. Canada: British Columbia, New Brunswick, Nova Scotia, Ontario, Quebec. United States: 39 States, with the exception of Arizona, Delaware, Maryland, Montana, Nevada, North Dakota, Oregon, South Dakota, Wyoming. April 18 (Miss.) to October 16 (Tenn.).

Plathemis subornata: A western species, inhabiting swales and seepage pools in desert and semidesert areas. Canada: British Columbia. United States: Arizona, California, Colorado, Kansas, Nebraska, Nevada, New Mexico, Oregon, Texas, Utah. Mexico: Chihuahua, Sonora. April (Calif.) to October 16 (Tex.).

ABBREVIATIONS

A —anal trachea
abt —abductor tendon
ac —anteclypeus
adt —adductor tendon
aet —anepisternum
al —articular rod of labium
an —anus
ant —antenna
as —antennal suture
asc —antennal sclerite
at —anterior tentorial pit
ata —anterior tentorial arm
atg —acrotergite
axc —axillary cord
bc —basicardo
bsc —basicostal suture
bcx —basicoxite
bs —basisternum
ce —cercus
cl —clypeus
cls —clypeolabral suture
co —condyle
cos —coronal suture
cs —clypeal suture
ct —corporotentorium
Cu —cubital trachea
cx —coxa
cxa —coxal articulation
cxc —coxal cavity
cxp —pleural coxal process
dc —disticardo
dh —dorsal hook
dps —distal palpal setae
dpt —distal palpal tooth
dsc —dorsal cervical sclerite
dta —dorsal tentorial arm
dts —distitarsus
em —epimeron
emp —empodium
ep —epiproct
es —epistomal suture
et —episternum
eye —compound eye
f —flagellum
fe —femur
fp —furcal pit
fr —frons
fs —furcasternum
ge —gena
gn —accessory genitalia
gp —genital pore
hap —hypopharyngeal apodeme
hy —hypopharynx
igm —insertions of gnathal muscles
il —inner lobe
in —incisor lobe
kem —katepimeron
ket —katepisternum

la —lamina sub-analis
lbp —labial palpus
lcd —laciniadentes
lgs —ligular seta
lhs —lateral suspensorial arm
lig —ligula
lk —lateral keel
lm —labrum
lps —lateral palpal seta
ls —laterosternite
lsc —lateral cervical sclerite
lsp —lateral spine
M —median trachea
md —mandible
mh —movable hook
mo —molar surface
mps —median palpal seta
ms —median sternite
mth —mouth
mx —maxilla
n —notum
nd —nodal region
ohs —oral suspensorial arm
ol —outer lobe
os —ocular suture
osc —ocular sclerite
p —pedicel
par —parietal lobe
pc —postclypeus
pf —palpifer
pfs —postfrontal suture
pge —postgena
pls —pleural suture
pm —pleurostoma
pms —pleurostomal suture
poc —postocciput
pocs —postoccipital suture
pp —paraproct
pr —precoxale
prm —prementum
prs —premental seta
ps —poststernum
psc —prescutum
psm —postmentum
pt —plantella
pta —posterior tentorial arm
R —radial trachea
Rs —radial sector trachea
s —scape
sa —lamina supra-analis
Sc —subcostal trachea
scl —scutellum
scs —sternacostal suture
sct —scutum
sp —spiracle
st —stipes
stn —sternum
ta —tergal apophysis
tb —tibia
ths —transverse suspensorial bar
tr —trochanter
ts —tarsus
un —ungue
ut —unguitractor plate
va —valvulae
w —wing

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PERMIAN BRACHIOPODS FROM CENTRAL OREGON

(With 12 Plates)

By
G. ARTHUR COOPER
Head Curator of Geology
United States National Museum
Smithsonian Institution

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PERMIAN BRACHIOPODS FROM CENTRAL OREGON

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INTRODUCTION

The Permian brachiopods described herein come from a little-known area of Paleozoic rocks lying about 30 miles east of the geographical center of Oregon. It is about 8 miles southwest of Suplee and about 15 miles southeast of Paulina. The country is in the headwaters of Grindstone and Twelvemile Creeks which are tributaries of the Crooked River. The area is one of great structural complexity which includes Mississippian, Pennsylvanian, and Permian beds overlain by Triassic and Jurassic deposits.

Washburne (1903) was the first to report the Paleozoic sediments of this region, but Packard (1928, 1932) was the first to recognize Mississippian and Permian deposits. In 1937 Merriam and Berthiaume (published in 1943) made studies and a geological map of part of the region. Read and Merriam (1940) visited this area and collected Paleozoic plants. Merriam (1942) described Mississippian and Permian corals from these rocks. The collections made by Merriam, Berthiaume, and Read, and those earlier assembled by Packard and his students, include many interesting Mississippian species as well as the Permian specimens described below. I was invited by Dr. Merriam to describe these fossils. The Permian (Coyote Butte formation) fossils are the first to be finished but description of the Mississippian brachiopods is scheduled for the near future.

The collection submitted by Dr. Merriam consists of materials collected by University of Oregon students prior to the studies of Merriam and Berthiaume. Unfortunately, the geographic and stratigraphic data with many of these specimens are inadequate. Nevertheless, for the sake of completeness it was necessary to describe and illustrate a few of them. The brachiopods described herein are of great interest because of their obvious affinities to Russian species and because of the occurrence of genera never, or only seldom, seen in more familiar areas of Permian rock in this country. When first reported these brachiopods were thought to be of Lower Permian age (Merriam and Berthiaume, 1943, p. 158) but this more detailed study requires a revision of this view. They now appear to be of Medial Permian age with probable affinities to the fauna of the lower part of the Word formation of west Texas.

DESCRIPTION OF COYOTE BUTTE FORMATION

The following description of the Coyote Butte formation is revised from Merriam and Berthiaume (1943). The youngest Paleozoic beds of the area comprise a sequence in which massive limestones form the most conspicuous exposures. These produce prominent ridges, buttes, and small circular hills or knobs subsidiary to the main ridge slopes. Steeply dipping strata forming the crest of Coyote Butte near the southern limit of the map (text fig. 1) constitute the type section of the formation. The Coyote Butte beds here lie in the north limb of a tight syncline overturned toward the south. Another bold outcrop of the formation appears in the belt extending north-northeast from the vicinity of Tuckers Butte for about 4 miles. A third area of Permian beds includes exposures in the northeast portion of the map, one tongue of which extends southwest beyond Twelvemile Creek where it is covered by Tertiary lava.

At the type section the lower portion of the Coyote Butte formation is generally a light olive-gray limestone, often crinoidal and locally containing fusulinids in great abundance. Higher in the section, at the summit of Coyote Butte, the limestone becomes purer, finer grained, deep olive gray in color and possesses more distinct bedding. In this upper portion fusulinids are less frequently met while brachiopods are common.

The character of the Coyote Butte limestone throughout the area is similar to that found at the type locality. Coarse crinoidal debris is abundant at several localities not far above the lower contact of the formation. Conglomeratic phases of the basal limestone also occur locally. At locality S73 in the eastern part of the area rounded chert pebbles and subangular chert grains are distributed throughout a crinoidal and fusulinid-bearing limestone. Another conglomeratic phase at the base of the limestone occurs on the west side of Spotted Ridge. Here pebbles of green, white, red, and black chert become so abundant as to form a calcareous conglomerate. It seems probable that these pebbly facies represent a local reworking of underlying Pennsylvanian sediments.

Limestones of the Coyote Butte formation are interbedded with large amounts of sandstones. Furthermore the discontinuous nature of some of the limestone exposures leads to the impression that these deposits are lenticular within the arenaceous facies. Generally speaking, exposures of the sands are poor, while the limestones form promi-

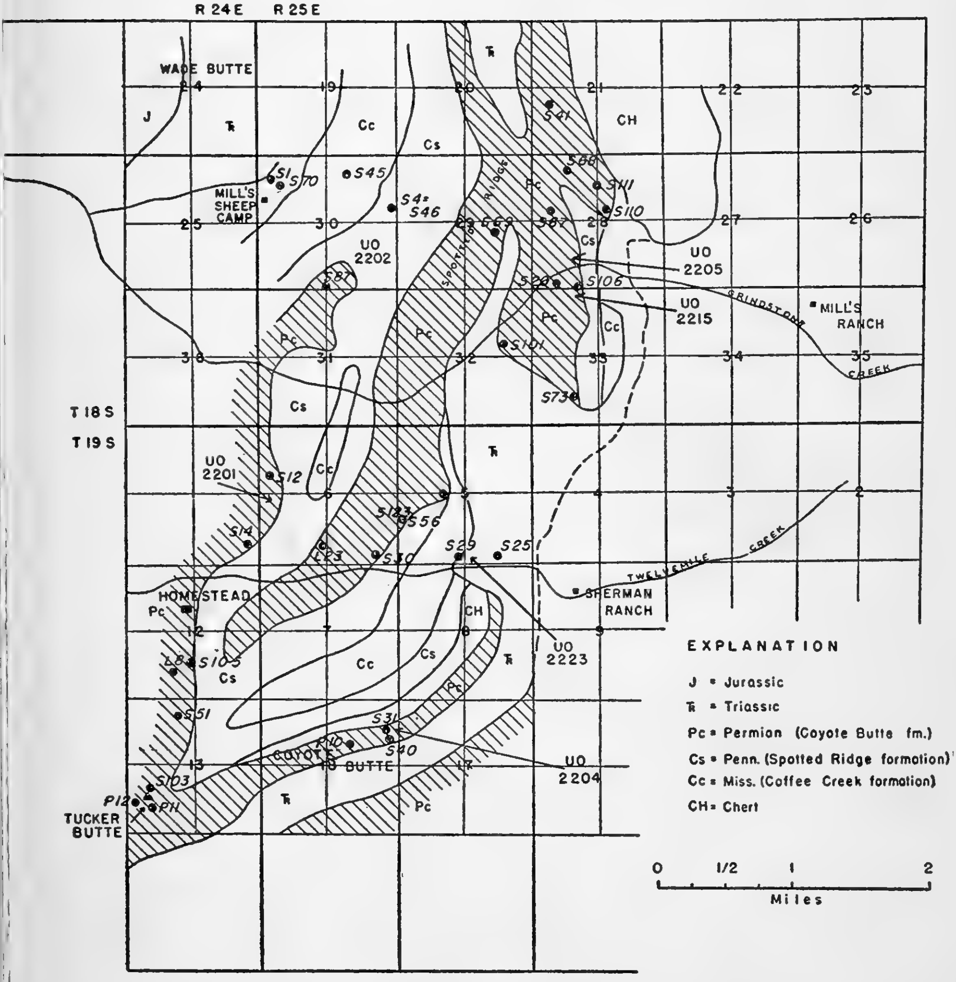

Fig. 1.—Map of Grindstone-Twelvemile Creeks area, central Oregon, showing distribution Permian rocks (oblique lines) and localities (numbers) from which brachiopods were taken. (Map redrawn after Merriam and Berthiaume, 1943.)

nent linear or circumscribed exposures. Northeast of locality S123 in the center of the map several zones of sandstone float alternately with fusulinid limestones.

Large amounts of insoluble materials, such as chert and sand grains, occur locally in the Permian limestone. At locality S68 in the northeastern portion of the area, dark, irregular chert layers up to 10 inches in thickness are interbedded with the limestone. In other occurrences the siliceous material replaces the limestone as irregular patches and permeates it in varying degree. In some instances, as along the southwest side of Spotted Ridge, the limestones are dolomitic and in extreme cases are apparently recrystallized, giving the rock a light gray or pale cream color.

Thickness.—At the type section on Coyote Butte the Permian beds measure approximately 900 feet. Estimates of thickness on Spotted Ridge and north of Tuckers Butte are approximately the same. However, exact thicknesses cannot be given because bedding is poor and folds within the massive limestone are difficult to unravel. Where the formation is to a great extent arenaceous, exposures are poorly developed. Unconformable relation of the Permian to overlying beds further conceals their thickness in some localities.

Stratigraphic relations.—The Coyote Butte is unconformable on the Pennsylvanian Spotted Ridge formation. This relation is suggested by pinching out of the Pennsylvanian strata in sec. 5, T. 19 S., R. 25 E., where the contact between Coyote Butte limestone and the Lower Carboniferous Coffee Creek formation is apparently depositional. At locality S105 north of Tuckers Butte an exposure of the lower contact of the Permian shows a slight angular discordance and a definite truncation of the conglomeratic and sandy beds of the underlying formation. On the basis of lithology and position the latter beds are presumed to be the Spotted Ridge formation. Furthermore, on the west side of Spotted Ridge and at several other localities the basal Coyote Butte strata are very pebbly limestones and calcareous conglomerates, probably indicating reworking of subjacent Pennsylvanian clastics.

LOCALITIES FROM WHICH BRACHIOPODS WERE COLLECTED

Some of the localities listed below are uncertain and sketchy because of the early lack of maps in this region. Inasmuch as good fossils are difficult to find in this complicated area, it seemed best to use all the specimens regardless of the sketchy quality of some of the locality descriptions. Completeness of faunal description seems a worthy aim in such a little-known region. Fortunately these specimens are few in number.

UNIVERSITY OF OREGON NUMBERS

U.O.

2201. Large limestone butte immediately south of the SW cor. NW¼ sec. 6, T. 19 S., R. 25 E., approximately = S12.

Echinoconchus inexpectatus Cooper

2201-1. On the north side of the butte at the base.

Anidanthus minor Cooper
Dielasma rectimarginatum Cooper
Echinoconchus inexpectatus Cooper
Kochiproductus transversus Cooper
Krotovia pustulata (Keyserling)
Pseudomartinia aff. *P. semiglobosa* (Tschernyschew)
Punctospirifer sp. 2
Rhynchopora magna Cooper
Squamularia rostrata (Kutorga)

2201-2. Between 50 and 100 feet up the side of the butte.

Anidanthus minor Cooper
Avonia oregonensis Cooper
Muirwoodia transversa Cooper
Proboscidella? carinata Muir-Wood and Cooper
Rostranteris sulcatum Cooper

2201-3. From the very top of the hill.

Chonetes sp. 1

2201-4. Outcrop just north of the main point right in the NE cor. sec. 1 = S12.

Alexenia? occidentalis Cooper
Probolionia posteroreticulata Cooper
Rhynchopora sp.
Spiriferella draschei (Toula)
Stenoscisma mutabile oregonense Cooper
S. cf. *S. plicatum* (Kutorga)

2202. "Triangulation Hill," a larger hill 2,800 feet from the SE cor. sec. 30, T. 18 S., R. 25 E., on section line fence = S87.

Echinoconchus inexpectatus Cooper
Kochiproductus cf. *K. porrectus* (Kutorga)

2202-1. Locality at the top of the hill.

Stenoscisma cf. *S. plicatum* (Kutorga)

2202-2. Ledge on south side of hill.

Alexenia? occidentalis Cooper
Antiquatonia sulcata Cooper
Avonia oregonensis Cooper
Chonetes sp. 1
Dielasma brevicostatum Cooper
Kochiproductus cf. *K. porrectus* (Kutorga)
Marginifera? costellata Cooper
Muirwoodia transversa Cooper
Neospirifer sp. 1
Probolionia posteroreticulata Cooper
Pseudomartinia aff. *P. semiglobosa* (Tschernyschew)
Rhynchopora magna Cooper
Spiriferella draschei (Toula)
Stenoscisma cf. *S. plicatum* (Kutorga)

U.O.

2202-3. Lowest ledge on north slope of hill.
Avonia oregonensis Cooper
Probolionia posteroreticulata Cooper
Probolionia elongata Cooper

2202-4. 100 yards due west of triangulation point.
Squamularia rostrata (Kutorga)

2202-5. Outcrop 450 feet due west of triangulation point.
Avonia oregonensis Cooper
Probolionia posteroreticulata Cooper

2202-6. East slope of hill 210 feet from top.
Avonia oregonensis Cooper
Stenoscisma cf. *S. plicatum* (Kutorga)

2204. Coyote Butte, fossil localities in E½NE¼ sec. 18 and NW¼ sec. 17, T. 19 S., R. 24 E., a string of hills trending northeast-southwest = S40.

2204-1. Westernmost butte of the string.
Anidanthus minor Cooper
Avonia oregonensis Cooper
Echinoconchus inexpectatus Cooper
Proboscidella? carinata Muir-Wood and Cooper
Rhynchopora magna Cooper
Squamularia rostrata (Kutorga)
Stenoscisma mutabile oregonense Cooper

2204-2. Approximately 1 mile southwest of Coyote Butte.
Alexenia? occidentalis Cooper

2204-3. From the top of the westernmost butte.
Alexenia ? occidentalis Cooper
Antiquatonia sulcata Cooper
Avonia oregonensis Cooper
Derbyia sp. 2
Dielasma brevicostatum Cooper
Echinoconchus inexpectatus Cooper
Krotovia pustulata (Keyserling)
Lingula sp.
Marginifera? profundosulcata Cooper
Muirwoodia transversa Cooper
Probolionia elongata Cooper
Spiriferella draschei (Toula)
S. parva Cooper
Squamularia rostrata (Kutorga)
Stenoscisma mutabile oregonense Cooper

2205. "Lunch Rock," just west of the road, north side of Grindstone Creek and east side of Lunch Creek, SW¼ sec. 28, T. 18 S., R. 25 E.

2205-1. The original locality just north of the road = 637.
Waagenoconcha parvispinosa Cooper

2205-5. 100 yards from "Lunch Rock" and the outcrops up Lunch Creek to the north for 250 yards = 636.
Cleiothyridina attenuata Cooper
Dielasma brevicostatum Cooper
Pleurohorridonia? elongata Cooper
Spiriferella draschei (Toula)
Stenoscisma biplicatoideum Cooper

2207. Central Bucher Butte, about 100 feet down the slope near the east central edge of sec. 17, T. 19 S., R. 24 E. (not shown on map).
Anidanthus minor Cooper
Spiriferella draschei (Toula)

U.O.

2207-2. Same.
Anidanthus minor Cooper

2210. Small limestone outcrop due west from Iron Mountain, and just west of the road, and N.15° W. of Christenson Brothers ranch, SE$\frac{1}{4}$ sec. 35, T. 17 S., R. 25 E. (not shown on map).
Spiriferella draschei (Toula)

2211. Small outcrop right behind Suplee, just due south of the Mesozoic rim, NE$\frac{1}{4}$ sec. 35, T. 17 S., R. 25 E. (not shown on map).

2211-2. On rim in limestone lens on central-north edge sec. 35 (not shown on map).
Alexenia? occidentalis Cooper

2215. Large limestone knob on the south side of Grindstone Creek, SW$\frac{1}{4}$ sec. 33, T. 18 S., R. 25 E.

2215-1. Same as above.
Anidanthus minor Cooper

2216. "Petrified snake locality," ledge of crinoidal limestone on second ridge south of Clark's place, SE$\frac{1}{4}$ sec. 33, T. 17 S., R. 25 E. (not shown on map).

2216-1. Same.
Anidanthus minor Cooper
Kochiproductus transversus Cooper
Probolionia posteroreticulata Cooper

2216-2. Same.
Dielasma brevicostatum Cooper

2218. Grindstone-Twelvemile Creeks area.

2218-2. Same.
Punctospirifer sp. 1

2219. Same as 2218.

2219-1. Same.
Pseudomartinia aff. *P. semiglobosa* (Tschernyschew)

2223. Small limestone outcrop near the south edge, center sec. 5, T. 19 S., R. 25 E., and just north of Twelvemile Creek and the road = S29.

2223-2. Float from SW cor. sec. 5 and on small hill just north of the dam.
Rostranteris sulcatum Cooper

2225. Same as 2218.
Pseudomartinia aff. *P. semiglobosa* (Tschernyschew)

613. Permian, Grindstone-Twelvemile Creeks area.
Rhynchopora magna Cooper

614. Permian, Grindstone-Twelvemile Creeks area.
Alexenia? occidentalis Cooper
Kochiproductus cf. *K. porrectus* (Kutorga)
Spiriferella draschei (Toula)

633? Permian, Grindstone-Twelvemile Creeks area.
Squamularia rostarta (Kutorga)

U.O.

636. "Lunch Creek" = U.O. 2205-5.
Avonia oregonensis Cooper
Echinoconchus inexpectatus Cooper
Rhynchopora magna Cooper
Waagenoconcha parvispinosa Cooper

637. "Lunch Creek" = U.O. 2205-1.
Leptodus? sp. 1
Meekella sp. 1
Rhynchopora magna Cooper

638. Permian, Suplee Anticline.
Alexenia? *occidentalis* Cooper
Antiquatonia sulcata Cooper
Echinoconchus inexpectatus Cooper
Krotovia pustulata (Keyserling)
Muirwoodia tranversa Cooper
Probolionia posteroreticulata Cooper
Proboscidella? *carinata* Muir-Wood and Cooper
Rhynchopora magna Cooper
Spiriferella draschei (Toula)
Squamularia rostrata (Kutorga)
Stenoscisma mutabile oregonense Cooper

639. Permian, Grindstone-Twelvemile Creeks area.
Alexenia? *occidentalis* Cooper
Echinoconchus inexpectatus Cooper
Rhynchopora magna Cooper
Spiriferella draschei (Toula)

MERRIAM AND BERTHIAUME NUMBERS

F-number localities

F. General float.
Alexenia? *occidentalis* Cooper
Echinoconchus inexpectatus Cooper
Muirwoodia transversa Cooper
Rhynchopora magna Cooper
Cooper
Waagenoconcha parvispinosa

L-number localities

L8. NW¼SE¼SW¼ sec. 12, T. 19 S., R. 24 E., 1 mile north of Tucker Butte.
Alexenia? *subquadrata* Cooper
Anidanthus minor Cooper
Avonia oregonensis Cooper
Cleiothyridina gerardi (Diener)
Composita sp. 1
Krotovia pustulata (Keyserling)
Marginifera? *profundosulcata* Cooper
Muirwoodia transversa Cooper
Rhynchopora magna Cooper
Spiriferella draschei (Toula)
Squamularia rostrata (Kutorga)
Stenoscisma biplicatoideum Cooper
S. mutabile oregonense Cooper

L23. W. side center line SE¼SW¼ sec. 6, T. 19 S., R. 25 E., about 1¾ miles west-northwest of Sherman Ranch.
Avonia oregonensis Cooper
Dielasma rectimarginatum Cooper
Spiriferella draschei (Toula)

P-number localities

P10. NE¼SW¼NE¼ sec. 18, T. 19 S., R. 25 E., northeast of Coyote Butte.

Alexenia? occidentalis Cooper
Antiquatonia reticulata Cooper
A. sulcata Cooper
Cleiothyridina gerardi (Diener)
Echinoconchus inexpectatus Cooper
Kochiproductus transversus Cooper
Krotovia parva Cooper
K. pustulata (Keyserling)
Muirwoodia transversa Cooper
Probolionia posteroreticulata Cooper
Rhynchopora magna Cooper
Spiriferella draschei (Toula)
Squamularia rostrata (Kutorga)
Stenoscisma biplicatoideum Cooper
S. mutabile oregonense Cooper

P11. NE¼SW¼SW¼ sec. 13, T. 19 S., R. 25 E., Tuckers Butte.

Echinoconchus inexpectatus Cooper
Kochiproductus transversus Cooper
Rostranteris merriami Cooper
Squamularia rostrata (Kutorga)

P12. Center NW¼SW¼SW¼ sec. 13, T. 19 S., R. 24 E., Tuckers Butte.

Alexenia? occidentalis Cooper
Anidanthus minor Cooper
Chonetes sp. 1
Cleiothyridina gerardi (Diener)
Dielasma brevicostatum Cooper
Squamularia rostrata (Kutorga)
Waagenoconcha parvispinosa Cooper

S-number localities

S1. SW¼NW¼NW¼ sec. 30, T. 18 S., R. 25 E., about 4 miles N. 35° W. of Sherman Ranch.

Echinoconchus inexpectatus Cooper

S4. See S46.

S12. NW¼SW¼NW¼ sec. 6, T. 19 S., R. 25 E., about 2½ miles N. 69° W. of Sherman Ranch.

Alexenia? occidentalis Cooper
Antiquatonia sulcata Cooper
Avonia oregonensis Cooper
Kochiproductus transversus Cooper
Marginifera? profundosulcata Cooper
Probolionia posteroreticulata Cooper
Proboscidella? carinata Muir-Wood and Cooper
Pseudomartinia berthiaumei Cooper
P. aff. *P. semiglobosa* (Tschernyschew)
Spiriferella draschei (Toula)

S14. Center E½SE¼SE¼ sec. 1, T. 19 S., R. 24 E., ½ mile northeast of Homestead.

Avonia oregonensis Cooper
Echinoconchus inexpectatus Cooper
Linoproductus cf. *L. lutkewitschi* (Stepanow)
Stenoscisma mutabile oregonense Cooper

S20. SE¼SW¼SW¼ sec. 28, T. 18 S., R. 25 E., about 2¼ miles north of Sherman Ranch.

Antiquatonia reticulata Cooper
Dielasma? truncatum Cooper
Neospirifer sp.
Rhynchopora magna Cooper
Stenoscisma americanum Cooper
S. mutabile oregonense Cooper

S25. SW cor. SE¼SE¼ sec. 5, T. 19 S., R. 24 E., about ¾ mile northwest of Sherman Ranch.

Chonetes sp. (not described or figured)
Echinoconchus inexpectatus Cooper
Hustedia sp. 1

S29. SE cor. SW¼ sec. 5, T. 19 S., R. 25 E., about 1 mile west-northwest of Sherman Ranch.

Echinoconchus inexpectatus Cooper
Probolionia posteroreticulata Cooper

S30. SW¼SE¼SE¼ sec. 6, T. 19 S., R. 25 E., 1½ miles west-northwest of Sherman Ranch.

Alexenia? occidentalis Cooper
Avonia oregonensis Cooper
Chonetes pygmoideus Cooper
Marginifera? brevisulcata Cooper
Probolionia posteroreticulata Cooper

S31. SE¼NE¼NE¼ sec. 18, T. 19 S., R. 25 E., Coyote Butte, about 1¾ miles southwest of Sherman Ranch.

Chonetes sp. 1

S39. Top of Coyote Butte (not located on map).

Alexenia? occidentalis Cooper
Echinoconchus inexpectatus Cooper
Marginifera? costellata Cooper
Rhynchopora magna Cooper

S40. NE cor. SE¼NE¼ sec. 18, T. 19 S., R. 25 E., east side of Coyote Butte.

Avonia oregonensis Cooper
Echinoconchus inexpectatus Cooper
Krotovia parva Cooper
K. pustulata (Keyserling)
Marginifera? profundosulcata Cooper
Muirwoodia transversa Cooper
Probolionia posteroreticulata Cooper
Rhynchopora magna Cooper
Spiriferella draschei (Toula)
Stenoscisma mutabile oregonense Cooper

S41. About center NW¼SW¼ sec. 21, T. 18 S., R. 25 E., about 3¾ miles north of Sherman Ranch.

Alexenia? occidentalis Cooper
Anidanthus minor Cooper
Krotovia pustulata (Keyserling)
Kochiproductus transversus Cooper
Marginifera? profundosulcata Cooper
Paeckelmannia aff. *Chonetes alatus* Stuckenberg
Rostranteris merriami Cooper
R. sulcatum Cooper
Squamularia rostrata (Kutorga)
Stenoscisma mutabile oregonense Cooper

S43. Equals S46.

S45. General float near center NW¼NE¼ sec. 30, T. 18 S., R. 25 E.

Avonia oregonensis Cooper
Cleiothyridina attenuata Cooper
Linoproductus cf. *L. lutkewitschi* (Stepanow)
Marginifera? brevisulcata Cooper

Echinoconchus inexpectatus Cooper
Rhynchopora magna Cooper

S46. SE¼SE¼NE¼ sec. 30, T. 18 S., R. 25 E., about 3¼ miles N. 25° W. of Sherman Ranch = S4.

Anidanthus minor Cooper
Antiquatonia sulcata Cooper
Avonia oregonensis Cooper
Crurithyris sp. 1
Echinoconchus inexpectatus Cooper
Krotovia pustulata (Keyserling)
Marginifera? costellata Cooper
Marginifera ? costellata
M.? multicostellata Cooper
Muirwoodia transversa Cooper
Probolionia elongata Cooper
P. posteroreticulata Cooper
Rhynchopora magna Cooper
Spiriferella draschei (Toula)
Squamularia rostrata (Kutorga)
Stenoscisma mutabile oregonense Cooper
Waagenoconcha parvispinosa Cooper

S47. NW¼SE¼ sec. 28, T. 18 S., R. 25 E., about 2½ miles north of Sherman Ranch (not located on map).

Antiquatonia sulcata Cooper
Chonetes sp. 1
Echinoconchus inexpectatus Cooper
Pleurohorridonia? elongata Cooper
Spiriferella draschei (Toula)
Stenoscisma biplicatoideum Cooper
S. mutabile oregonense Cooper

S49. Several zones of the Permian at Coyote Butte (not located on map).

Alexenia? occidentalis Cooper
Avonia oregonensis Cooper
Linoproductus cf. *L. lutkewitschi* (Stepanow)
Marginifera? brevisulcata Cooper
M.? profundosulcata Cooper
Probolionia elongata Cooper
P. posteroreticulata Cooper
Proboscidella? carinata Muir-Wood and Cooper
Rhynchopora magna Cooper
R. sp.
Spiriferella draschei (Toula)

S50. General collection of Permian including several zones, Coyote Butte (not located on map).

Alexenia? occidentalis Cooper
Anidanthus minor Cooper
Echinoconchus inexpectatus Cooper
Kochiproductus transversus Cooper
Lingula sp.
Muirwoodia transversa Cooper
Proboscidella? carinata Muir-Wood and Cooper
Rostranteris merriami Cooper
Spiriferella draschei (Toula)
Stenoscisma mutabile oregonense Cooper

S51. About center NE¼NW¼ sec. 13, T. 19 S., R. 24 E., about ½ mile north-northeast of Tuckers Butte.

Antiquatonia sulcata Cooper
Pleurohorridonia? elongata Cooper
Spiriferella draschei (Toula)

S56. SW¼NW¼SW¼ sec. 5, T. 19 S., R. 25 E., about 1½ miles northwest of Sherman Ranch.

Krotovia pustulata (Keyserling)
Rhynchopora magna Cooper
Spiriferella draschei (Toula)

Marginifera? profundosulcata Cooper
Squamularia rostrata (Kutorga)

S67. Just south of center SW¼NW¼ sec. 28, T. 18 S., R. 25 E., 2 miles northwest of Mills Ranch.

Antiquatonia reticulata Cooper
A. sulcata Cooper

S68. Center W½NE¼NW¼ sec. 28, T. 18 S., R. 25 E., about 3½ miles north of Sherman Ranch.

Chonetes sp. 1
Derbyia sp. 2
Probolionia elongata Cooper
Spiriferella draschei (Toula)

S69. SE cor. NE¼NW¼SE¼ sec. 29, T. 18 S., R. 25 E., 2¾ miles N. 12° W. of Sherman Ranch.

Probolionia posteroreticulata Cooper

S70. SW cor. SE¼NW¼NW¼ sec. 30, T. 18 S., R. 25 E., about 4 miles N. 30° W. of Sherman Ranch and near Mills sheep camp.

Echinoconchus inexpectatus Cooper
Krotovia pustulata (Keyserling)

S87. Just N. of center S. line sec. 30, T. 18 S., R. 25 E., ¾ mile southeast of Mills sheep camp.

Anidanthus minor Cooper
Avonia oregonensis Cooper
Cleiothyridina attenuata Cooper
Dielasma brevicostatum Cooper
Echinoconchus inexpectatus Cooper
Kochiproductus cf. *K. porrectus* (Kutorga)
Krotovia pustulata (Keyserling)
Pleurohorridonia? elongata Cooper
Probolionia posteroreticulata Cooper
Rhynchopora magna Cooper
Spiriferella draschei (Toula)
Spiriferellina pauciplicata Cooper
Stenoscisma cf. *S. plicatum* (Kutorga)
Wellerella multiplicata Cooper

S101. SW¼SE¼NE¼ sec. 32, T. 18 S., R. 25 E., 2 miles N. 15° W. of Sherman Ranch.

Derbyia sp. 1
D. sp. 2
Krotovia aff. *K. barenzi* (Miloradovitch)
Neospirifer sp. 1
Pseudomartinia berthiaumei Cooper
Punctospirifer sp. 1
Rhipidomella sp. 1
Spiriferellina sp. 1.

S103. SW¼NW¼SW¼ sec. 13, T. 19 S., R. 24 E., Tuckers Butte.

Alexenia? occidentalis Cooper
Anidanthus minor Cooper
Antiquatonia sulcata Cooper
Avonia oregonensis Cooper
Chonetinella sp. 1
Cleiothyridina gerardi (Diener)
Derbyia sp. 1
Dielasma brevicostatum Cooper
Linoproductus cf. *L. lutkewitschi* (Stepanow)
Muirwoodia transversa Cooper
Neospirifer sp. 1
Probolionia posteroreticulata Cooper
Rhynchopora magna Cooper
R. sp.
Spiriferella draschei (Toula)

Kochiproductus transversus Cooper
Krotovia pustulata (Keyserling)
Squamularia rostrata (Kutorga)
Stenoscisma cf. *S. plicatum* (Kutorga)
Waagenoconcha parvispinosa Cooper

S106. SW¼SE¼SW¼ sec. 28, T. 18 S., R. 25 E., 2½ miles due north of Sherman Ranch.

Alexenia? *subquadrata* Cooper
Avonia oregonensis Cooper
Kochiproductus cf. *K. porrectus* (Kutorga)
Probolionia posteroreticulata Cooper
Squamularia rostrata (Kutorga)
Stenoscisma cf. *S. plicatum* (Kutorga)

S111. About ¼ mile north of center sec. 28, T. 18 S., R. 25 E., 1¾ miles northwest of Mills Ranch.

Chonetes sp. 1
Linoproductus cf. *L. lutkewitschi* (Stepanow)

CORRELATION OF THE PERMIAN OF OREGON

Any correlation based on a single group of animals, unless that group is an accepted standard of comparison, must be regarded as tentative. In view of the fact that goniatites and fusulines at present are regarded as the most reliable groups in the Permian, some conflict with a correlation based on brachiopods alone may be expected. The brachiopods of the upper Paleozoic are still too little known for all the superfamilies represented to be reliable. Furthermore, some of the genera such as *Composita* have few morphological characters on the exterior and, at present, are of no value in correlation. Investigation of the interior of such brachiopods may prove them to be more useful but development of the interior will require much skill and more time than most paleontologists are willing to give.

The Permian assemblage from Oregon is a varied one but it contains a number of genera that can be excluded from consideration because of their present slight correlative value. These are *Lingula, Rhipidomella, Derbyia, Composita, Squamularia,* and *Hustedia.* In addition *Neospirifer, Crurithyris,* and *Punctospirifer* are added to this list, not because of any implied lack of correlative value, but because the specimens available are too poor or insufficiently represented to use.

Another special problem in this exercise in correlation is the fact that some of the genera and species are unlike any described American Permian species. Comparison with European forms, and especially Russian ones, is difficult because comparative material does not exist in this country. Furthermore the modern illustrations of some of the

Russian species are not good, and the good available pictures, those of Tschernyschew, are often provided with a stratigraphic assignment of dubious value.

DISCUSSION OF THE SPECIES

Meekella in the Oregon fauna appears to have little value in correlating these rocks. The species represented is unlike any of the European species but is most like *M. striatocostata* (Cox) from the Wolfcampian in Kansas. It also resembles *M. difficilis* Girty from the Bone Spring and Leonard formations of Texas and *M. skenoides* Girty from the Word and Delaware Mountain formations of Texas.

Of the two species of *Chonetes* in the Oregon fauna, one is like *C. timanicus* of the *Schwagerina* zone of the Timan, and the other, the larger of the two, is most like three Word species: *C. deliciasensis* King, *C. monosensis* Cooper, and *C. phosphoriensis* Branson. The indication is thus of a post-Leonardian age. The fragmentary *Chonetinella* is not of much help because it cannot be related to known species. The last chonetid from Oregon is *Paeckelmannia* cf. *C. alatus* Stuckenberg which has no known counterpart in American described species but is reported from the Artinskian of the Urals.

The one species of *Leptodus?* from Oregon is an equivocal form. Comparison with numerous specimens in the National Museum collection suggests that it is most related to some of the small subconical forms common in the upper part of the Leonard formation of the Glass Mountains. These are undescribed; consequently, nothing definitive about the relationships of the Oregon species can be stated.

The productoids in the Oregon fauna are a numerous and varied group. They also contain a number of genera and species that have considerable value in correlation. Some uncertainty, however, exists in the stratigraphic assignments of some of the Russian species. In general, the present assigned stratigraphic levels of these are far lower than similar species in North America.

Avonia oregonensis Cooper, n. sp., is similar to *A. tuberculatus* (Moeller) from the *"Schwagerina"* horizon in Russia. In North America *A. subhorrida* (Meek) from the Phosphoria formation appears to be a related species. Other related species occur in the Word formation, and similar forms appear in the Leonard but the latter are smaller and probably unrelated. They do, however, indicate that the genus has a fairly long range.

Two species of *Antiquatonia* occur in the Oregon fauna. This genus is not yet well known in North America but indications in the collections of the National Museum are that it ranges through much of the Pennsylvanian and into the Permian. The Oregon specimens are related to *A. hessensis* (King) from the upper Leonard of the Glass Mountains.

A number of Oregon specimens are referred to two species of *Alexenia,* a genus described in Russia. This genus embraces shells like the familiar *"Marginifera" lasallensis* of the American Pennsylvanian and Permian. The generic assignment is not entirely a happy one because the interior of the American shells does not agree well with the published diagram of the interior of the type species. Nevertheless, the American shells are long ranged and seem to embrace the Oregon specimens. The genus in America goes to lower Word. The Oregon specimens are not especially distinctive.

Two species of *Kochiproductus* are recognized in the Oregon fauna, one of them new but the other assigned to the Russian species *K. porrectus* (Kutorga) from the *Cora* and *"Schwagerina"* beds of Timan and the Urals. This genus in North America is common in the Wolfcampian but is rare above. A species occurs in the Bone Spring formation but it is not yet known from the Word or higher beds. In Greenland, however, *Kochiproductus* occurs in the late Permian. It does not therefore give definitive aid in correlation but it is definitely in the *"Schwagerina"* beds of Tschernyschew.

For correlation one of the best species in the Oregon fauna is *Muirwoodia transversa* Cooper, n. sp. In North America this genus is not known below the Word formation. It appears in the Lower Word in great abundance and is common in a larger form in the Phosphoria formation and its equivalents in Nevada, Utah, Wyoming, and Mexico. The genus is also known in Greenland. In Russia, however, it may have a longer range than in North America. It is recorded there from the *"Schwagerina"* horizon and is known from the Jisu Honguer limestone in Mongolia and elsewhere in China.

At one time *Waagenoconcha* was regarded as an excellent guide to the Permian, but now it is known from the Pennsylvanian of this country and occurs in pre-Permian rocks in Russia. The Oregon species is a small one but is like small individuals of *W. montpelierensis* Girty.

Krotovia is represented by three species, one of them new. Of the previously described species, *K.* aff. *K. barenzi* is from the *"Schwagerina"* beds in Russia and from the Upper Marine group in northeast Greenland. *Krotovia pustulata* (Keyserling) is from the *"Schwagerina"* beds of Russia and the Maping limestone of China. In North America no other described Permian productoid like this one is known.

One species is referred to *Pleurohorridonia* with a query. This genus was recently described by Dunbar from Greenland and is assigned to late Permian. The Oregon specimen is too poor and uncertainly identified to use in correlation.

One species is referred to *Linoproductus lutkewitschi* which is not definitely located stratigraphically but comes from the *Productus* beds in Greenland.

Anidanthus is a distinctive linoproductid known from Russia, North America, and Australia. In North America it is abundant at the top of the Leonard and the base of the Word formations. A Russian species *A. aagardi,* which is similar to the Oregon species, is known from the *"Schwagerina"* beds and the Artinskian.

Echinoconchus inexpectatus Cooper, n. sp., is most like *E. fasciatus* (Kutorga) which occurs in the *"Schwagerina"* limestone of Russia. In the United States outside Oregon *Echinoconchus* is an exceedingly rare fossil in the Permian.

Marginifera is so uncertainly identified in the Oregon fauna that it cannot be used in correlation. The new genus *Probolionia* has a structure like that of the Mississippian genus *Diaphragmus* and cannot be evaluated in correlation at the present time.

The pretty little shell here referred to *Proboscidella*(?) is like *P.*? *kutorgae* from the *"Schwagerina"* beds of Russia but unlike any known American productoid.

The Rhynchonellacea are not well represented in the Oregon fauna. The one *Wellerella* is like *W. pinguis* (Girty) from the Leonard and Word and *W. shumardiana* (Girty) from the Capitan limestone. *Rhynchopora magna* is so close to other rhynchoporas and the range of the genus is so long that it has little value in correlation.

The Stenoscismatacea are common in Oregon and give close ties with Russia. Several species of *Stenoscisma* are all close to Russian forms from the *"Schwagerina"* beds.

Cleiothyridina is rare in the Permian of North America. A species of small size is known from the Wolfcamp formation of the Glass Mountains. *Cleiothyridina gerardi* (Diener) to which one Oregon species is referred is a member of the fauna of the *"Schwagerina"* beds. *Pseudomartinia berthiaumei* is closest to species from the *"Schwagerina"* beds of Russia.

Spiriferella draschei (Toula) is a Russian species identified in Oregon which belongs in the *"Schwagerina"* beds and the Artinskian. It has also been identified in the Cache Creek series of British Columbia.

Spiriferellina pauciplicata Cooper, n. sp., from Oregon is most like

S. pyramidata (Tschernyschew) which occurs in the Russian *"Schwagerina"* beds.

Rostranteris is a little-known terebratuloid genus described from Sicily where it is said to be Word in age (Miller, 1933). The Oregon species, *R. merriami* Cooper, n. sp., is most like *Rhynchonella keyserlingi* Moeller from the *"Schwagerina"* beds of Russia. The other Oregon species, *R. sulcatum* Cooper, n. sp., is most like *R. nucleola* (Kutorga) also from the *"Schwagerina"* beds but identified widely in other formations throughout the world.

Of the three species of *Dielasma* described from the Oregon fauna, *D.? truncatum* Cooper, n. sp., is eliminated from consideration because of the uncertainty of its stratigraphic position. The other two species, both new, are not very distinctive. *Dielasma breviplicatum* Cooper, n. sp., is most like *D. prolongatum* Girty from the Delaware Mountain formation.

CORRELATION OF THE OREGON FAUNA WITH PERMIAN FAUNAS OF NORTH AMERICA

It is difficult to correlate Permian faunas on the basis of brachiopods because little is known about them. In North America only three studies are available for consultation: Girty's (1909) report on the Guadalupian fauna of west Texas, which, although massive, is incomplete; King's (1930) report on the Glass Mountains, Texas, brachiopods; and Dunbar and Condra (1932) on the Pennsylvanian brachiopods of Nebraska. The title of the last monograph is misleading because the report contains descriptions of many Lower Permian species.

Inspection of the Oregon fauna will at once show its Middle Permian affinities. It is therefore unnecessary to consider Wolfcampian or the higher Guadalupian. In comparing with the Glass Mountains sequence, in which the brachiopods are perhaps better known than in any other fauna, it is necessary to make an explanation of the Leonard and Word formations.

Glass Mountains.—The Leonard fauna is a varied one. The assemblage at the base and for some hundreds of feet is characterized by *Scacchinella* and is quite different from the fauna found in the upper part. The fauna of the Leonard described by King in 1930 is characterized by a number of genera which, in the Glass Mountains, are confined to this interval: *Institella* and *Uncinuloides.* In the eastern part of the mountains the Word formation overlying the Leonard is distinguished by the bituminous and laminated nature of the limestones. These limestones are exactly like the Bone Spring limestone of the Guadalupe Mountains. Furthermore, some of the fossils of the Lower Word (limestone No. 1) are those of the underlying Leonard: *Dictyoclostus bassi* and *Perrinites,* a goniatite.

According to A. K. Miller (1945, p. 14) *Perrinites* characterizes the Leonard but the Lower Word is actually also in the zone of *Perrinites.* Furthermore, a few brachiopods that appear first in Word limestone No. 1 are prophetic of the higher Word. The most important one of these is *Muirwoodia,* which has not yet been seen in the Leonard. Chiefly on the basis of the presence of *Muirwoodia* the Oregon Permian seems to ally itself with the Word limestone No. 1. No other brachiopod species or genera in the Oregon Permian are violently in conflict with this notion.

A correlation of the Oregon Permian with the lower Word also suggests alliance of the fauna with that of the Phosphoria of Idaho where *Muirwoodia* is also present, together with other species that are in line with this correlation. The Monos formation of Mexico has been allied with the Phosphoria, but it seems to have affinities rather with the middle or upper Word than with the lower part.

British Columbia.—The Cache Creek formation of British Columbia has long been known to be of Permian age. Parts of it have been correlated with Wolfcampian and Leonardian (Thompson and Verville, 1950) but still younger Permian, the Guadalupian, has also been recognized (Thompson, Wheeler, and Danner, 1950). Kindle (1926) described a species of *Leptodus* from this formation in British Columbia, and Girty (*in* Daly 1915, pp. 121-122) listed some Russian species that are the same as some listed herein. However, the formation or series was dated as Pennsylvanian rather than Permian.

Crockford and Warren (1935) published a list of fossils from the Cache Creek series which includes names similar to or identical with those recorded in Oregon. These authors indicate the Eurasiatic affinities of the fauna and the slight resemblance to the faunas of the Glass Mountains and the Phosphoria. They did not, however, offer a specific correlation.

It seems safe to say that the Oregon fauna is represented in the Cache Creek series, not in the lower or Wolfcampian part but in post-Wolfcampian beds. The fossils listed by Crockford and Warren came from the upper part of the series, and it is to this part that the Oregon fauna is related.

CORRELATION OF THE OREGON FAUNA WITH THE PERMIAN FAUNA OF RUSSIA

The Permian fauna of Oregon has obvious and close affinity to the fauna of part of the Russian Permian sequence. The published Russian work which illustrates these fossils best is that by Tschernyschew (1902), especially the species described from the Ufa Plateau. Unfortunately, these are not adequately located stratigraphically.

Tschernyschew described brachiopods from two regions in his great monograph: From the Timan arch in northeastern Russia and the Ufa Plateau in southeastern Russia. According to Dunbar (1940) Tschernyschew established a sequence in the Timan area consisting of the *Omphalotrochus* beds, *Cora* beds, and *Schwagerina* beds in ascending order. In attempting to apply this sequence to the strata of the Ufa Plateau far to the south, Tschernyschew made some mistakes. The fossils he used for correlation purposes were not his zone guides, the fusulines, but the brachiopods which accompany them. Consequently, in the Ufa Plateau with its reefy developments, facies fossils were mistaken for guide fossils with the result that the *Schwagerina* zone was identified far above its true position. The "*Schwagerina*" zone of the Ufa Plateau region thus contains brachiopods that do not occur in the true *Schwagerina* zone.

Lately the "*Schwagerina*" zone of the Ufa Plateau has been divided into four formations in ascending order: Chernya Rechka, Irghina, Sarga, and Krasnoufimsk formations. These make up the Artinskian in this region (Tolstikhina, 1935). Lists of species from these formations are given by Fredericks (1934), Gorsky (1937), and Tolstikhina (1937). Most of the Russian species identified in the Oregon Permian and other closely related forms range throughout these formations. These Russian species are *Kochiproductus porrectus* (Kutorga), *Krotovia pustulata* (Keyserling), *Stenoscisma mutabile* Tschernyschew, *Cleiothyridina gerardi* (Diener), *Squamularia rostrata* (Kutorga), and *Spiriferella draschei* (Toula).

These Russian species therefore permit correlation with the Artinskian. It is more difficult to delimit the part of the Artinskian represented in Oregon. The Chernya Rechka formation can be eliminated from consideration because it contains *Scacchinella* and other fossils indicating a late Wolfcampian or early Leonardian age. The Oregon fauna thus seems best to conform with the Irghina and Sarga faunas and is thus correlative to medial or late Artinskian.

Study of the Permian brachiopod fauna thus indicates that correlation in the United States is with the fauna of the basal Word which contains the Leonardian elements *Perrinites* and *Dictyoclostus bassi*. In Russia the correlation is with medial to late Artinskian.

Another and perhaps more positive correlation will be afforded by study of the fusulines which are common in the Permian rocks of the Grindstone-Twelvemile Creeks area. It is possible, however, that the correlation based on the fusulines will be at variance with the present one derived from study of the brachiopods. Correlations based on a single group of animals are seldom reliable unless the animal group used is an already established zone fossil. Zoning of the late Paleozoic has hitherto been based on the fusulines. The brachiopods of the Pennsylvanian and Permian, however, are still too poorly known to be reliable as zone fossils. They will increase in correlative value as more collections and critical studies are made.

DESCRIPTION OF THE SPECIES

In the descriptions full synonymies are not cited. Citation to the original description is generally given. This is followed by one or more references where full synonymies appear.

Class GASTROCAULIA

Superfamily OBOLACEA Schuchert, 1896

Family OBOLIDAE King, 1846

LINGULA sp.

Plate 1A, figures 1-3

Shell small for the genus, length twice the width, strongly convex in anterior and posterior profile but slightly convex in lateral profile. Beak bluntly pointed; sides gently rounded but anterior margin narrowly rounded. Interior with a long ridge extending along the axis of the valve nearly from the beak to about the middle where it ends at a callus swelling on the floor. Traces of two pallial trunks appear anterior to the callus.

Measurements in mm.—Length 17.3, width at middle 8.8.

Types.—Figured specimens, U.S.N.M. 125311, 125531.

Localities.—S50; U.O. 2204-3.

Discussion.—*Lingula* is rare in any Permian rocks in the United States and is apparently not frequently met elsewhere. This is a more elongated and more acutely pointed species than *L. carbonaria exporrecta* Girty from the Phosphoria formation in Wyoming. The material available is not sufficient for the establishment of a species, as it consists only of a pedicle valve and a crushed brachial valve.

Class PYGOCAULIA

Suborder DALMANELLOIDEA Moore, 1952

Superfamily Dalmanellacea Schuchert and Cooper, 1931

RHIPIDOMELLA sp. 1

Plate 1F, figure 12

This genus is represented by a single specimen, a small brachial valve having a length of 5.6 mm. and a width at the widest point, slightly anterior to the middle, of 5.4 mm. Anterior profile somewhat strongly convex and slightly narrowed in the median region. Lateral profile most convex in the umbonal region and becoming less convex anteriorly. Lateral margins broadly rounded; anterior margin broadly rounded; posterior margin somewhat narrowly rounded. Beak small, protruding slightly posterior to the posterior margin. Median region marked by a faint sulcus. Costellae narrowly rounded, about 4 to the millimeter at the front margin.

Type.—Figured specimen, U.S.N.M. 125314.

Locality.—S101.

Discussion.—This is obviously a juvenile specimen and is thus difficult to relate to any of the known species from Russia or the United States.

Suborder STROPHOMENOIDEA Maillieux, 1932

Superfamily Orthotetacea Williams, 1956

Family ORTHOTETIDAE MacEwan, 1939

DERBYIA sp. 1

A single imperfect brachial valve is the only representative of the large Derbyias usually so common in the Permian. It is 48 mm. long and more than 60 mm. wide. The lateral profile has moderate convexity. These measurements thus indicate a large species but no specific characters of significance can be determined.

Type.—Described specimen, U.S.N.M. 125532.

Localities.—S101, S103.

DERBYIA sp. 2

Plate 1B, figures 4-7

About medium size for the genus, wider than long, semiconical in outline. Sides rounded; anterior margin broadly rounded. Surface costellate, costellae numbering 2 to 3 to the millimeter at the front margin.

Pedicle valve with uneven lateral profile, flattened in the umbonal region, but gently convex in the anterior region; anterior profile broadly convex but with steep lateral margins. Interarea moderately long, triangular; pseudodeltidium narrow and strongly convex; palintrope steeply apsacline. Sides of interarea forming an angle of about 110°. Median septum, short, off-center.

Brachial valve evenly and moderately convex in lateral profile; anterior profile broadly convex but with a narrow median depression. Lateral slopes moderately steep. Umbo somewhat swollen; sulcus originating at the beak narrow and shallow to the front margin. Cardinal process moderately long.

Types.—Figured specimens, U.S.N.M. 125312, 125315.

Localities.—S68, S101; U.O. 2204-3.

Discussion.—The specimens assigned here are poorly preserved. They suggest an undescribed species from the upper Leonard of the Glass Mountains, Texas, but may be the young of *Derbyia* sp. 1 above.

MEEKELLA sp. 1

Plate 1D, figure 9

This genus is represented by a single specimen broken nearly through the middle but preserving the dental plates and most of the pseudodeltidium. The specimen represents a small species about 19 mm. long, about the same in width, and having a thickness of about 18 mm. Width of hinge 15 mm. The beak is erect and the interarea shows only slight curvature. The surface was marked by about 14 plications. The brachial valve is thickest posteriorly, and its beak is strongly incurved as is usual in the genus.

Type.—Figured specimen, U.S.N.M. 125313.

Locality.—637.

Discussion.—None of the Russian meekellas is like this one. *Meekella eximia* (Eichwald) is larger and more strongly plicated; *Meekella uncitoides* Tschernyschew is not strongly plicated and is a much more elongated species. Specimens figured by Tschernyschew (1902, pl. 24, figs. 7a,b) as *M. striatocostata* (Cox) are suggestive but the ribbing is more subdued. None of the Alpine species described by Schellwien (1900) even remotely resembles the Oregon species.

Compared to American Permian species the Oregon form is most like *M. striatocostata, M. difficilis* Girty, and *M. skenoides* Girty. These species are small compared with the generality of American meekellas. The ribbing of *M. difficilis* is similar to that of the Oregon species but is not so sharp and strongly elevated. Furthermore the shape of the two is different, the Texas form having a more elongated and attenuated beak of the pedicle valve. In *M. skenoides* the inclination of the interarea is like that of the Oregon species but the ribbing of the Texas species is stronger and broader. Actually the American species most like the Oregon one is from the early Permian of Kansas and now called *M. striatocostata* (Cox). The latter species, which is identified in Pennsylvanian as well as Permian rocks, is in serious need of revision.

Suborder CHONETOIDEA Muir-Wood, 1955

Superfamily CHONETACEA Shrock and Twenhofel, 1953

Family CHONETIDAE Hall and Clarke, 1895

CHONETES sp. 1

Plate 1I, figures 27-35

Shell of about medium size for the genus, transversely subrectangular in outline; hinge narrower than the widest part which is just posterior to the middle; sides gently rounded; anterior margin broadly rounded. Surface marked by fine costellae about 4 in 1 mm. at the front margin.

Pedicle valve moderately convex in lateral profile, broadly convex in anterior profile; beak small, incurved; umbo low and only gently swollen; sulcus varying from shallow to moderately deep, extending from the umbo to the front margin; flanks moderately swollen; slopes to cardinal extremities flattened and steep.

Brachial valve gently concave; umbo deeply concave, the concavity widening anteriorly but flattening and becoming imperceptible in the anterior half. Posterolateral extremities flattened.

Measurements in mm.—Figured specimen, U.S.N.M. 125470a, length 14.6, brachial valve length 13.2, maximum width 20.9, hinge width 18.3, thickness 3.7 (this is the actual measure but the valve is exfoliated on the dorsal side; the true thickness must have been about 4.0), height 5.3; figured specimen, U.S.N.M. 125318, length 15.5, maximum width 23.1, hinge width 19.0, height 4.4?.

Types.—Figured specimens, U.S.N.M. 125318, 125319, 125470a,b.

Localities.—P12; S31, S47, S68, S111; U.O. 2201-3, 2202-2.

Discussion.—This is a large species but the specimens in the collection are few and poorly preserved. Of North American described chonetids the Oregon specimens are most like *C. deliciasensis* King (1930) in the flatness of the brachial valve and the shallowness of the median sulcus of the pedicle valve, but the latter feature may be a variable one. *Chonetes monosensis* Cooper (1953) is also suggestive because of its fine ornamentation but its brachial valve is even flatter than that of the Oregon one.

The Oregon specimens indicate a variable species or possibly more than one species. The specimen from S68 is best preserved and has both valves. The sulcus of the pedicle valve is shallow but a specimen from U.O. 2201-3 has the same form but a deep sulcus. The specimen is much exfoliated and this may emphasize the depth of the sulcus. However, a specimen from S111 is flatter and with a shallower sulcus. The description above was composed on the basis of the complete specimen, and the above comparisons were made with it.

Chonetes phosphoriensis Branson (1930) is similar internally to the Oregon species, Branson's figure 6 on plate 5 being very like the impression of the pedicle valve from S111. His species, however, appears to be more strongly costellate than the Oregon specimens.

CHONETES PYGMOIDEUS Cooper, new species

Plate 1H, figures 19-26

Shell small for the genus, subcircular in outline with maximum width at the middle, well-rounded sides and anterior margin; surface costellate, costellae numbering about 5 to the millimeter.

Pedicle valve strongly convex in lateral profile, especially in the umbonal region which is strongly swollen; anterior profile strongly and narrowly convex; median region strongly inflated; sulcus originating on the umbo, shallow but fairly broad and extending to the anterior margin; flanks not prominent; lateral slopes steep. Beak strongly incurved, overhanging the moderately long and curved interarea.

Brachial valve nearly flat in both profiles; umbonal region fairly deeply concave forming a subcircular pit under the beak; fold originating on the anterior side of the pit, low and widening moderately to the anterior margin; flanks and cardinal extremities flattened.

Measurements in mm.—Holotype, length 10.0, brachial length 7.7, maximum width 11.2, hinge width 6.7, thickness 4.9, height 5.1.

Type.—Holotype, U.S.N.M. 125469.

Locality.—S30.

Discussion.—The shape and general expression of this shell suggest an abnormal specimen, but study of it indicates that it is normal but of unusual shape for a chonetid. *Chonetes timanicus* Tschernyschew is of about the same size and shape but it is more deeply sulcate.

CHONETINELLA sp. 1

Plate 1E, figures 10, 11

Small, wider than long and with greatly extended ears; hinge forming widest part; sides sloping medially; anterior margin broadly rounded; surface marked by flattened costellae, about 5 costellae in 1 mm. at the anterior.

Pedicle valve strongly convex in lateral profile; unevenly convex in anterior profile, with narrow, rounded but sulcate median region and long, concave lateral slopes. Umbo swollen; sulcus originating on umbo, narrow and deep; flanks bounding sulcus narrowly rounded; lateral slopes concave.

Brachial valve unknown.

Measurements in mm.—U.S.N.M. 125468, length 9.6, midwidth 14.7?, hinge width (based on half measure) 17.6, height 3.7.

Type.—Figured specimen, U.S.N.M. 125468.

Locality.—S103.

Discussion.—Like the other chonetids in the collection this one is poorly preserved and not complete along the anterior margin. It is very deeply sulcate and unlike any of the species figured by King (1930) from the Glass Mountains. The Oregon specimen is a much larger species than *C. victoriana* Girty from the Sierra Diablo, Texas. *Chonetes uralica* Moeller from Russia is suggestive in the young form but the adult loses the deep sulcus at the anterior.

PAECKELMANNIA aff. CHONETES ALATUS Stuckenberg

Plate 1C, figure 8

Chonetes alatus Stuckenberg, Mém. Com. Géol., St. Petersburg, vol. 16, No. 1, p. 353, pl. 5, figs. 1a-b, 1898.

Shell small with the width about 3½ times the length; cardinal extremities acute, mucronate; hinge forming the greatest shell width. Lateral margins sloping inward; anterior margin gently curved. Strongly convex in lateral profile; anterior profile broadly convex, most convex in median region with sides gently concave. Surface smooth. Interior of pedicle valve, when the shell is moistened, with a thin, short median septum. Two spine bases visible on the hinge.

Measurements in mm.—Length 3.8, width 13.2, height 0.5.

Type.—Figured specimen, U.S.N.M. 125316.

Locality.—S41.

Discussion.—The specimen described above is very suggestive of one figured by Tschernyschew (1902, pl. 56, fig. 8), an impression of the interior. This specimen, although larger than the Oregon one, is about 3 times as wide as long but the cardinal extremities are not preserved. A short and very thin median septum is visible just anterior to the beak. According to Tschernyschew his figured specimen was compared with Stuckenberg's. The Tschernyschew specimen is from the *Schwagerina* zone on the Issin-jelga River.

Suborder OLDHAMINOIDEA Williams, 1953

Superfamily OLDHAMINACEA Williams, 1953

Family OLDHAMINIDAE Schuchert and LeVene, 1929

LEPTODUS? sp. 1

Plate 1J, figures 36-39

Known from an impression of the pedicle interior which does not indicate any of the exterior details and does not show the usual form of the genus. The specimen is 28.7 mm. long by 33.7 mm. wide at the widest part which is slightly anterior to the middle. The septal apparatus is moderately simple, consisting of four lobes on each side of the median axial thickening. Axis thick, moderately elevated, bounded on each side by a narrow groove from which are given off the oblique lobes. Angle of divergence of lobes from lateral grooves 50°. Ridges between lobes thick and rounded. Troughs between the lateral ridges marked by oblique striations on the sides but by a low, rounded ridge on their floor.

Type.—Figured specimen, U.S.N.M. 125325.

Locality.—637.

Discussion.—The specimen on which the foregoing description is based is an impression of the interior of the pedicle valve prepared by removing much of the shell from the grooves. Not sufficient of the specimen is preserved to make an accurate generic or specific determination. It is referred to *Leptodus,* but without information on the exterior, especially the posterior attachment surface, the determination cannot be regarded as positive. The specimen is suggestive of some of the small stout leptodids from the upper part of the Leonard formation in the Glass Mountains but these have not been described.

The Oregon example is quite unlike the specimen from the Cache Creek fauna of British Columbia described by Kindle (1926). The Canadian specimen has the grooves nearly parallel and nearly at right angles to the axis of the shell, whereas the Oregon specimen has the grooves directed anterolaterally.

Suborder PRODUCTOIDEA Maillieux, 1940

Superfamily Productacea Waagen, 1883

Family PRODUCTIDAE Gray, 1840

PROBOLIONIA Cooper, new genus

Shells usually of small or medium size, subrectangular; hinge wide, usually equal to width at middle or wider; ears prominent, acute or forming a right angle; surface costellate but with visceral disk also rugose and usually strongly reticulate; spines few in number, generally 6 large spines: 1 on each ear, 1 on each flank just above the ear, and 1 on the trail near the sulcus midway between the point of geniculation and the front margin. Additional spines present as shown by scattered bases but not forming a definable pattern.

Pedicle valve with reticulated visceral disk, strong sulcus and well-rounded flanks; interior with crenulated ridge bounding inner side of ear; adductor scars elevated on an elongated platform. Diductor scars broad and flabellate.

Brachial valve concave with strongly reticulate visceral disk, and with median fold corresponding to sulcus of pedicle valve; cardinal process small, bilobed on ventral face, sessile, trilobed on posterior face and surrounded on the dorsal side by a low collar; lateral ridge strong; brachial ridges narrow and strongly thickened; visceral disk anterior extended anteroventrally to form a strong shelf or diaphragm from ear to ear; diaphragm forming interior edge of successive trails, several of which may be preserved. Breviseptum short and slender.

Type species.—Probolionia posteroreticulata Cooper, new species.

Discussion.—This genus is characterized by its elongate form, strong costellae and strongly reticulate visceral disk, paucispinose exterior, and the extreme development of the marginal rim or diaphragm. The development of the rim and the successive trails connected with it are much like the same features in the Mississippian genus *Diaphragmus* (text fig. 2D).

The one described genus having greatest similarity to *Probolionia* is *Kozlowskia*. In this genus the spines of the exterior are arranged like those of the Oregon shell but *Kozlowskia* is not deeply sulcate and the costellae are never clearly in relief nor as conspicuous as they are in the Oregon shell. Furthermore, *Kozlowskia* is not so strongly geniculated and does not have a strongly reticulated visceral disk. The interiors of both valves of *Kozlowskia* are similar to the interior of *Probolionia* but a strong difference in the marginal shelf is apparent, that of the Oregon genus being much more strongly developed.

The external ornamentation of *Marginifera* with its strong costellae on a long trail, strongly sulcate trail, and rugose visceral disk is like that of *Probolionia.* A major difference on the exterior appears in the strong row of spines on the flanks of *Marginifera* which extend from the anterior margin nearly to the beak and overhang the naked ears. On the inside another difference between the two genera is apparent. The marginal shelf in *Marginifera* is an overhanging ledge as it is in *Probolionia* but it does not bear a series of trails as in the Oregon genus (text fig. 2C). The shelf in *Marginifera* appears to have been built out from the visceral disk but no additional trail added; the shelf thus forms a ledge over the trail rather than being the trail attachment of the brachial valve.

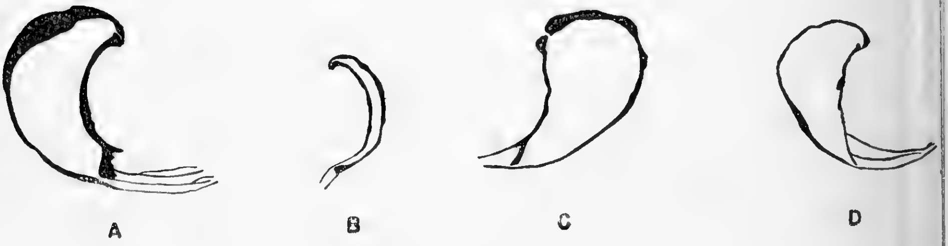

FIG. 2.—Longitudinal sections of productoid genera.

A. *Probolionia posteroreticulata* Cooper, new species. Longitudinal section showing the diaphragm and numerous trails of the pedicle valve, × 2, paratype, U.S.N.M. 125366e. Compare with figures C and D. Locality S103.

B. *Proboscidella? carinata* Muir-Wood and Cooper, new species. Longitudinal section showing the thickened subperipheral rim on the pedicle valve, × 2.5, hypotype, U.S.N.M. 126981a. Locality 2204-1.

C. *Marginifera typica* Waagen. Longitudinal section showing margin on brachial valve and lack of trails on exterior of that valve, × 2, hypotype, U.S.N.M. 124032b.
Permian, ¼ mile southeast of Fazawadi Dhok, above Warcha Mandi, Salt Range, Pakistan.

D. *Diaphragmus cestriensis* (Worthen). Longitudinal section showing diaphragm and trails on brachial valve, × 2.25, hypotype, U.S.N.M. 124040.
Fayetteville formation ½ mile south of Glendale School, just east of east line of sec. 20, T. 15 N., R. 20 E., Muskogee County, Oklahoma.

No other genus having a shelf in the brachial valve like *Marginifera* appears to be related to the Oregon genus more than in a family relationship. *Eomarginifera* has spines like *Probolionia* but the ornamentation and marginal ridge are quite different. *Spinomarginifera* has a different arrangement to the spines, and *Paramarginifera* is differently ornamented, is transverse, and has a strong marginal ridge in the pedicle valve.

PROBOLIONIA ELONGATA Cooper, new species

Plate 8B, figures 6-12

Shell fairly large for the genus, longer than wide with a short body and long trail. Width of hinge about equal to half the length of an adult; lateral margins slightly rounded; front margin broadly rounded to nearly straight. Body marked by fine, rounded costellae and concentric undulations that are cancellated by the costellae on the visceral disk; trail marked by longitudinal costellae. Entire surface covered by fine concentric growth lines.

Pedicle valve having visceral region about 10 mm. long where the valve geniculates at about 90°. Geniculated part of trail continued for a distance nearly twice that of the length of the visceral part and strongly convex in lateral profile. Sulcus originating at about 5 mm. from the beak and extending to the front margin, deepest on the geniculated portion of the valve and becoming somewhat shallower anteriorly; in section or profile the sulcus makes a broad U with narrowly rounded rather than sharp trough. Beak and umbo somewhat elongated, moderately convex; visceral region moderately inflated and with steep lateral slopes. Cardinal extremities auriculate; ears forming a right angle in the adult, acute in the young. Areas bounding sulcus on body and trail rounded and with steep lateral slopes.

Brachial valve short and moderately concave, with a concave umbonal region and moderately concave flanks bounding a short, low fold that originates at about the middle of the visceral area. Cardinal extremities flattened. Visceral region strongly and coarsely reticulated. Flange well-developed.

Interior of brachial valve with long and prominent flange around the margin of the visceral disk and with the trail given off from the flange at an acute angle. Inner flange or margin about 2 mm. in length.

Measurements in mm.—Holotype, total surface length of pedicle valve 37.2, length 21.2, length of visceral region 9.2, length from geniculated part to front margin measured on surface 28, hinge width 20, width 20, height 13; paratype, U.S.N.M. 125372, total surface length 41, length 23.0, length of visceral region 10, length from geniculation to front margin 31, hinge width 20.6, width 19, height 17.

Types.—Holotype, U.S.N.M. 125371a; figured paratype, U.S.N.M. 125372; unfigured paratype, U.S.N.M. 125371b.

Localities.—S46, S49, S68; U.O. 2202-3, 2204-3.

Discussion.—This species is the largest of the marginiferids found in the Oregon Permian. Besides this feature it has a strongly convex visceral disk region, a deep sulcus, and strongly rounded flanks. It differs from *M. posteroreticulata,* new species, in size, in being shallower, and in having a less strongly reticulate visceral disk. This species is uncommon in the Oregon section.

PROBOLIONIA POSTERORETICULATA Cooper, new species

Plate 7A, figures 1-23; text figure 2A

Shell of about medium size for the genus, with length and width about equal; sides gently rounded and sloping gently toward the valve middle; anterior margin gently rounded to straight. Visceral region of both valves coarsely reticulate; trail marked by closely crowded costellae. Spines forming a horizontal row of 4 near middle, 1 on flank near ear and 1 on flank near sulcus.

Pedicle valve with visceral region occupying about one-third the surface length, strongly reticulated and gently convex in lateral profile; geniculation strong; trail long, moderately convex in lateral profile. Sulcus originating 4 or 5 mm. anterior to the beak, narrow and moderately deep throughout its extent to the front margin. Flanks bounding sulcus narrowly rounded and with steep lateral slopes. Beak small; umbo narrow and gently swollen.

Brachial valve with visceral region strongly and coarsely reticulated; valve short, moderately deep, marked medianly by an obscure, low fold. Inner flange long and prominent.

Measurements in mm.

		Surface length	Length	Hinge width	Width	Height	Thickness	Length visceral disk
Holotype		23.0	12.4	15.2	12.9	7.6	?	8.0
Paratype	(125366b)	24.0	13.2	14.1	13.6	8.0	?	7.5
"	(125366c)	24.0	13.7	17.6	14.6	10.0?	?	?
"	(125369)	25.0	14.6	16.4	14.3	9.8	?	9.0
"	(125374)	22.0+	13.2+	?	13.5	?	5.3	7.0
"	(125367)	24.5	14.4	14.6	13.4	8.7	?	6.5

Types.—Holotype, U.S.N.M. 125369; figured paratypes, U.S.N.M. 125366a-f,j, 125367, 125374, 125550; unfigured paratypes, U.S.N.M. 125366g-i, 125375, 125455.

Localities.—638; P10; S12, S29, S30, S40, S46, S49, S69, S87, S103, S106; U.O. 2201-4, 2202-2, 2202-5, 2216-1.

Discussion.—This is the most common marginiferoid in the Oregon Permian, being most abundant at S103. The species is characterized by a strongly reticulate visceral disk, the deep sulcus originating just anterior to the visceral disk, and a long, prominent flange around the margin of the visceral disk. This species cannot be confused with the much larger *P. elongata,* new species, and differs from the other smaller, described marginiferas in having an inner flange in the brachial valve.

Family DICTYOCLOSTIDAE Stehli, 1954

Subfamily Dictyoclostinae Stehli, 1954

AVONIA OREGONENSIS Cooper, new species

Plate 2C, figures 13-24

Shell large for the genus, subquadrate in outline with the width slightly exceeding the length; cardinal extremities nearly a right angle; lateral margins gently rounded; anterior margin broadly rounded.

Pedicle valve strongly convex with a strongly incurved beak and strongly convex umbo. Outline of umbonal region forming approximately a right angle. Median region inflated, with very steep slopes to the margins. Sulcus shallow, originating just anterior to the umbo, poorly defined, not always reaching the anterior margin. Hinge just slightly narrower than the maximum shell width which is located at about the middle. Ears ill defined. Surface marked by scattered pustules bearing long, slender spines; pustules continued into more or less long, rounded radial ridges most numerous and longest anteriorly.

Brachial valve about 20 percent shorter than the pedicle valve, and having a decidedly rectangular outline, strongly convex in profile, thus producing a thin visceral cavity; umbo deeply concave; fold poorly defined, anterior to umbo and extending to the front margin; areas bounding fold deeply concave with the greatest concavity located at about the middle; ears well defined, deflected toward the pedicle valve and slightly concave. Surface marked by irregularly arranged, shallow, elongate pits corresponding to the spine-bearing pustules of the pedicle valve.

Measurements in mm.—Holotype, length 24.6, width 29.1, thickness at middle 3.7, height from margin to point of maximum convexity of pedicle valve 15.2, surface measure 40+, length of brachial valve 20; paratype, U.S.N.M. 125322, length 19.0, width 25.4, thickness at middle 3.7, height 9.7, surface measure 30+, length of brachial valve 15.6.

Types.—Holotype, U.S.N.M. 125323a; figured paratypes, U.S.

N.M. 125321a,b, 125322, 125323b, 125324; unfigured paratypes, U.S.N.M. 125320a,b.

Localities.—636; L8, L23; S12, S14, S30, S40, S43, S45, S46, S49, S87, S103, S106; U.O. 2201-2, 2202-2, 2202-3, 2202-5, 2202-6, 2204-1, 2204-3.

Discussion.—This species is characterized by its large size and its surface covered by elongate, distant pustules or spine ridges. It is most suggestive of *Productus tuberculatus* Moeller but differs in having an obscure median sulcus on the pedicle valve rather than a distinct and fairly deep one as on the Russian species. Furthermore, the spine bases of the American species are more elongated than those of the Russian species and are somewhat more abundant. This species is fairly common in the Oregon Permian.

Productus subhorridus Meek is an American form that may be related but it differs markedly in form, profile, and the arrangement of the spines. This stock of productoids appears in the early Permian, is common in the Leonard, and reaches a large size in the Word.

KROTOVIA aff. K. BARENZI (Miloradovitch)

Plate 10C, figures 12-17

Krotovia barenzi Miloradovitch, Trans. Arctic Inst., vol. 37, p. 139, pl. 5, fig. 12, 1935; Branson, Geol. Soc. Amer. Mem. 26, p. 378, 1948.

Material poorly preserved and consisting of several pedicle valves; small, length and width nearly equal, outline suboval; lateral margins gently rounded, anterior margin broadly rounded; hinge slightly narrower than the maximum width which is near the middle. Lateral profile strongly convex; anterior and posterior profiles narrowly domed. Beak narrow and incurved, protruding beyond the posterior margin. Umbo swollen. Surface ornamented by distant growth varices and small closely crowded spines covering all parts of the pedicle valve.

Measurements in mm.—Figured specimen, U.S.N.M. 125336b, length 16.2, width 15+, hinge width 12.9, surface measure 27.5; figured specimen, U.S.N.M. 125336a, length 13.2, width 11.6, hinge width ?, surface measure 22.

Types.—Figured specimens, U.S.N.M. 125336a,b.

Locality.—S101.

Discussion.—This species is characterized by its small size and elongate form. The specimens closely resemble those figured by Tschernyschew (1902, pl. 30, fig. 8).

KROTOVIA PARVA Cooper, new species

Plate 2B, figures 5-12

Shell small, about one-third wider than long; lateral margins narrowly rounded, anterior margin broadly rounded; cardinal extremities nearly a right angle. Surface covered by small, fairly densely crowded spines that arise from short, low pustules.

Pedicle valve strongly convex in lateral profile with the greatest convexity at about the middle; anterior profile strongly convex in the midregion but with the sides inclined. Beak strongly incurved over the hinge; umbo narrow, swollen, and with steep slopes to the hinge and cardinal extremities. Midregion of valve swollen, with steep lateral slopes but the anterior slope somewhat less steep.

Brachial valve concave with the deepest part in the median region and posterior to the umbonal region. Cardinal extremities slightly flattened.

Measurements in mm.—Holotype, length 10.9, surface length 11, width at middle 14.5, hinge width 12.0, height 5.6?; paratype, U.S.N.M. 125355b (brachial valve), length 88, midwidth 12.6, hinge width 11.8.

Types.—Holotype (pedicle valve), U.S.N.M. 125355a; figured paratype, U.S.N.M. 125465; unfigured paratype (impression of brachial exterior), U.S.N.M. 125355b.

Localities.—P10; S40.

Discussion.—This species is characterized by its small size, transverse outline, and numerous fine spines. Its transverse form and numerous spines distinguish it from *K. barenzi* (Miloradovitch) from Russia and Greenland. No American species is like it in size or ornamentation. It differs from *K. pustulata* young in its finer spines. This species is also suggestive of *K. nielsoni* Dunbar, but the Greenland species, although nearly of the same size as the Oregon species, is a much rounder form in outline and thus much less transverse.

KROTOVIA PUSTULATA (Keyserling)

Plate 8A, figures 1-5

Productus pustulata Keyserling, Tschernyschew, Mém. Com. Géol., St. Petersburg, vol. 16, No. 2, p. 617, pl. 30, figs. 1,2; pl. 53, figs. 5,6, 1902.

Krotovia pustulata (Keyserling) Branson, Geol. Soc. Amer. Mem. 26, p. 379, 1948.

This species can be recognized by its large size and the peculiar arrangement of the spines on the surface. The shell is transversely subrectangular in outline with a moderately convex pedicle valve marked anteriorly to the beak by a shallow sulcus. The brachial valve shares the curvature of the pedicle valve, thus producing a shell with only a thin body cavity. The spines of the pedicle valve are short and have a crude quincuncial arrangement. The brachial valve impression is pitted, each pit corresponding to a spine on the pedicle valve. A typical specimen (hypotype, U.S.N.M. 124021) is 28 mm. long, 41 mm. wide, and 4 mm. thick at the umbo. The height from the margins to the point of greatest curvature is about 12 mm. The specimen figured by Tschernyschew (1902, pl. 30, figs. 2a-c), has almost the same measurements as the figured Oregon specimen.

Types.—Figured hypotype, U.S.N.M. 124021.

Localities.—638; L8; P10; S40, S41, S43, S46, S56, S70, S87, S103; U.O. 2201-1, 2204-3.

ANTIQUATONIA RETICULATA Cooper, new species

Plate 3A, figures 1-9

Large, subquadrate in outline but with the width slightly greater than the length; margins not clearly preserved; somewhat more than posterior half finely reticulate; trail costellate, costellae unequal in size, narrowly rounded and separated by spaces about equal in width to the width of the costellae; costellae numbering about 4 in 5 mm. at the anterior part of the trail.

Pedicle valve unevenly convex in lateral profile, the anterior third, except for the beak and umbo, gently convex; median third narrowly convex and anterior third or trail gently convex. Beak strongly incurved but not protruding beyond the hinge line. Umbo broadly swollen and with steep lateral slopes. Sulcus originating about 10 mm. anterior to the beak, shallow at its origin but becoming deeper anteriorly where it forms a deep, broadly V-shaped trench in the trail. Flanks bounding sulcus in the visceral region moderately swollen but on the trail they are strongly swollen and have steep, rounded lateral slopes.

Brachial valve gently concave in lateral profile but with a short trail geniculated at about a right angle to the visceral region. Umbo moderately deeply sulcate. Median fold low, fairly broad but becoming nearly obsolete on the trail.

Measurements in mm.—Holotype, length 44.0, width at middle 50.4+, surface length 90, height 33.5?; brachial valve, paratype, U.S.N.M. 125349, length 36.3, width 48.1, surface length 52.

Types.—Holotype, U.S.N.M. 125348; figured paratypes, U.S.N.M. 125347, 125349.

Localities.—P10; S20, S67.

Discussion.—This species is characterized by its subquadrate form, strong convexity, strongly reticulate visceral region and strong sulcus. This species is more like *A. hessensis* than it is like its associate in the Oregon fauna. It is more convex and longer than *A. sulcatus* and is differently ornamented. It differs from *A. hessensis* in being larger, somewhat more strongly ribbed, with a larger reticulate area and more convex profile.

ANTIQUATONIA SULCATA Cooper, new species

Plate 5C, figures 18-22

Shell fairly large for the genus, wider than long with the hinge forming the widest part. Lateral margins gently rounded; anterior margin broadly rounded, emarginate medially. Slightly less than posterior half of the shell reticulate, the trail costate, the costae narrowly rounded and separated by spaces not quite equal to the costae in width, and 7 to 8 costae occupying a space of 10 mm. on the front half.

Profile of pedicle valve strongly convex with the greatest curvature slightly posterior to the middle; reticulate or visceral portion strongly convex with strongly curved beak which, however, protrudes slightly beyond the posterior margin. Umbonal region slightly convex but with steep slopes to the cardinal extremities. Sulcus originating 10 to 12 mm. anterior to the beak as a narrow groove, deepening rapidly but not materially widening in its extent to the front margin. Flanks bounding sulcus strongly rounded with steep lateral slopes to the margins; ears prominent, moderately extended, narrowly rounded in profile. Lateral slopes over ears marked by a low curving ridge bearing a row of spines; ridge variable in elevation and definition.

Brachial valve forming with the pedicle valve a moderately deep visceral chamber; visceral area nearly flat in profile but with a concave umbo and concave area in front of umbo extending for about 8 or 9 mm. anterior to the beak where the concavity changes to a low and narrow fold with gently sloping sides that extend to the front margin. Areas surrounding the sulcus on the visceral region slightly convex especially in the neighborhood of the cardinal extremities. Brachial valve geniculating about 20 mm. anterior to the beak strongly in the direction of the brachial valve. Geniculate area narrowly rounded in profile; trail very slightly convex in profile, steep; ears of brachial valve moderately long, narrowly rounded in profile, a narrow, curved groove anterior to the ear corresponding to the ridge on the slope of the pedicle valve.

Measurements in mm.—Holotype, length 34.7, width at middle 46, hinge width 44+, surface length 56, thickness through middle of visceral area 8.5, height 14.

Types.—Holotype, U.S.N.M. 125327; figured paratype, U.S.N.M. 125329.

Localities.—638; P10; S43, S46, S47, S51, S67, S103; U.O. 2202-2, 2204-3.

Discussion.—This species is characterized by its wide hinge, the big ears, and deep sulcus, although this last feature is somewhat variable. Few described species of *Antiquatonia* from the Permian are available for comparison.

Antiquatonia planumbona Stehli from the Bone Spring formation in the Sierra Diablo, Texas, is sulcate but not so deeply as the Oregon species. The Texas shell is also more finely reticulate than the Oregon species.

The holotype of *Productus hessensis* King is a poorly preserved specimen, but nevertheless shows the elevated ridge characteristic of *Antiquatonia*. It is also a sulcate form but is a larger and more finely ornamented species than *A. sulcata*.

Productus semireticulatus arcticus Whitfield is a deeply sulcate species similar to the Oregon form but it is not certain to what genus it belongs. In any case, the type as illustrated by Whitfield is a narrower species than the Oregon *Antiquatonia*.

PROBOSCIDELLA? CARINATA Muir-Wood and Cooper, new species

Plate 3B, figures 10-17; text figure 2B

Specimens rare, showing the pedicle valve only in a hard matrix; small, with the hinge forming the widest part; length less than the width. Pedicle valve with visceral area slightly wider than long. Semicircular in lateral profile, more broadly arched in anterior profile; beak narrow, protruding posterior to the hinge; umbonal region narrowly swollen; sulcus originating about 5 mm. anterior to the beak, shallow and narrow, terminating in a trough 9 to 12 mm. (surface measure) from the beak. Visceral region marked by radiating costellae cancellated by concentric undulations. Trail moderately convex in lateral profile, separated from the visceral area by a slight peripheral depression; trail anterior to median troughlike depression nasute and carinate; flanks of trail moderately convex and descending nearly vertically from the visceral area. Trail ornamented by costellae.

Brachial valve closely fitting the concavity of the pedicle valve interior, as seen in longitudinal section, otherwise unknown.

Interior of pedicle valve unknown except for the presence of a subperipheral marginal thickening.

Measurements in mm.—Holotype, surface length 18, length 11.1, hinge width 13.0+, length of visceral area and trail about equal (9 each), height 7.0.

Types.—Holotype, U.S.N.M. 124156a; figured paratypes, U.S.N.M. 124157, 125533, 126981a; unfigured paratypes, U.S.N.M. 124156b, 126981b.

Localities.—638; S12, S49; U.O. 2201-2, 2204-1.

Discussion.—This interesting little productoid is unique among American species in having the median trough anterior to the visceral area and in having a long carinate trail. The only productoid like it is *Proboscidella? kutorgae* Tschernyschew (1902, p. 643, pl. 59, figs. 1-3) from the *"Schwagerina"* limestone of the Urals. The Russian species differs from the Oregon one in its larger size, finer and more abundant reticulation, and in the absence of the strong carina on the trail. Nothing at present is known of the interior of the Russian species.

PLEUROHORRIDONIA? ELONGATA Cooper, new species

Plate 7C, figures 30-33

Large, narrowly elongate; hinge slightly narrower than the width; cardinal extremities auriculate, ears small and rounded. Beak incurved but not protruding beyond the posterior margin; umbo narrow, sulcate; sulcus deep, widening and deepening anteriorly but narrow throughout the shell length. Flanks narrowly and strongly rounded; sides steep; surface smooth on the posterior third but longitudinally and irregularly costellate on the anterior two-thirds. Brachial valve unknown.

Measurements in mm.—Holotype, length 40.5, midwidth 31.4, maximum width 33.2, surface length 80, hinge width 26.6.

Type.—Holotype, U.S.N.M. 125346.

Localities.—S47, S51, S87; U.O. 2205-5.

Discussion.—This species is difficult to place, and few good specimens are available for study. The posterior or umbonal region appears to be quite smooth but the trail and steep lateral slopes have numerous longitudinal subdued ribs. These also appear in the deep and narrow sulcus. The only genus like this is the newly erected *Pleurohorridonia* of Dunbar. The Oregon specimens are not characteristic of the genus because they are much narrower and the ears of the cardinal extremities are not so extended. Unfortunately, the brachial valve and spines of the Oregon species are not preserved; consequently, it is impossible to compare these features with Dunbar's species. The Oregon species differs from *P. scoresbyensis* Dunbar in its narrower outline, smaller ears, and narrower, deeper sulcus.

Subfamily LINOPRODUCTINAE Stehli, 1954

LINOPRODUCTUS cf. L. LUTKEWITSCHI (Stepanow)

Plate 6D, figures 27-29

Productus lutkewitschi STEPANOW, Leningrad State Univ., Sci. Bull., Geol.-Geogr. ser., vol. 2, p. 127, pl. 1, figs. 5a-c, 1936.

Linoproductus lutkewitschi (Stepanow) BRANSON, Geol. Soc. Amer. Mem. 26, p. 393, 1948.

Fairly large for the genus, length slightly less than the width; sides gently rounded, front margin broadly rounded as shown by the growth lamellae; costellae narrowly rounded and separated by spaces about equal to the width of the costellae; 5 or 6 costellae in 5 mm. at the valve middle.

Pedicle valve moderately convex in lateral profile, more narrowly convex in anterior profile but with the median region flattened and the sides steep. Umbo moderately swollen, beak small; median region flattened to gently concave; sides gently convex but steep. Cardinal extremities somewhat flattened, marked by a few prominent wrinkles.

Brachial valve moderately concave in both profiles; most concave in the median region. Umbo a shallow pit. Fold broad, low, indistinct and best defined near the middle. Posterolateral extremities flattened and marked by 5 or 6 prominent wrinkles which extend as indistinct concentric undulations on the concave portions of the valve.

Measurements in mm.—Figured hypotype, surface length 80+, length 56.1+, width (based on half measure) 62.8.

Types.—Figured hypotype, U.S.N.M. 125326.

Localities.—S14, S45, S49, S103, S111.

Discussion.—The inconspicuous beak of this species is its most striking feature.

ANIDANTHUS MINOR Cooper, new species

Plate 6A, figures 1-17

Shell small, length and width nearly equal; cardinal extremities forming small ears; sides nearly parallel; front margin broadly rounded. Surface costellate, with low, rounded costellae separated by spaces of about equal width to that of the costellae; 2 or 3 costellae occupying the space of 1 mm. at the front margin and 12 to 15 costellae in 5 mm. Brachial valve with concentric lamellae crowded anteriorly.

Pedicle valve with profile unequally convex, anterior half gently convex but posterior half almost semicircular. Anterior profile moderately rounded. Beak protruding over hinge; umbo somewhat swollen and the costellae cancellated by a few low rugae. Median region swollen and tumid, fold low, indistinct, and narrow, occupying the front half. Lateral slopes moderately steep.

Brachial valve moderately concave, most concave in the midregion.

Interior unknown.

Measurements in mm.

	Surface length	Length	Width	Height
Holotype	30.0	15.0	17.0 ?	10.0
Paratype (125351)	26.0	15.0	14.0	10.0
Paratype (125466)	?	7.0	10.4	?

Types.—Holotype, U.S.N.M. 125361; figured paratypes, U.S.N.M. 125351, 125360, 125466, 125534, 125535.

Localities.—L8; P12; S41, S43, S46, S50, S87, S103; U.O. 2201-1, 2201-2, 2204-1, 2204-2, 2207, 2207-2, 2215-1, 2216-1.

Discussion.—No American species like *A. minor* are known. Certain small linoproductids such as *L. waagenianus* Girty are known to be generically distinct from *Anidanthus* and are thus excluded. However, one Russian species, *A. aagardi* (Toula), is similar to the Oregon species. The Russian form, however, is larger and less strongly convex than the American species. The costellae of the Oregon species are stronger than those of the Russian form.

MUIRWOODIA TRANSVERSA Cooper, new species

Plate 5A, figures 1-13

Shell fairly large, width almost twice the length; cardinal extremities acutely angular; lateral margins nearly straight but oblique; front margin bilobed. Shell strongly geniculated 16 mm. from the beak; angle of geniculation 65° to 75°. Geniculated trail slightly longer than the visceral region. Surface costellate, with about 8 costellae in the space of 5 mm. at the point of geniculation and at the front margin.

Pedicle valve with visceral region gently convex in lateral profile, geniculated area narrowly rounded; trail gently convex in profile, slightly more so than the visceral area. Sulcus originating about

3 mm. anterior to the beak, deepening gradually but with nearly parallel sides to the place of geniculation; sulcus on trail somewhat shallower and wider but very pronounced nevertheless. Flanks bounding sulcus on visceral area moderately swollen, most so at the place of geniculation; slopes of flanks long and gentle; region about cardinal extremities flattened. Trail strongly bilobed in anterior profile, with posterolateral portions nearly flat in profile. Beak small, strongly incurved.

Brachial valve fitting closely into the pedicle valve to make a narrow or thin visceral cavity; umbonal region sulcate; fold originating just anterior to the umbonal sulcus, low, somewhat narrowly rounded to subangular, strongest just before geniculation, less well defined anterior to geniculation. Flanks bounding fold gently concave. Two spines just anterior to geniculation moderately long, strongly divergent.

Measurements in mm.—Holotype, length 21.1, surface length 34+, hinge width based on half-measure 35.8+, midwidth (based on half measure) 30.8, thickness 4.9, height 13.2; paratype, U.S.N.M. 125337, length 19.2, surface length 36.5, hinge width 33+, midwidth 30.3; paratype, U.S.N.M. 125343, length 18, surface length 33+, hinge width 35+, midwidth 29.5.

Types.—Holotype, U.S.N.M. 125339; figured paratypes, U.S.N.M. 125337, 125338, 125340, 125342, 125343, 125345; unfigured paratypes, U.S.N.M. 125341, 125344.

Localities.—638; F; L8; P10; S40, S43, S46, S50, S103; U.O. 2201-2, 2202-2, 2204-3.

Discussion.—This species is characterized by its transverse outline and strong geniculation. It is smaller and more strongly geniculated than *M. multistriata* (Meek) of the Word and Phosphoria formations. It is larger and more strongly geniculated than *M. geniculata* Girty of the Park City formation. The Oregon species is similar to specimens of a *Muirwoodia* that occurs in abundance in the bituminous limestones of the lower Word formation in the Glass Mountains. The Texas species has a deep sulcus and a long trail but none of the specimens in the national collection appears to be as strongly geniculated or to have as long and prominent a trail as the Oregon species.

Of European species of *Muirwoodia* the Oregon species is most like *M. mammatus* (Keyserling) but the latter is a variable species. The specimens figured by Tschernyschew (1902, pl. 35, figs. 4 and 5) are much smaller and with a shallower sulcus than the Oregon specimens. The forms figured by Chao (1927, figs. 10-14) are about the same size as *M. transversa* and have a similar ornamentation, but the Chinese species is not so strongly geniculated nor does it have as strong a sulcus as the American species.

Muirwoodia greenlandica Dunbar from Greenland is perhaps the nearest like the Oregon species but the extremely acute angle of geniculation separates these two species as it separates the Oregon shell from all others.

Subfamily MARGINIFERINAE Stehli, 1954

MARGINIFERA? BREVISULCATA Cooper, new species

Plate 7B, figures 24-29

Shell of about usual size for the genus, known only from the pedicle valve; length and width about equal; outline subquadrate. Sides and anterior margin gently rounded. Hinge equal to the greatest shell width. Surface with coarsely rugose visceral area with some reticulation, fine radial costellae on the trail and a few strong, radial plications. Spines few, but their pattern is difficult to determine.

Visceral region somewhat swollen, equal in length to less than half the surface length of the valve; lateral profile of visceral area nearly flat except for the narrowly convex umbo; beak incurved over hinge. Slopes to cardinal extremities fairly steep. Cardinal extremities produced into small ears having an agle of about 90°. Sulcus just barely perceptible at the anterior end of the visceral area just before the geniculated part of the valve. Angle of geniculation obtuse; trail gently convex in profile with moderately steep lateral slopes. Sulcus shallow, almost completely confined to the trail.

Measurements in mm.—Holotype, surface length 23, length 13.5, length of visceral area 9.5, width at hinge 15.5, height 13.3.

Types.—Holotype, U.S.N.M. 125363a; figured paratype, U.S. N.M. 125362; unfigured paratypes, U.S.N.M. 125363b-d.

Localities.—S30, S45, S49.

Discussion.—This species can be readily identified by its small size, short trail with sulcus confined to trail. It differs from *Probolionia posteroreticulata,* new species, in its shorter trail, less reticulate visceral disk and shallower, shorter sulcus. No details of the interior of this species are known; consequently, the generic assignment to *Marginifera* is queried. The exterior, however, is like that of all the other species described herein that are referred to *Marginifera.*

MARGINIFERA? COSTELLATA Cooper, new species

Plate 6C, figures 22-26

Shell small to medium size for the genus, transversely subrectangular in outline. Hinge forming widest part; lateral margins directed toward the valve middle, slightly convex; anterior margin broadly rounded. Surface marked by subdued, rounded costellae separated by spaces of much less width than the costellae. Visceral disk not strongly reticulated. Spines few, but 4 large ones located in a horizontal row on flanks and trail.

Pedicle valve having a visceral area about 10 mm. long, after which the valve is strongly geniculated. Trail moderately convex in profile and about 1½ times as long as the visceral area. Beak protruding slightly posterior to the hinge; umbo somewhat swollen, narrow; visceral region inflated; umbonal slopes and slopes of flanks of visceral region moderately steep. Ears small but prominent, narrowly rounded, forming right angles; sulcus originating about 3 mm. anterior to the beak, extending to the anterior margin as a trough, deep and narrowly U-shaped in profile. Flanks narrowly rounded and with steep slopes to the margins. Four long spines, two on each side of the sulcus, given off at nearly a right angle from flanks bounding sulcus of trail and forming a horizontal row.

Brachial valve closely fitting the pedicle valve, deeply concave at the point of geniculation; umbo concave; fold originating about 3 to 4 mm. anterior to the umbo, moderately narrowly rounded; flanks moderately concave; ears deflected and flattened.

Interior.—A longitudinal section of a complete specimen gives no indication of a marginal rim.

Measurements in mm.—Holotype, surface length 28, length 13.6, length of visceral area 9, hinge width 18.6; height 10.

Types.—Holotype, U.S.N.M. 125368; figured paratype, U.S. N.M. 125370a; unfigured paratypes, U.S.N.M. 125370b-c.

Localities.—S39, S43, S46; U.O. 2202-2.

Discussion.—This species is characterized by its strong costellae and deep sulcus. It is similar to *Probolionia posteroreticulata,* new species, in exterior appearance but is wider, has a less reticulate visceral disk region, and the sulcus is broader. The interior is not definitely known and a margin was not seen, nor is it indicated on the exterior.

MARGINIFERA? MULTICOSTELLATA Cooper, new species

Plate 5B, figures 14-17

Shell of about medium size for the genus, known from the pedicle valve only. Subrectangular in outline and the visceral region occupying nearly half the surface length. Visceral region coarsely reticulated; trail strongly and evenly costellated. Costellae numbering about 7 in 5 mm. at the front margin. Sulcus originating about 5 mm. anterior to the beak, broad and shallow from point of origin to front margin. Beak small, umbo moderately swollen. Visceral region moderately convex in lateral profile; trail more convex than the visceral region in lateral profile. Flanks bounding sulcus gently swollen and with steep lateral slopes.

Measurements in mm.—Holotype, surface length 18.0, length 9.9, hinge width 15.6, midwidth 12.8, height 6.2.

Types.—Holotype, U.S.N.M. 125365.

Locality.—S46.

Discussion.—This species is characterized by its broad but shallow sulcus, short trail, wide hinge, and strong costellae. It is most like *Marginifera profundosulcata,* new species, but differs from it in having a shallower sulcus, finer costellae, and rounded flanks. The interior, however, is unknown; consequently, it could not be assigned to the new genus *Probolionia.*

MARGINIFERA? PROFUNDOSULCATA Cooper, new species

Plate 6B, figures 18-21

Shell of about usual size for the genus, subrectangular in outline; lateral margins sloping toward the valve middle; anterior margin medially emarginate; ears prominent, subalate. Visceral disk region obscurely reticulate; trail marked by low, broadly rounded costellae.

Pedicle valve with visceral region about 8 mm. long and trail about 10 mm. long; visceral region nearly flat in lateral profile; umbo narrowly swollen; umbonal slopes gentle. Trail strongly geniculated from visceral region, gently convex in lateral profile. Sulcus originating about 3 mm. anterior to the beak, narrow and deep, widening and deepening anteriorly to form a deep U-shaped trough. Flanks bounding sulcus narrowly rounded and with long, precipitous lateral slopes.

Brachial valve deeply concave; umbo forming a deep trough; median fold strong, originating about 4 mm. anterior to the beak. No diaphragm.

Measurements in mm.—Holotype, surface length 18, length 11.9, hinge width 17.9, midwidth 15.2, height 7.6; thickness of a complete specimen (U.S.N.M. 125364b) near middle 2.8.

Types.—Holotype, U.S.N.M. 125364a; unfigured paratype, U.S. N.M. 125364b.

Localities.—L8; S12, S40, S41, S49, S56; U.O. 2204-3.

Discussion.—This species is characterized by its deep and wide sulcus. It differs from all others described herein by this feature, but its interior is unknown and the generic assignment therefore is uncertain.

ALEXENIA? OCCIDENTALIS Cooper, new species

Plate 2D, figures 25-34

Shell of about medium size, slightly wider than long but with a long trail. Greatest width at middle, hinge narrow, ears strong, obtuse, flattened but not extended. Margins strongly rounded; posterior third moderately coarsely reticulate. Anterior two-thirds costellate with costellae narrowly rounded and separated by spaces nearly as wide as the costellae. Costellae numbering about 5 to the millimeter on the trail.

Lateral profile of pedicle valve strongly curved. Ears broken. Umbo narrowly but strongly swollen, with steep slopes; median region inflated. Sulcus originating 10 to 15 mm. anterior to the beak, shallow and broadly U-shaped, disappearing or becoming faintly defined anteriorly on the trail. Flanks bounding sulcus broadly inflated; lateral slopes rounded. Location of spines not clearly defined but spine bases are scattered over trail and lateral slopes.

Brachial valve gently concave, most so in the umbonal region which forms a shallow pit and in anterolateral extremities. Median region defined by a low, narrow fold originating just posterior to the middle of the visceral disk region but becoming poorly defined or obsolete anteriorly. Cardinal process moderately long, slender, with bilobed ventral face.

Measurements in mm.—Holotype, length 28.3, width at middle 32.7, surface length 54, height 14.5; paratype, U.S.N.M. 125334 (brachial valve) length 23.2, width 31.4, surface length 34, height 10.

Types.—Holotype, U.S.N.M. 125350; figured paratypes, U.S.N.M. 125334, 125335.

Localities.—614, 638, 639; F; P10, P12; S12, S30, S39, S41, S49, S50, S103; U.O. 2201-4, 2202-2, 2204-3, 2211-2.

Discussion.—This species is characterized by the finely reticulate visceral disk and the long trail. The interior is imperfectly known because none of the Oregon species shows the marginal ridges, but one specimen, U.S.N.M. 125334, does show the cardinal process and this agrees with the interior of *Alexenia? parvispinosa* Stehli, the only described Permian species like the Oregon one.

Alexenia? occidentalis differs from the west Texas species in having a larger size, longer trail, less transverse outline, and more concave brachial valve. The visceral disk region of a specimen of *A.? parvispinosa* is gently but definitely swollen to form a slightly convex area. The spines of the Texas species are fine and numerous but indications from the few spine bases seen on *A.? occidentalis* suggest much stronger spines. This would be in agreement with the larger size of the Oregon species.

Shells similar to the Permian *Alexenia?* are common in the Pennsylvanian and occur fairly frequently in the Wolfcamp and Leonard formations of the Glass Mountains. None of these, except Stehli's species, appears to have been named.

ALEXENIA? SUBQUADRATA Cooper, new species

Plate 2A, figures 1-4

Shell small, slightly wider than long; lateral margins gently rounded; anterior margin gently rounded; anterolateral extremities moderately rounded; posterior half fairly strongly reticulated; anterior half costellate; costellae subequal, separated by spaces narrower than the costellae, numbering about 6 in 5 mm. at the front margin.

Pedicle valve with lateral profile moderately convex and with the geniculation at about the middle and forming an angle of 90°. Posterior half somewhat less convex than the anterior half or trail. Beak narrow, incurved, scarcely protruding beyond the hinge line. Umbo narrowly and strongly swollen and with precipitous slopes to the ears. Sulcus originating about 12 mm. anterior to the beak, narrow and shallow but extending to the anterior margin and forming a broad V in profile. Flanks bordering sulcus moderately broad and moderately swollen and with steep slopes to the margins. Ears small. Spines concentrated on lateral slopes, scattered on trail.

Measurements in mm.—Holotype, length 22.1, width at middle 26.1, width at ears 26.0, surface length 40.0, height 13.8.

Type.—Holotype, U.S.N.M. 125328.

Localities.—L8; S106.

Discussion.—This species is characterized by its subquadrate form, deep sulcus, and strong convexity. It differs from *A.? occidentalis,* new species, in its narrower outline, shorter trail, deeper sulcus, and more strongly convex lateral profile. The species is represented by a single specimen only, but it is fairly well preserved.

Family ECHINOCONCHIDAE Stehli, 1954

KOCHIPRODUCTUS TRANSVERSUS Cooper, new species

Plate 4A, figures 1-6

Shells moderately large, wider than long and with moderate depth. Sides rounded, anterior margin broadly rounded; anterolateral extremities narrowly rounded. Surface marked by discontinuous costellae swollen anteriorly to form spine bases.

Pedicle valve with moderately convex lateral profile; anterior profile moderately convex but with steep lateral slopes and sulcate median region. Umbo greatly swollen, beak strongly incurved. Sulcus originating on the umbo near the beak, extending to the anterior margin, becoming broader and deeper to the valve middle but becoming still broader but shallower anterior to the middle. Flanks bounding sulcus narrowly rounded. Cardinal extremities not alate. Anterior margin with short, ventrally deflected frill.

Brachial valve gently concave in lateral view but nearly flat when seen from the posterior. Umbo marked by a shallow pit anterior to which a low, broad fold rises and extends to the anterior margin. Fold steepest and somewhat carinate near the valve middle, flattening and broadening anterior to the middle but remaining prominent. Shell bounding fold gently concave; posterolateral extremities nearly flat. Cardinal process long and slender, curved.

Measurements in mm.

	Length	Middle width	Surface length	Thickness
Holotype	36.6	44.5	56.0	16.1
Paratype (125331)	42.7?	55.4	62.0?	?

Types.—Holotype, U.S.N.M. 125332; figured paratype, U.S.N.M. 125331.

Localities.—P10, P11; S12, S41, S50, S103; U.O. 2201-1, 2216-1.

Discussion.—This species is characterized by its medium size for the genus, transverse form and broad sulcus becoming obsolete anteriorly. The specimens assigned to this new species appear to be adults and not the young of *K. porrectus* which is more strongly ornamented. The adult character appears in the short ventrally deflected rim along the margin of the pedicle valve (pl. 4A, fig. 4).

The development of a rim seldom takes place in productoids except in the adult.

This species differs from *K. porrectus* in other features beside the ornamentation as mentioned above. The sulcus originates near the beak and is broader than that of the Russian species. *Kochiproductus transversus* is a smaller and wider species than the two known American species, *K. peruviana* (d'Orbigny) and *K. victorioensis* (R. E. King).

KOCHIPRODUCTUS cf. K. PORRECTUS (Kutorga)

Plate 4B, figure 7

Productus porrectus Kutorga, Verhandl. Russ.-Kais. Min. Ges., St. Petersburg, 1844, p. 96, pl. 10, fig. 3; Tschernyschew, Mém. Com. Géol., St. Petersburg, vol. 16, No. 2, pp. 301, 634, pl. 55, fig. 1, pl. 56, fig. 4, pl. 62, fig. 2; p. 637, fig. 7, 1902.

The specimen placed under this heading is a large productoid, the largest occurring in the fauna under consideration and one of the largest known in this country. Only part of both valves are preserved and these have become somewhat displaced so that the beak is shoved some distance over the hinge line. The beak is narrow and the umbo strongly swollen. A shallow sulcus originates on the umbo but its anterior extent and depth cannot be ascertained. The brachial valve is gently concave but shows evidence of the origin of a low fold about 18 mm. anterior to the beak. The surface is costellate and reticulate. The costellae are narrowly rounded and separated by spaces wider than the costellae. The reticulation is produced by narrow, concentric rugae. Where an undulation and costella meet, a node is produced which probably was the seat of origin of a short spine.

Detailed measurements are not possible because the specimen is so incomplete but its length and width were in excess of 70 mm. The size and ornamentation of the Oregon specimen are similar to those of a specimen figured by Tschernyschew (1902, pl. 55, figs. 1a, 1b.)

Type.—Figured specimen, U.S.N.M. 125333.

Localities.—614; S87, S106; U.O. 2202-2.

WAAGENOCONCHA PARVISPINOSA Cooper, new species

Plate 4C, figures 8-12

Shell small for the genus, wider than long, but somewhat rectangular in outline; sides rounded; front margin subtruncated. Surface covered by a mat of fine spines arranged quincuncially, about 9 to 16 in 4 square mm. near the front.

Pedicle valve moderately convex in lateral profile and with the greatest convexity located in the umbonal region; beak strongly incurved; umbonal region narrowly swollen and marked off from main body of valve by steep slopes; sulcus shallow, equal in width to about one-quarter the valve width or less, originating about 4 mm. anterior to the curved umbo; areas bounding sulcus moderately swollen; slopes to margins steepening posteriorly and steepest along the umbo; cardinal extremities flattened.

Brachial valve nearly flat in profile, but strongly geniculated around the margin; point of geniculation 15 mm. anterior to beak; umbonal region concave; fold low, widening anteriorly and originating about 5 mm. anterior to the beak. Grooves bounding sulcus shallow, deepest near the middle; flanks slightly swollen.

Measurements in mm.—Holotype (pedicle valve), length 17.6, width (based on half measure) 24, height 6.5; paratype, U.S.N.M. 125462a (brachial valve), length 16.1, hinge width 17.1; midwidth 23.6.

Types.—Holotype, U.S.N.M. 125353; figured paratypes, U.S.N.M. 125352a, 125354; unfigured paratypes, U.S.N.M. 125352b, 125462a,b.

Localities.—636; F; P12; S46, S103; U.O. 2205-1.

Discussion.—This species is characterized by its small size, the geniculated anterior margin of the brachial valve and the very fine spines. The largest specimen from Oregon is about the same size as the type specimen of *W. montpelierensis* figured by Girty (1910), but the Oregon species is more deeply sulcate on the pedicle valve and has a somewhat more prominently folded brachial valve and finer spines. Girty's illustrations do not indicate the strong geniculation of the anterior margin of *W. montpelierensis* that is such a prominent character of the Oregon species. If this were present in the Idaho form, a fairly deep trough would appear parallel to the margin.

ECHINOCONCHUS INEXPECTATUS Cooper, new species

Plate 8C, figures 13-26

Shell small to medium size for the genus, somewhat trapezoidal to pentagonal in outline; sides broadly rounded; greatest width located at about two-thirds the length from the umbo. Hinge narrower than the shell at its widest part, equal to about two-thirds the width. Anterolateral extremities narrowly rounded; front margin gently rounded. Surface of both valves marked by conspicuous concentric growth lamellae bearing rows of spines of more than one size.

Pedicle valve strongly convex in lateral profile with the beak and umbo curved over the hinge line; beak curved over and pointing at the dorsal umbo. Umbonal region narrowly convex and with steep, almost vertical slopes to the cardinal extremities. Median region somewhat inflated; lateral slopes and anterior slope very steep to the margins. Cardinal extremities auriculate, ears small, forming an obtuse angle (118°). Median portion of valve slightly depressed by an almost imperceptible sulcus which may or may not reach the anterior margin.

Brachial valve trapezoidal in outline, moderately concave with the deepest part located just anterior to the umbo. In front of this deep part a barely perceptible fold extends anteriorly to the front margin. Areas extending obliquely to anterolateral extremities and bounding the fold moderately deep. Cardinal extremities deflected in a dorsal direction, flattened; marginal parts of valve forming a well bounding the concave portion.

Measurements in mm.—Holotype, length 27.8, width 30.4, thickness at middle 12.2, height 15.7, length of brachial valve 21.8, surface measure 50; paratype, U.S.N.M. 125357, length 25, width 25.5, thickness at middle 9, height 12.8, length of brachial valve 20.9; paratype, U.S.N.M. 125358, length 22.5, width 23.9, thickness at middle 8.8, height 11.3, surface length 36, length of brachial valve 18.7; paratype, U.S.N.M. 125454 (brachial valve), length 21.2, midwidth 32.2, hinge width 20.7, surface length 37.

Types.—Holotype, U.S.N.M. 125551; figured paratypes, U.S.N.M. 125356, 125357, 125359, 125454; unfigured paratype, U.S.N.M. 125358.

Localities.—636, 638, 639; F; P10, P11; S25, S29, S39, S40, S45, S46, S47, S50, S70, S87; U.O. 2201, 2201-1, 2202, 2204-1, 2204-3.

Discussion.—This species is most suggestive of *Echinoconchus fasciatus* (Kutorga) of described European Permian species. It differs, however, in having different dimensions, the Oregon species being shorter and wider with a broader anterior and more flaring sides.

Echinoconchus inexpectatus, new species, is a fairly common species in the Oregon Permian and is usually found in dense, hard, brownish-gray limestone having a very fine grain.

Suborder RHYNCHONELLOIDEA Moore, 1952

Superfamily RHYNCHONELLACEA Schuchert, 1896

Family CAMAROTOECHIIDAE Schuchert and LeVene, 1929

WELLERELLA MULTIPLICATA Cooper, new species

Plate 10B, figures 7-11

Shell of about medium size for the genus, subtriangular in outline; wider than long and with the greatest width at about the middle; sides rounded; front margin truncated, posterolateral margins forming an obtuse angle; paucicostate, having 5 costae on the fold of the brachial valve and 4 costae in the sulcus of the pedicle valve, and the flanks with 4 costae.

Pedicle valve gently convex in lateral profile, nearly flat in anterior profile; beak small, incurved; umbo gently swollen; sulcus originating just anterior to the middle and occupied by 4 costae; costae extending posteriorly for a short distance onto the umbo. Tongue long, geniculated at right angles, truncated anteriorly; flanks bounding sulcus not strongly elevated, flattened.

Brachial valve moderately convex in lateral profile but strongly convex in anterior profile; umbo smooth and swollen; fold originating at about the valve middle, nearly flat in anterior profile and only moderately elevated; flanks gently rounded but sloping steeply to the margins.

Measurements in mm.—Holotype, length 10.5, brachial valve length 9.5, maximum width 12.0, thickness 7.8; paratype, U.S.N.M. 125467b, length 9.8, brachial valve length 8.9, maximum width 10.7, thickness 9.1.

Types.—Holotype, U.S.N.M. 125467a; unfigured but measured paratype, U.S.N.M. 125467b.

Locality.—S87.

Discussion.—This species is characterized by its globular form, its low fold, and the presence of 4 costae in the sulcus and 5 on the fold. This species has an exterior resemblance to *W. pinguis* (Girty) and *W. shumardiana* (Girty) but it differs from both of them in being much smaller and in having more costae in the sulcus and on the fold. *Allorhynchus? permianus* Stehli has a fold and sulcus with a similar number of costae but this species is costate over the umbones as well as on the anterior half. Furthermore, Stehli's species has more costae on the flanks than the Oregon species. No other described *Wellerella* is close to this one.

Superfamily STENOSCISMATACEA Shrock and Twenhofel, 1953

Family STENOSCISMATIDAE Muir Wood, 1955

STENOSCISMA MUTABILE OREGONENSE Cooper, new subspecies

Plate 9C, figures 15-28

Shell of about medium size for the genus, body slightly wider than long, somewhat triangular in outline with beak and sides forming an angle of about 90°; greatest width anterior to the middle; posterolateral margins narrowly rounded; front margin nearly straight.

Surface marked by 10 to 11 rounded costae separated by spaces narrower than the costae; sulcus marked by 4 costae, the median 2 of which extend to the umbo and the other 2 intercalated outside the median costae and appearing at about the middle or slightly posterior to the middle; fold marked by 5 costae, the 3 median ones strong and extending to the umbo, the 2 outside ones appearing on the sides of the outer 2 strong median costae but not extending posterior to the middle. Flanks marked by 2 or 3 costae.

Ornamentation in addition to costae consisting of wide and wrinkled frills extending laterally for fully 7 mm. on each side of the valve and for an undetermined distance anteriorly.

Pedicle valve gently convex with the greatest convexity located in the umbonal region. Beak strongly incurved; sulcus originating about one-third the length from the umbo, shallow throughout but becoming very wide anteriorly and occupying slightly less than two-thirds the valve width at the front. Tongue moderately long, truncated anteriorly. Flanks narrow, flattened anteriorly but with steep slopes and rounded sides posteriorly.

Brachial valve moderately convex in lateral profile and more strongly convex in anterior profile; maximum convexity slightly posterior to the middle. Umbonal region gently convex; fold originating about one-third the length anterior to the umbo, low, gradually widening but occupying only half the width at the front margin. Flanks narrowly rounded and with steep slopes to the margins.

Measurements in mm.

	Length	Brachial length	Width	Width with frill	Thickness
Holotype	11.8	10.6	14.5	?	8.0
Paratype (125379)	12.2	11.0	15.0	29.6	?
Paratype (125377)	12.5	11.1	16.4	?	8.0

Types.—Holotype, U.S.N.M. 125378; figured paratypes, U.S.N.M. 125377, 125379, 125380.

Localities.—638; L8; P10; S14, S20, S40, S41, S46, S50; U.O. 2201-4, 2204-1, 2204-3.

Discussion.—This subspecies is represented by 4 specimens, all of them approximately of the same size, about one-half inch in width. Small size is the chief distinction between the Russian species *S. mutabile* and its American subspecies. A comparison of Tschernyschew's figures of *S. mutabile* of comparable size (Tschernyschew, 1902, pl. 45, figs. 2 and 4) shows the development of the costae in the fold and sulcus to be essentially the same as that of the American specimens, with the exception that the intercalated costae on each side of the median 2 in the sulcus are longer than in the Russian specimen of comparable size. Furthermore, the costae of the Oregon specimens are somewhat more slender than those of the Russian specimens. In Russia the species attains a width of about 1 inch or about twice the size of the Oregon specimens.

STENOSCISMA AMERICANUM Cooper, new species

Plate 9D, figures 29-33

Shell small, valves of subequal depth, subtriangular in outline, incomplete (lacking the frills), slightly wider than long. Posterolateral margins straight, lateral margins narrowly rounded, anterior margin truncated; valves paucicostate, the umbo of both valves smooth but the remainder costate. Costae numbering about 15 or 16, 4 on the fold, 1 on each side of the fold, and 4 or 5 on the flanks.

Pedicle valve slightly less deep than the brachial valve, gently convex in lateral profile, flattened in anterior profile; sulcus originating just anterior to the umbo, shallow but wide, occupying more than half the width at the front; sulcus occupied by 3 primary costae, but 1 or 2 costae are intercalated on the slope on each side of the primary 3; tongue bent nearly at a right angle, long, and broadly rounded; flanks bounding sulcus narrowly rounded.

Brachial valve gently convex in lateral profile, strongly rounded in anterior profile; fold originating just anterior to the smooth umbo, low but wide, and occupied by 4 primary costae. Secondary costae intercalated on sloping sides of fold; flanks bounding fold convex but depressed below the fold; umbo swollen.

Measurements in mm.—Holotype, length 11.2, brachial length 9.7, width 12.0, thickness 9.0.

Type.—Holotype, U.S.N.M. 125381.

Locality.—S20.

Discussion.—This species is similar to *S. mutabile oregonense* but differs in its ornamentation and the smooth umbones of both valves. It is similar to *S. karpinskyi* (Tschernyschew) but differs in having smooth umbones rather than plicated ones and the details of the ornamentation are somewhat different. On the pedicle valve of *S. americanum,* new species, the fold has only 4 costae but 2 additional ones are intercalated on the sloping side of the fold, unlike *S. karpinskyi* as illustrated by Tschernyschew (1902, pl. 60, figs. 2, 3), in which the adult has 6 costae on the fold. In the brachial valve the lateral intercalations in the sulcus are shorter than those in the Russian species which extend up to the umbo.

STENOSCISMA BIPLICATOIDEUM Cooper, new species

Plate 9E, figures 34-54

Shell of about medium size for the genus, transversely pentagonal in outline, beak obtuse; sides narrowly rounded. Surface sparsely costate, the fold provided with 3 costae, the sulcus with 2, and the flanks with 2 distinct but short costae and a third obscure one.

Pedicle valve moderately convex in lateral profile; umbonal region gently convex; sulcus originating at about the middle, shallow and occupying slightly less than half the width at the front. Tongue moderately long, narrowly rounded; costae in sulcus strongest near anterior margin. Flanks gently convex with gentle slopes to the margin.

Brachial valve slightly deeper and more convex than the pedicle valve; moderately convex and with the greatest convexity at the middle in lateral profile; fold originating about one-third the length from the dorsal beak, not strongly elevated, with costae fairly broad and separated by spaces narrower than the costae. Slopes of fold steep; flanks somewhat narrowly rounded and with steep slopes to the margins.

Measurements in mm.—Holotype, length 17.0, brachial length 14.8, width 16.9, thickness 11.3.

Types.—Holotype, U.S.N.M. 125382; figured paratypes, U.S.N.M. 125383, 125384a-d; unfigured paratype, U.S.N.M. 125461.

Localities.—L8; P10; S47; U.O. 2205-5.

Discussion.—This species differs from *S. biplicata* (Stuckenberg) as figured by Tschernyschew in its more transverse outline and the lesser development of the costae which in the American species are distinct only to about the middle of the valves. Furthermore, the sulcus is shallower and the fold somewhat narrower and lower than that of the Russian species. The most significant difference appears in the anterolateral angles which are narrower in the American form than in the Russian one and the tongue of the pedicle valve of the American species is more extended to give the valve a somewhat nasute appearance.

STENOSCISMA cf. S. PLICATUM (Kutorga)

Plate 10E, figures 32-35

Pentamerus plicatus Kutorga, Verhandl. Russ-Kais. Min. Ges., St. Petersburg, p. 89, pl. 9, fig. 3, 1844.

Camarophoria plicata (Kutorga) Tschernyschew, Mém. Com. Géol., St. Petersburg, vol. 16, No. 2, pp. 92, 502, pl. 21, fig. 1, pl. 50, figs. 17, 18, 1902.

Several specimens of a large but poorly preserved *Stenoscisma* are compared to Kutorga's species. An uncrushed pedicle valve is 27 mm. long by 30 mm. wide at the widest part which is anterior to the middle. The sulcus originates near the middle and is occupied by 5 costae and the flanks by 6 costae.

A crushed complete specimen shows a long tongue on the pedicle valve and a low fold occupied by 6 costae. Although the two specimens do not attain the full size of Kutorga's species, the characters indicated are in accord with the Russian species.

Types.—Figured specimens, U.S.N.M. 125385a,b.

Localities.—S87, S103, S106; U.O. 2201-4, 2202-1, 2202-2, 2202-6.

Superfamily RHYNCHOPORACEA Moore, 1952

Family RHYNCHOPORIDAE Muir-Wood, 1955

RHYNCHOPORA MAGNA Cooper, new species

Plate 9A, figures 1-10; plate 10D, figures 18-31

Shell large for the genus, pentagonal in outline, triangular in lateral profile. Beak obtuse, greatest width slightly anterior to the middle. Greatest thickness at the anterior. Anterior margin slightly convex. Shell provided with 24 to 26 costae, with 8 on the fold, 7 in the sulcus, and 9 on the flanks.

Pedicle valve gently convex in lateral profile, with the anterolateral flanks reflected. Maximum convexity slightly posterior to the middle. Umbo and median region slightly inflated; sulcus originating at the middle, shallow and broad, slightly swollen in the middle and occupying slightly more than half the width. Flanks bounding sulcus slightly concave posteriorly but anterolaterally folded into a low plica. Tongue long and truncated in front. Interior with long, stout dental plates.

Brachial valve gently convex in lateral view, narrowly convex in anterior profile; umbonal and median regions slightly swollen. Fold low and broad, originating at about the middle, protruding slightly anteriorly; flanks rounded and extended, with steep slopes and with sharp geniculation to unite with the reflected anterolateral extremities of the pedicle valve.

Measurements in mm.

	Length	Width	Thickness
Holotype	18.6	20.9	17.8
Paratype (125389)	19.1	22.8	19.0
" (125393)	16.5	19.2	14.5
" (125391a)	11.8	13.8	9.4
" (125390)	10.6+	12.4	9.6

Types.—Holotype, U.S.N.M. 125392; figured paratypes, U.S.N.M. 125388, 125389, 125390, 125391a, 125393, 125552; unfigured paratype, U.S.N.M. 125391b.

Localities.—613, 636, 637, 638, 639; F; L8; P10; S20, S39, S40, S45, S46, S49, S56, S87, S103; U.O. 2201-1, 2202-2, 2204-1.

Discussion.—This is the largest species of *Rhynchopora* yet found in the United States. It is coarser ribbed than large specimens of either *R. illinoisensis* (Worthen) or *R. carbonaria* (McChesney). *Rhynchopora taylori,* best-known species from the Permian, is a smaller shell with a narrower fold and sulcus. In the Oregon species the fold and sulcus occupy most of the anterior part, the flanks being small and restricted. None of the numerous specimens of *Rhynchopora* from the Leonard and Word formations of the Glass Mountains approaches *R. magna* in size or in the strength of the costation.

RHYNCHOPORA sp.

Plate 9B, figures 11-14

The specimen illustrated is probably an aberrant specimen of *Rhynchopora magna* Cooper, new species, which may have, because of unfavorable or unusual conditions, attained adulthood without ever growing to normal size. Adult characters in this specimen appear in the long tongue of the pedicle valve and the great depth of the brachial valve.

Type.—Figured specimen, U.S.N.M. 125387.

Localities.—S49, S103; U.O. 2201-4.

Suborder SPIRIFEROIDEA Allen, 1940

Superfamily SPIRIFERACEA Waagen, 1883

Family SPIRIFERIDAE King, 1846

Subfamily AMBOCOELIINAE George, 1931

CRURITHYRIS sp. 1

Plate 1G, figures 13-18

Longer than wide, maximum width at about the middle, lateral margins narrowly rounded; anterior margin truncate. Anterior commissure faintly sulcate. Surface smooth.

Pedicle valve having the greater depth; strongly convex in lateral profile especially just anterior to the umbo. Beak long and strongly incurved. Umbo narrow, elongate. Median region swollen.

Brachial valve convex in about the posterior third but flattened anteriorly. Anterior profile nearly flat. Posterolateral extremities deflected toward the pedicle valve, rounded.

Measurements in mm.—Figured specimen, U.S.N.M. 125463, length 6.6., brachial length 5.2, maximum width 5.6, hinge width 3.4, thickness 4.0.

Type.—Figured specimen, U.S.N.M. 125463.

Locality.—S46.

Discussion.—The small size of this *Ambocoelia* makes it unusual in the American Permian. It is longer than wide whereas most other species are wider than long. *Ambocoelia arcuata* Girty from the Phosphoria formation is a larger species and has a different outline. It is also not flattened anteriorly as is the Oregon species. Schellwien's *A. telleri* and Netschajew's *A. nucella* are small species but they are strongly biconvex, quite unlike typical *Ambocoelia* or *Crurithyris*. The specimen figured herein is the only one in the Oregon collection; consequently, it is impossible to tell whether it is a young form or an adult.

Subfamily TRIGONOTRETINAE Schuchert, 1893

SPIRIFERELLA DRASCHEI (Toula)

Plate 11C, figures 7-20

Spirifera draschei TOULA, Neues Jahrb. Mineral., Geol., Palaeont., p. 239, pl. 7, fig. 4, 1875.

Spiriferella draschei (Toula) BRANSON, Geol. Soc. Amer. Mem. 26, p. 506, 1948.

Spiriferina (*Spiriferella*) *salteri* TSCHERNYSCHEW, Mém. Com. Géol., St. Petersburg, vol. 16, No. 2, pp. 128, 528, pl. 6, fig. 5, pl. 12, figs. 5, 6, 1902.

Smaller than the type, moderately thin-shelled; longer than wide, with a pentagonal outline. Sides slightly convex, anterior margin subtruncate. Surface fascicostellate and pustulose; shell substance impunctate.

Pedicle valve with beak strongly curved over dorsal umbo giving the shell a top-heavy appearance. Greatest curvature umbonally, convexity moderate in the anterior half. Sulcus originating at the beak and extending to the front margin, widening gradually anteriorly to occupy about half the width at the front. Tongue long and sharply pointed. Flanks narrowly rounded and marked by about 5 fascicles of costellae; sulcus marked by a few costellae.

Brachial valve at least one-quarter the length shorter than the ventral valve, moderately convex in lateral profile but carinate in anterior profile. Fold strongly elevated, angular in section but bearing a narrow groove down the center. Flanks flattened and with long oblique slopes to the margins.

Measurements in mm.—Hypotype, U.S.N.M. 125400, length 26.9, width 22.3, thickness 17.8, length of brachial valve 20; U.S.N.M. 125406, length 34, length of brachial valve 21.9, width at middle 29+, thickness 23.5.

Types.—Figured hypotypes, U.S.N.M. 125400, 125401, 125402, 125404, 125406.

Localities.—614, 638, 639; L8, L23; P10; S4, S12, S40, S46, S47, S49, S50, S51, S56, S68, S87, S103; U.O. 2201-4, 2202-2, 2204-3, 2205-5, 2207, 2210.

Discussion.—None of the specimens of this species from Oregon is well preserved, but all appear to be typical of the Russian species.

SPIRIFERELLA PARVA Cooper, new species

Plate 11A, figures 1-5

Shell small for the genus, elongate-oval in outline; sides nearly parallel; cardinal extremities probably produced into small ears; surface fascicostellate.

Pedicle valve strongly convex in lateral profile with strongly incurved beak; umbonal and curved portion of valve approximating one-third the shell; sulcus originating at the beak, widening gradually anteriorly to occupy about half the width at the front; anterior produced into a long, sharply pointed tongue. Flanks rounded and with very steep sides. Surface marked by 5 fascicles of about 3 costellae; sulcus marked by numerous radial costellae. Deltidium prominent.

Brachial valve moderately convex with the maximum convexity located slightly posterior to the middle; carinate in anterior profile; fold originating at the beak, high and narrow, marked by slight median depression. Flanks convex and steep-sided.

Measurements in mm.—Holotype, length 22.7, width 14.9(?), thickness 17.0, length of brachial valve 16.3.

Type.—Holotype, U.S.N.M. 125405.

Locality.—U.O. 2204-3.

Discussion.—This species is characterized by its laterally compressed form and narrow fold. It is a small species, smaller than *S. draschei* (Toula). It differs from the latter by its narrower form, more incurved beak of the pedicle valve, strongly elevated and extremely narrow fold. A single specimen is all that has been taken from the Oregon Permian.

NEOSPIRIFER sp. 1

This genus is represented by fragmentary and crushed specimens, not one of them in a condition good enough for description. The shells are finely ribbed.

Types.—Mentioned specimens, U.S.N.M. 126984a,b.

Localities.—S101, S103; U.O. 2202-2.

Subfamily MARTINIINAE Waagen, 1883

PSEUDOMARTINIA BERTHIAUMEI Cooper, new species

Plate 12G, figures 50-54

Shell of about medium size for the genus, longer than wide, sides gently convex; anterior margin subtruncate. Surface mostly smooth but with obscure radial lines on the flanks.

Pedicle valve moderately convex in lateral profile with the greatest curvature in the umbonal region. Beak strongly curved over the interarea; delthyrium and interarea visible; interarea short; hinge narrow, equal to slightly less than half the shell width. Beak acute; umbo somewhat swollen; sulcus originating near the middle but well defined only in the anterior third, broad and shallow and occupying about half the width at the front. Tongue short, narrowly rounded. Flanks steep-sided and gently convex.

Brachial valve less deep than the pedicle valve, gently convex in lateral profile, subcarinate in anterior profile; fold originating at about the middle, low, clearly defined in the anterior third only, flanks steep-sided and flattened in profile. Umbonal region swollen.

Measurements in mm.—Holotype, length 22.7, length of brachial valve 18.2, width 19.7, thickness 15.8.

Type.—Holotype, U.S.N.M. 125395.

Localities.—S12, S101.

Discussion.—This species is characterized by its elongate-oval outline, the maximum width at about the middle, and the soft contours of the fold and sulcus. *Pseudomartinia berthiaumei,* new species, is unlike any described American Permian species. It is differently shaped and does not have the elongated anterior and nearly obsolete sulcus of *P. martinesi* Cooper from the Monos formation of Sonora, Mexico. It is smaller than, and with completely different outline from, Girty's two species from the Guadalupe Mountains of west

Texas, *P. shumardiana* and *rhomboidalis.* Both of these species are more nasute than the Oregon species.

Of species described outside North America, *P. berthiaumei,* new species, is very close to *P. semiglobosa* (Tschernyschew) from the *"Schwagerina"* limestone of the Urals but differs in having a more convex brachial valve and less strongly rounded sides. Another Russian species having some similarity is *P. uralica* (Tschernyschew), but that one is more elongated and has a very modest development of the fold and sulcus, even less than in the Oregon species.

Although the holotype specimen is somewhat crushed, the growth lines are clear in places and show the lateral margin to have been only gently convex.

PSEUDOMARTINIA aff. P. SEMIGLOBOSA (Tschernyschew)

Martinia semiglobosa TSCHERNYSCHEW, Mém. Com. Géol., St. Petersburg, vol. 16, No. 2, p. 564, pl. 17, figs. 6-10, 12, 13, 1902.

A fragmentary specimen is referred to Tschernyschew's species but it is impossible to make a more satisfactory identification. The profile and size of the valves agree as far as they are preserved. The fold and sulcus are indicated as low and of gentle contours and the tongue of the pedicle valve is short and rounded. These are features shared by Tschernyschew's type specimens. The umbo of the brachial valve of the Oregon specimen is narrower and the beak smaller than that of the Russian specimens. This is, however, the only important difference between the two.

Measurements in mm.—Described specimen, U.S.N.M. 125456, brachial valve length 21.2, width 23.2 (based on half measure), height about 6.

Type.—Described specimen, U.S.N.M. 125456.

Localities.—S12; U.O. 2201-1, 2202-2, 2219-1, 2225.

Subfamily PHRICODOTHYRINAE Caster, 1939

SQUAMULARIA ROSTRATA (Kutorga)

Plate 10F, figures 36-42

Spirifer rostratus KUTORGA, Verhandl. Russ.-Kais. Min. Ges., St. Petersburg, 1842, p. 25, pl. 5, fig. 10.

Reticularia rostrata TSCHERNYSCHEW, Mém. Com. Géol., St. Petersburg, vol. 16, No. 2, p. 575, pl. 20, figs. 17 and 18, 1902.

Squamularia rostrata (Kutorga) BRANSON, Geol. Soc. Amer. Mem. 26, p. 521, 1948.

A single specimen is referred to this species, although differences are apparent between it and Tschernyschew's figure of Kutorga's specimen *S. rostrata.* The latter has a considerably narrower and more elevated beak than the one from Oregon. Nevertheless, the specimen figured by Tschernyschew (1902, pl. 20, fig. 17), which comes from the *"Schwagerina"* zone, is very close to the Oregon species. This Russian specimen has not the strongly elevated beak of Kutorga's type and may ultimately prove to be distinct. The matter, however, cannot be settled on the single Oregon specimen, which is slightly crushed.

Type.—Hypotype, U.S.N.M. 125396.

Localities.—633?, 638; L8; P10, P11, P12; S41, S43, S46, S56, S103, S106; U.O. 2201-1, 2202-4, 2204-1, 2204-3.

Superfamily ROSTROSPIRACEA Schuchert and LeVene, 1929

Family ATHYRIDAE Davidson, 1884

CLEIOTHYRIDINA ATTENUATA Cooper, new species

Plate 11D, figures 21-27

Small, suboval in outline, length and width nearly equal; maximum width at middle; posterolateral margins nearly straight and forming an angle of 90° at the beak; sides strongly rounded; anterior margin strongly rounded; anterior commissure rectimarginate. Surface details indistinct but marked by closely spaced concentric lamellae bearing spines.

Pedicle valve gently convex in lateral profile, strongly convex in anterior profile; beak and umbo narrow; umbo narrowly swollen; median region swollen; flanks flattened but steep. Beak incurved and extending posterior to the margin of the brachial valve.

Brachial valve shallower than the pedicle valve, gently convex in lateral profile but strongly convex in anterior profile; umbonal region somewhat narrowed; median region strongly swollen and forming the most convex part. All slopes to the margins steep.

Measurements in mm.—Holotype, length 12.3, brachial length 11.2, maximum width 11.9, thickness 7.2.

Types.—Holotype, U.S.N.M. 125394a; unfigured paratype, U.S. N.M. 125394b.

Localities.—S45, S87; U.O. 2205-5.

Discussion.—This species is characterized by small size and small attenuate beak. This genus is at present not described from the American Permian, although it occurs in the Wolfcamp of west and north-central Texas. The Wolfcamp species is a small one but does not have the narrowed beak of the Oregon species. The same difference separates the Oregon species from *C. pectinifera* (Sowerby) as figured by Tschernyschew (1902, pl. 43, fig. 4). The species of *Cleiothyridina* from Pakistan and Timor are all large forms.

Netschajew (1911, pl. 13) figures a variety of small to medium-sized *Cleiothyridina* under the name of *C. pectinifera* (Sowerby), some of which are somewhat attenuated but none of which are like the Oregon species.

CLEIOTHYRIDINA GERARDI (Diener)

Plate 11E, figures 28-31

Athyris gerardi Diener, Palaeont. Indica, Geol. Surv. India, ser. 15, vol. 1, pt. 2, p. 56, pl. 6, figs. 12-14, 1899.

Cleiothyridina gerardi (Diener) Branson, Geol. Soc. Amer. Mem. 26, p. 317, 1948.

Two specimens of a large and transverse *Cleiothyridina* have features of this species. The figured specimen preserves both valves but the beak of the pedicle valve is missing. The pedicle valve is gently convex in profile and is devoid of a sulcus, although the anterior is considerably flattened. The brachial valve is slightly deeper than the pedicle valve and moderately convex in lateral profile. The anterior profile is strongly convex but with long and steep lateral slopes. The median region is swollen from the umbo to the anterior margin, thus forming a poorly defined fold to accommodate the anterior flattening of the opposite valve.

Only approximate measurements in millimeters are possible: Figured specimen, U.S.N.M. 125398, length 17 (probably 19 in a complete specimen), width 21, brachial length 16.7, thickness 10 or 11 (?).

A second specimen of the brachial valve has spines measuring about 2.5 mm. long.

Types.—Figured specimen, U.S.N.M. 125398; mentioned specimen, U.S.N.M. 126983.

Localities.—L8; P10, P12; S103.

COMPOSITA sp. 1

A single pedicle valve of a somewhat elongate species of *Composita* is the only representation of this genus to appear in the entire collection.

Types.—Mentioned specimen, U.S.N.M. 126982.

Locality.—L8.

Superfamily Punctospiracea Cooper, 1944

Family SPIRIFERINIDAE Davidson, 1884

Subfamily Spiriferellininae Paeckelmann, 1931

SPIRIFERELLINA PAUCIPLICATA Cooper, new species

Plate 12F, figures 45-49

Shell of moderately large size, length and width about equal; sides gently rounded, sloping slightly toward the middle; anterior margin broadly rounded. Hinge forming the greatest width; ears acute. Surface plicate, plicae strong, direct, and angular, 2 large ones on each flank and 2 smaller ones near the ears. Surface covered by concentric plaits.

Pedicle valve unevenly subpyramidal in profile with the longer side gently convex and the shorter gently concave; sulcus deep and wide, originating at the beak and occupying about one-third the valve width at the anterior margin; tongue long and angular. Flanks bounding sulcus somewhat depressed below the strong costae bounding the sulcus; interarea long and wide, gently concave, and strongly apsacline.

Brachial valve gently convex in lateral profile with the most noticeable curvature in the umbonal region. Anterior profile broadly and gently convex; fold narrow, subangular, and strongly elevated anteriorly; flanks depressed, gently convex and marked by 2 strong and 2 weak costae.

Interior unknown.

Measurements in mm.—Holotype, length 23, brachial valve length 17.0, midwidth 24.1, hinge width (based on half measure) 25.0, thickness 15.8.

Type.—Holotype, U.S.N.M. 125464.

Locality.—S87.

Discussion.—This species is especially distinguished by its fairly large size, subangular and distant costae, and the broad, strongly apsacline interarea. No other American species of *Spiriferellina* approaches it in this combination of characters. *Spiriferellina laxa* Girty is a strongly costate species but it is much smaller than the Oregon one and has a shorter and much less inclined interarea. The species nearest like the Oregon one is a Russian shell, *Spiriferina pyramidata* Tschernyschew. The two species share a similarity of ornament, each having the same type and number of costae, but the Russian species is a larger one, is wider, and the long interarea is still more steeply inclined in the apsacline position.

PUNCTOSPIRIFER sp. 1

Plate 11B, figure 6

A single poorly preserved brachial valve and a few other fragments assignable to this genus have a broad but fairly strongly elevated and angular fold. The flanks are depressed and marked by 5 subangular costae. The best brachial valve (U.S.N.M. 125407) is 16 mm. long and 19 mm. wide. The external ornamentation is not preserved on the figured specimen but a fragment of another specimen has marked varices of growth and small papillae.

Types.—Figured specimen, U.S.N.M. 125407.

Localities.—S101; U.O. 2218-2.

Discussion.—The specimen on which the foregoing description is based is poorly preserved and the pedicle valve is missing. Nevertheless, there is a striking resemblance to a Russian specimen referred to Waagen's *S. ornata* by Tschernyschew (1902, pl. 37, fig. 9). The Oregon species also bears a resemblance to *S. holzapfeli* which is similar to Tschernyschew's specimens of *S. ornata.* The Oregon species differs from both of them in having a broader and much less elevated fold.

PUNCTOSPIRIFER sp. 2

A spiriferinoid having closely spaced concentric lamellae is assigned to this genus but the specimen is too fragmentary for description or figuring. It is mentioned only for completeness sake.

Type.—Mentioned specimen, U.S.N.M. 128253.

Locality.—U.O. 2201-1.

Family RHYNCHOSPIRINIDAE Schuchert and LeVene, 1929

Subfamily RETZIINAE Waagen, 1883

HUSTEDIA sp. 1

Plate 12E, figures 42-44

Small, longer than wide, elongate oval in outline; posterolateral margins concave; lateral margins narrowly rounded; anterior margin broadly rounded. Lateral profile gently convex, anterior profile moderately convex; umbo narrowly swollen, the swelling continued throughout the median region. Surface marked by 12 costae.

Measurements in mm.—Figured specimen, length 8.0, width 6.4.

Type.—Figured specimen, U.S.N.M. 127578.

Locality.—S25.

Discussion.—This is a poorly preserved specimen and might belong to any of two or three species. It is similar to *H. remota* (Eichwald) as figured by Tschernyschew (1902, pl. 47, fig. 11).

Suborder TEREBRATULOIDEA Muir-Wood, 1955

Superfamily TEREBRATULACEA Waagen, 1883

Family CENTRONELLIDAE Waagen, 1882

Subfamily CENTRONELLINAE Waagen, 1882

ROSTRANTERIS MERRIAMI Cooper, new species

Plate 12B, figures 12-26

Shell small, longitudinally ovoid in outline, globular in profile. Sides and front rounded; anterior costate; 5 costae marking the brachial valve and 6 are on the pedicle valve.

Pedicle valve forming almost a semicircle in lateral profile with the maximum convexity a short distance posterior to the middle. Umbonal region narrowly swollen; beak strongly incurved over the dorsal umbo. Anterior two-thirds marked by a low fold consisting of 2 costae separating a narrow and fairly deep groove. Flanks convex and very steep to the margins, marked by 2 additional costae.

Brachial valve having about half the depth of the ventral valve, gently convex in the posterior two-thirds but strongly geniculated in a ventral direction about 5 mm. anterior to the beak. Maximum convexity at the point of geniculation. Anterior half marked by a fold, defined only at the front and consisting of 3 costae, a median one corresponding to the ventral groove and 2 lateral ones. Flanks moderately convex but with steep slopes to the margins. In anterior view this valve is provided with a long tongue that dovetails with a reentrant formed by the fold of the pedicle valve.

Measurements in mm.

	Length	Width	Thickness
Holotype	8.0	6.2	7.2
Paratype (125409b)	8.0	6.5	6.8

Interior.—Loop about 4 mm. long in a shell 6.5 mm. long and 5.4 mm. wide; median process of loop extending nearly to the front margin and slightly more than 2.3 mm. long.

Types.—Holotype, U.S.N.M. 125409a; figured paratypes, U.S. N.M. 125409b, 125560; unfigured paratypes, U.S.N.M. 125409c, 126985a,b.

Localities.—P11; S41, S50.

Discussion.—This species is unique in known American faunas. Most of the small terebratuloid species referred to *Notothyris* have no hinge plate and are referable to other genera. None of the species referred to *Notothyris* has the long median process on the loop as seen in *Rostranteris*. The Oregon species referred here to *Rostranteris* is quite clearly an adult shell and is therefore congeneric with Gemmellaro's genus. It does not, however, resemble any of the Sicilian species. The Oregon form is reminiscent of *Rhynchonella keyserlingi* Moeller, 1862, which is referred by Tschernyschew to the genus *Pugnax*. The original of this species, figured by Tschernyschew (1902, pl. 21, fig. 18), shows a small but extremely thick shell similar to *R. merriami*, new species. The Oregon species differs from the Russian one in stronger and more elevated costae, a well-defined fold on the pedicle valve made up of 2 costae with a wide sulcus between. The brachial sulcus is occupied by a single costa quite unlike the Russian species.

ROSTRANTERIS SULCATUM Cooper, new species

Plate 12A, figures 1-11

Shell small, longitudinally ovoid in outline, unequally biconvex in profile; sides convex; anterior narrowly rounded. Surface semicostate, shell substance punctate.

Pedicle valve deep, strongly and evenly convex in lateral profile, with the greatest convexity at about the middle. Beak strongly incurved; umbonal region narrowly convex. Pedicle valve marked by a broad and shallow sulcus defined by 2 prominent costae that originate near the middle of the valve and extend to the front margin, heightening and strengthening anteriorly. The sulcus is occupied by a low costa beginning anterior to the middle and strengthening in an anterior direction. Sulcus produced into a long, tapering tongue. Flanks convex, steeply sloping to the margins and provided with a single obscure costa.

Brachial valve shallower than the pedicle valve, slightly convex in lateral profile, fairly strongly convex in anterior profile. Umbo narrowly swollen; median area slightly swollen; fold originating slightly anterior to the middle short, narrow, low, and marked in the middle by a narrow sulcus corresponding to the median costa that occupies the sulcus of the ventral valve. Flanks steep-sided and convex, marked anteriorly by a single obscure costa.

Measurements in mm.

	Length	Width	Thickness
Holotype	8.6	6.3	6.0
Paratype (125408)	7.7	6.4	5.3

Types.—Holotype, U.S.N.M. 125410; figured paratype, U.S.N.M. 125408.

Localities.—S41; U.O. 2201-2, 2223-2.

Discussion.—This species has its closest affinities with *R. nucleola* (Kutorga) as redescribed by Tschernyschew. It is somewhat more elongate and slightly smaller than the Russian species and possesses a sulcate fold on the brachial valve which is not shown by Tschernyschew's specimens. It differs from *R. merriami,* new species, in its subnasute anterior, the more erect pedicle beak, and the less numerous costae on the anterior part of the valves.

Family DIELASMATIDAE Schuchert and LeVene, 1929

Subfamily DIELASMATINAE Schuchert, 1913

DIELASMA? TRUNCATUM Cooper, new species

Plate 10A, figures 1-6

Shell small for the genus, pyriform in outline, with a moderately long posterior third; rounded lateral margins but truncated front. Beak incurved, foramen labiate. Pedicle valve most convex in the posterior half and particularly in the umbonal region. Median region slightly swollen and with gentle slopes to the lateral and front margins. Brachial valve most convex in the posterior half; umbonal region swollen with moderate slopes to the posterolateral margins. Midregion gently convex.

Measurements in mm.—Holotype, length 10.6, width 8.5, thickness 6.2, length of brachial valve 8.8.

Type.—Holotype, U.S.N.M. 125411.

Locality.—S20.

Discussion.—This species is represented by two specimens only, and it is not certain that the species belongs to *Dielasma.* It is different from all the other terebratuloids seen in the Oregon Permian in its truncated front margin and rectimarginate commissure.

DIELASMA BREVICOSTATUM Cooper, new species

Plate 12D, figures 32-41

Of about medium size for the genus, longer than wide; valves unequally convex, the pedicle valve the deeper and more convex;

lateral margins gently rounded, front margin emarginated. Pedicle valve having a prominent and deep sulcus originating 15 mm. surface measure anterior to the beak; sulcus narrow and deepening anteriorly, about 21 mm. long, surface measure. Anterolateral extremities narrowly rounded. Brachial valve nearly flat, with narrow and elongate beak; anterior profile broadly convex. Anterior margin flexed dorsally to accommodate the short ventral tongue but no appreciable amount of folding takes place on the valve.

Measurements in mm.—Holotype, length 21, length of brachial valve 18.7, width 15.2, thickness 10.8; paratype, U.S.N.M. 125413b, surface length 36, length of brachial valve 20, width 15?, thickness 13.

Types.—Holotype, U.S.N.M. 125413a; figured paratypes, U.S. N.M. 125413b, 125415.

Localities.—P12; S87, S103; U.O. 2202-2, 2204-3, 2205-5, 2216-2.

Discussion.—This species is characterized by its flat brachial valve and anteriorly sulcate pedicle valve. The species most like it is *D. prolongatum* Girty but the Oregon species differs in having a much shorter sulcus in the pedicle valve and a flatter brachial valve. The sulcus in the Oregon species is deep only in the anterior third or quarter.

DIELASMA RECTIMARGINATUM Cooper, new species

Plate 12C, figures 27-31

Shell of about usual size for the genus, narrowly elliptical in all profiles; maximum width anterior to the middle; anterolateral margins broadly rounded; anterior margin truncated. Surface smooth. Anterior commissure faintly uniplicate, but no fold and sulcus defined.

Pedicle valve slightly deeper than the brachial valve, gently convex in lateral and anterior profiles; median region gently inflated.

Brachial valve gently convex in lateral profile, more strongly convex in anterior profile; beak small and acutely pointed; umbo and median region gently inflated; anterior slope long and gentle; lateral slopes steep near the margins.

Interior of pedicle valve with low median ridge extending from beak for three-fourths the length of the valve.

Measurements in mm.—Holotype, length 19.6+, brachial length 17.6, maximum width 16.3, thickness 13.0+.

Type.—Holotype, U.S.N.M. 125414.

Localities.—L23; U.O. 2201-1.

Discussion.—This species is characterized by the slender profiles, lack of marked anterior folding, and the sharp, somewhat elongated beak of the brachial valve. It differs from all Girty's species, *D. prolongatum, cordatum, sulcatum,* and *spatulatum,* in lacking anterior folding and having only a faint trace of sulcation on the pedicle valve.

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EXPLANATION OF PLATES

Plate 1

Page

A. *Lingula* sp. 20

(1, 2) Respectively × 1 and × 2 views of a pedicle valve showing an impression of the interior with its long, low, median ridge, figured specimen, U.S.N.M., 125311. Locality U.O. 2204-3.

(3) Plasticine impression showing a replica of the exterior of a crushed brachial valve, × 1, figured specimen, U.S.N.M. 125531. Locality S50.

B. *Derbyia* sp. 2.. 21

(4, 5, 7) Respectively posterior, side, and ventral views of a pedicle valve showing interarea, × 1, figured specimen, U.S.N.M. 125315. Locality S101.

(6) Exterior of a poorly preserved brachial valve, × 1, figured specimen, U.S.N.M. 125312. Locality U.O. 2204-3.

C. *Paeckelmannia* aff. *Chonetes alatus* Stuckenberg.................... 25

(8) Exterior of an imperfect pedicle valve with outline restored, × 3, figured specimen, U.S.N.M. 125316. Locality S41.

D. *Meekella* sp. 1.. 22

(9) Side view of a specimen broken through the middle, × 1, figured specimen, U.S.N.M. 125313. Locality 637.

E. *Chonetinella* sp. 1.. 25

(10, 11) Exterior of an imperfect pedicle valve showing deep sulcus, × 1 (with outline restored) and × 2, figured specimen, U.S.N.M. 125468. Locality S103.

F. *Rhipidomella* sp. 1.. 21

(12) Exterior of a small pedicle valve, × 2, figured specimen, U.S.N.M. 125314. Locality S101.

G. *Crurithyris* sp. 1.. 55

(13) Dorsal view of a complete specimen with broken margin, × 1, figured specimen, U.S.N.M. 125463; (14-18) respectively posterior, ventral, anterior, dorsal (with margin restored), and side views of the same specimen, × 2. Locality S46.

H. *Chonetes pygmoideus* Cooper, new species.............................. 24

(19-23) Respecively anterior, posterior, ventral, side, and dorsal views of the holotype, U.S.N.M. 125469; (24-26) respectively side, dorsal, and ventral views of the holotype, × 2. Locality S30.

I. *Chonetes* sp. 1.. 23

(27-31) Respectively dorsal, ventral, anterior, posterior, and side views of a complete but somewhat exfoliated specimen, × 1, figured specimen, U.S.N.M. 125470a; (32) same specimen as preceding, × 2, showing pits left by pseudopunctae when shell was exfoliated; (33) rubber replica of the exterior of a brachial valve showing the costellae, × 2, figured specimen, U.S.N.M. 125470b. Locality S68.

(34) Impression of the interior of a pedicle valve showing median

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ridges, × 1, figured specimen, U.S.N.M. 125319. Locality S111.

(35) Impression of the interior of another pedicle valve, × 1, figured specimen, U.S.N.M. 125318. Locality U.O. 2201-3.

J. *Leptodus?* sp. 1 26

(36-38) Respectively posterior, ventral, and anterior views of the internal impressions of a pedicle valve showing stout median ridge and lateral lobes, × 1, figured specimen, U.S.N.M. 125325; (39) rubber cast prepared from the preceding mold showing a replica of the interior of the pedicle valve, × 1, with its ridges and channels. Locality 637.

Plate 2

A. *Alexenia? subquadrata* Cooper, new species 45

(1-4) Respectively anterior, ventral, side, and posterior views of a pedicle valve, × 1, holotype, U.S.N.M. 125328. Locality L8.

B. *Krotovia parva* Cooper, new species 33

(5-7) Respectively side, ventral, and posterior views of the holotype, a pedicle valve, × 1, U.S.N.M. 125355a; (8) ventral view of the same specimen, × 2, showing arrangement of fine spines. Locality S40.

(9-11) Respectively dorsal, ventral, and side views of a complete but silicified specimen showing beak, × 1, paratype, U.S.N.M. 125465; (12) dorsal view of same specimen showing deeply concave brachial valve and beak, × 2. Locality P10.

C. *Avonia oregonensis* Cooper, new species 31

(13) Impression of the exterior of a brachial valve, × 1, paratype, U.S.N.M. 125321b; (14) ventral view of a pedicle valve showing elongated spine bases, × 1, paratype, U.S.N.M. 125321a. Locality S49.

(15-17) Respectively side, ventral, and dorsal views of a complete specimen, × 1, paratype, U.S.N.M. 125322. Locality S46.

(18) Impression of the exterior of an exceptionally large brachial valve, × 1, paratype, U.S.N.M. 125324. Locality S30.

(19, 20) Ventral and side views of an average-sized pedicle valve, × 1, paratype, U.S.N.M. 125323b; (21-24) respectively posterior, ventral, anterior, and side views of a large specimen, × 1, holotype, U.S.N.M. 125323a. Locality U.O. 2204-3.

D. *Alexenia? occidentalis* Cooper, new species 44

(25-29) Respectively posterior, side, dorsal, ventral, and anterior views of a complete specimen, × 1, holotype, U.S.N.M. 125350. Locality 638.

(30-33) Respectively posterior, side, ventral, and anterior views of a pedicle valve preserving the trail, × 1, paratype, U.S.N.M. 125335. Locality U.O. 2204-3.

(34) Poorly preserved interior of a brachial valve showing part of cardinal process, × 1, paratype, U.S.N.M. 125334. Locality U.O. 2201-4.

PLATE 3

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A. *Antiquatonia reticulata* Cooper, new species.......................... 34

(1) Impression of the exterior of a brachial valve showing the reticulate visceral region, × 1, paratype, U.S.N.M. 125349. Locality S67.

(2-5) Respectively side, dorsal, anterior, and ventral views of a small individual without complete trail, × 1, paratype, U.S.N.M. 125347. Locality P10.

(6-9) Respectively posterior, ventral, side, and anterior views of a large specimen with strongly reticulate visceral region and long trail, × 1, holotype, U.S.N.M. 125348. Locality S20.

B. *Proboscidella? carinata* Muir-Wood and Cooper, new species.......... 36

(10) Ventral view of a well-preserved pedicle valve showing long carinate trail, × 1, holotype, U.S.N.M. 124156a; (11-14) respectively anterior, ventral, side, and posterior views of the holotype, × 2, Locality S12.

(15) Impression of the interior of a pedicle valve showing groove left by solution of subperipheral rim, × 1, paratype, U.S.N.M. 124157. Locality S49.

(16, 17) Anterior and ventral views of another pedicle valve showing depression just posterior to line of geniculation, × 2, paratype, U.S.N.M. 125533. Locality U.O. 2201-2.

PLATE 4

A. *Kochiproductus transversus* Cooper, new species...................... 46

(1-3) Respectively ventral, side, and dorsal views of a complete specimen showing fold on brachial valve, × 1, holotype, U.S.N.M. 125332. Locality P10.

(4-6) Respectively ventral, posterior, and side views of a larger specimen showing part of ventrally deflected anterior border, × 1, paratype, U.S.N.M. 125331. Locality U.O. 2201-1.

B. *Kochiproductus* cf. *K. porrectus* (Kutorga)......................... 47

(7) Dorsal view of a large but fragmentary specimen, × 1, figured specimen, U.S.N.M. 125333. Locality U.O. 2202-2.

C. *Waagenoconcha parvispinosa* Cooper, new species.................... 47

(8) Rubber replica of the exterior of a large brachial valve showing minute spine bases, × 1, paratype, U.S.N.M. 125354. Locality S46.

(9, 10) Ventral and side views of a pedicle valve with outline restored, × 1, holotype, U.S.N.M. 125353. Locality 636.

(11, 12) Respectively × 1 and × 2 views of another pedicle valve younger than the preceding, paratype, U.S.N.M. 125352a. Locality P12.

PLATE 5

A. *Muirwoodia transversa* Cooper, new species.......................... 39

(1) Ventral view of a specimen preserving one of the long anterior spines, × 1, paratype, U.S.N.M. 125340. Locality S43.

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(2, 3) Posterior and dorsal views of a specimen preserving both valves, × 1, holotype, U.S.N.M. 125339. Locality U.O. 2201-2.

(4, 5) Anterior and ventral views of a young specimen, × 1, paratype, U.S.N.M. 125342. Locality S103.

(6) Plasticine replica of the exterior of a brachial valve, × 1, paratype, U.S.N.M. 125345. Locality L8.

(7-9) Respectively ventral, side, and anterior views of a large pedicle valve showing strong geniculation, × 1, paratype, U.S.N.M. 125337. Locality P10.

(10-12) Respectively ventral, side, and anterior views of another pedicle valve showing scar of large anterior spine (in fig. 12), × 1, paratype, U.S.N.M. 125343. Locality S46.

(13) Posterior view of another pedicle valve showing deep median sulcus, × 1, paratype, U.S.N.M. 125338. Locality U.O. 2204-3.

B. *Marginifera? multicostellata* Cooper, new species.................... 43

(14-17) Respectively side, ventral, anterior, and posterior views of the holotype showing reticulate visceral disk region, × 1, U.S.N.M. 125365. Locality S46.

C. *Antiquatonia sulcata* Cooper, new species.......................... 35

(18-21) Respectively posterior, anterior, side, and ventral views of the holotype, showing deep sulcus, × 1, U.S.N.M. 125327. Locality S51.

(22) Impression of the exterior of a brachial valve showing reticulate visceral region and prominent depression (shown as a fold) around the ear, × 1, paratype, U.S.N.M. 125329. Locality S43.

PLATE 6

A. *Anidanthus minor* Cooper, new species.............................. 38

(1-4) Respectively ventral, anterior, posterior, and side views of broad but crushed specimen, × 1, paratype, U.S.N.M. 125351. Locality S87.

(5-7) Respectively side, posterior, and ventral views of nasute specimen, × 1, paratype, U.S.N.M. 125360. Locality S46.

(8, 9) Side and posterior views, × 2, showing the wide hinge and ears, paratype U.S.N.M. 125535. Locality S103.

(10-12) Respectively posterior, ventral, and side views of a large, broad specimen, × 1, holotype U.S.N.M. 125361; (13, 14) side and ventral views of the holotype, × 2, showing costellae. Locality U.O. 2201-1.

(15) Posterior of another pedicle valve showing beak and ears, × 2, paratype, U.S.N.M. 125534. Locality L8.

(16, 17) Respectively × 1 and × 2 enlargements of an impression of the exterior of a brachial valve showing concentric lamellae, paratype, U.S.N.M. 125466. Locality U.O. 2207-2.

B. *Marginifera? profundosulcata* Cooper, new species.................... 43

(18-21) Respectively ventral, posterior, anterior, and side views of the holotype showing the wide and deep sulcus, × 1, U.S.N.M. 125364a. Locality S49.

C. *Marginifera? costellata* Cooper, new species........................ 42

(22-25) Respectively ventral, anterior, posterior, and side views, × 1, of the holotype, U.S.N.M. 125368. Locality S46.

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(26) Ventral view of a specimen showing two of the large steadying spines on the trail, × 1, paratype, U.S.N.M. 125370a. Locality S43.

D. *Linoproductus* cf. *L. lutkewitschi* (Stepanow) 38

(27-29) Respectively side, posterior, and dorsal views of an imperfect specimen with margin restored, × 1, figured hypotype, U.S.N.M. 125326. Locality S14.

PLATE 7

A. *Probolionia posteroreticulata* Cooper, new species 30

(1-3) Respectively side, posterior, and ventral views of a pedicle valve, × 1, paratype, U.S.N.M. 125366b; (7-9) respectively posterior, ventral, and side views of another pedicle valve, paratype, U.S.N.M. 125366a; (10-12) posterior, side, and ventral views of the preceding paratype, × 2, partially exfoliated and showing impression of cincture on interior of pedicle valve; (17) fragmentary pedicle valve showing one of the lobes of the brachial ridges, × 2, paratype, U.S.N.M. 125366d; (18) anterior view of same paratype, × 2, showing steep, endospinose trail and anterior edge of diaphragm; (19) interior of a silicified but imperfect pedicle valve showing the elevated adductor ridge, × 2, paratype, U.S.N.M. 125366j; (20) specimen with part of the pedicle valve broken away to show the position of the brachial valve, the depth of the visceral cavity, and the diaphragm, × 2, paratype, U.S.N.M. 125366c; (21) posterior of an exfoliated pedicle valve showing a cardinal process etched into relief by acid, × 4, paratype, U.S.N.M. 125366f; (22) polished transverse section showing diaphragm and successive trails of the brachial valve, × 2, paratype, U.S.N.M. 125366e. Locality S103.

(4-6) Respectively ventral, side, and posterior views of a large pedicle valve, × 1, paratype, U.S.N.M. 125367. Locality S87.

(13-15) Respectively posterior, ventral, and side views of a large and well-preserved pedicle valve, × 2, holotype, U.S.N.M. 125369. Locality S40.

(16) Dorsal view of a specimen showing the brachial valve but with the trail broken along the diaphragm, × 1, paratype, U.S.N.M. 125374. Locality 638.

(23) Impression of the exterior of a brachial valve showing the long diaphragm around the visceral disk, × 1, paratype, U.S.N.M. 125550. Locality U.O. 2202-2.

B. *Marginifera? brevisulcata* Cooper, new species 41

(24-26) Respectively ventral (with margin restored), posterior, and side views of an exfoliated specimen, × 1, paratype, U.S.N.M. 125362. Locality S49.

(27-29) Respectively posterior, side, and ventral views of the holotype, U.S.N.M. 125363a. Locality S30.

C. *Pleurohorridonia? elongata* Cooper, new species 37

(30-33) Respectively posterior, anterior, ventral, and side views, × 1, of the holotype, U.S.N.M. 125346. Locality S51.

Plate 8

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A. *Krotovia pustulata* (Keyserling).................................. 33

(1-5) Respectively posterior, dorsal, ventral, side, and anterior views, × 1, of a nearly complete specimen with outlines restored and pits left by spines of the brachial valve in figure 3, hypotype, U.S.N.M. 124021. Locality U.O. 2204-3.

B. *Probolionia elongata* Cooper, new species.......................... 29

(6-8) Respectively side, anterior, and posterior views of the holotype, U.S.N.M. 125371a. Locality U.O. 2202-3.

(9) Anterior view of another specimen larger than the preceding, × 1, paratype, U.S.N.M. 125372. Locality S49.

(10) Dorsal view of an imperfect specimen showing brachial valve, diaphragm, and ear, × 1, paratype, U.S.N.M. 125373; (11, 12) respectively × 1 and × 2 views of the counterpart of the preceding specimen showing impression of visceral disk and part of diaphragm. Locality S46.

C. *Echinoconchus inexpectatus* Cooper, new species..................... 48

(13-17) Respectively dorsal, anterior, side, posterior, and ventral views of a complete specimen (beak restored), × 1, U.S.N.M. 125357. Locality 638.

(18) Plasticine replica of the exterior of brachial valve, × 1, made from paratype, U.S.N.M. 125359. Locality U.O. 2204-3.

(19-22) Respectively side, posterior, anterior, and ventral views of pedicle valve, × 1, showing rows of pits representing spines, paratype, U.S.N.M. 125454. Locality U.O. 2201-1.

(23) Ventral view of a large pedicle valve showing spine-bearing lamellae, × 1, paratype, U.S.N.M. 125356. Locality S25.

(24-26) Respectively posterior, side, and dorsal views of a large specimen preserving the beak, × 1, holotype, U.S.N.M. 125551. Locality U.O. 2201-1.

Plate 9

A. *Rhynchopora magna* Cooper, new species............................ 54

(1-5) Respectively anterior, ventral, side, dorsal, and posterior views of a nearly perfect young specimen, × 1, paratype, U.S.N.M. 125391a. Locality S40.

(6-10) Respectively ventral, posterior, side, dorsal, and anterior views of a well-preserved young individual, × 1, paratype, U.S.N.M. 125390. Locality 639.

B. *Rhynchopora* sp. 55

(11-14) Respectively ventral, dorsal, side, and anterior views, × 1, figured specimen, U.S.N.M. 125387. Locality U.O. 2201-4.

C. *Stenoscisma mutabile oregonense* Cooper, new subspecies............... 50

(15-19) Respectively dorsal, posterior, side, anterior, and ventral views of a nearly complete specimen, × 1, holotype, U.S.N.M. 125378; (20) plasticine replica of the exterior of the holotype, × 1, showing lateral frills, prepared from natural impression of the ventral side of the holotype; (21-25) respectively ventral, posterior, side,

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anterior, and dorsal views of a specimen larger than the holotype, × 1, paratype, U.S.N.M. 125377. Locality 638.

(26) Ventral view of another paratype showing part of the anterior frill, × 1, U.S.N.M. 125380. Locality U.O. 2204-3.

(27, 28) Respectively × 1 and × 2 views of the dorsal side of a well-preserved specimen preserving most of the lateral frills, paratype, U.S.N.M. 125379. Locality S40.

D. *Stenoscisma americanum* Cooper, new species...................... 52

(29-33) Respectively posterior, anterior, side, dorsal, and ventral views of the holotype, U.S.N.M. 125381. Locality S20.

E. *Stenoscisma biplicatoideum* Cooper, new species...................... 53

(34-38) Respectively ventral, posterior, side, anterior, and dorsal views, × 1, of the holotype, U.S.N.M. 125382. Locality U.O. 2205-5.

(39-41) Respectively dorsal, posterior, and ventral views, × 1, showing the anterior part of the frill, paratype, U.S.N.M. 125384a; (47-50) respectively dorsal, posterior, anterior, and side views, with outlines restored, × 1, of a large specimen, paratype, U.S.N.M. 125384b; (51-53) respectively posterior, ventral, and dorsal views of a specimen still larger than the preceding showing a section of the spondylium, × 1, paratype, U.S.N.M. 125384c; (54) ventral view of the largest specimen of this species, × 1, paratype, U.S.N.M. 125384d. Locality L8.

(42-46) Respectively ventral, anterior, posterior and dorsal views of a large specimen with outlines restored, × 1, paratype, U.S.N.M. 125383. Locality P10.

PLATE 10

A. *Dielasma? truncatum* Cooper, new species............................ 66

(1-5) Respectively ventral, anterior, posterior, side, and dorsal views of the holotype, × 1, U.S.N.M. 125411; (6) dorsal view of the holotype, × 2. Locality S20.

B. *Wellerella multiplicata* Cooper, new species.......................... 49

(7-11) Respectively ventral, posterior, side, anterior, and dorsal views of the holotype, × 1, U.S.N.M. 125467a. Locality S87.

C. *Krotovia* aff. *K. barenzi* (Miloradovitch)........................... 32

(12-14) Respectively ventral, side, and posterior views of a small individual, × 1, figured specimen, U.S.N.M. 125336a; (15-17) respectively ventral, side, and posterior views of a specimen larger than the preceding, × 1, figured specimen, U.S.N.M. 125336b. Locality S101.

D. *Rhynchopora magna* Cooper, new species............................ 54

(18-22) Respectively ventral, side, dorsal, anterior, and posterior views of a large specimen with margins restored, × 1, holotype, U.S.N.M. 125392. Locality U.O. 2202-2.

(23, 24) Posterior and anterior views of a somewhat crushed specimen, × 1, paratype, U.S.N.M. 125388. Locality U.O. 2204-1.

(25-27) Respectively side, ventral, and posterior views of a specimen smaller than the holotype, × 1, paratype, U.S.N.M. 125393. Locality S87.

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(28) Interior of a silicified pedicle valve showing the long dental lamellae, × 2, paratype, U.S.N.M. 125552. Locality S103.

(29-31) Respectively side, anterior, and ventral views of a large but poorly preserved specimen, × 1, paratype, U.S.N.M. 125389. Locality 638.

E. *Stenoscisma* cf. *S. plicatum* (Kutorga)........................... 54

(32-34) Respectively posterior, side, and anterior views of a longitudinally crushed specimen, × 1, figured specimen, U.S.N.M. 125385a. Locality S103.

(35) Ventral view of a pedicle valve with outline restored, × 1, figured specimen, U.S.N.M. 125385b. Locality U.O. 2201-4.

F. *Squamularia rostrata* (Kutorga)................................. 59

(36-40) Respectively side, ventral, posterior, anterior, and dorsal views of a complete specimen, × 1, hypotype, U.S.N.M. 125396; (41) dorsal view of the preceding specimen, × 2; (42) median portion of the same specimen, × 3, showing surface with concentric rows of small holes representing spines. Locality P12.

PLATE 11

A. *Spiriferella parva* Cooper, new species.............................. 57

(1-5) Respectively ventral, posterior, side, anterior, and dorsal views, × 1, of the holotype, U.S.N.M. 125405. Locality U.O. 2204-3.

B. *Punctospirifer* sp. 1... 63

(6) Dorsal view of an exfoliated brachial valve, × 1, figured specimen, U.S.N.M. 125407. Locality U.O. 2218-2.

C. *Spiriferella draschei* (Toula)..................................... 56

(7-10) Respectively side, anterior, ventral, and dorsal views of a large but imperfect specimen, × 1, hypotype, U.S.N.M. 125406; (19) portion of a pedicle valve showing papillae on exterior, × 3, hypotype, U.S.N.M. 125402. Locality S46.

(11-13) Respectively side, ventral, and dorsal views of a small adult specimen, × 1, hypotype, U.S.N.M. 125400. Locality S50.

(14-17) Respectively dorsal, ventral, side, and posterior views of a fragmentary pedicle valve showing pseudodeltidium (fig. 14) and ribbing, × 1, hypotype, U.S.N.M. 125401; (18) portion of right side of previous specimen enlarged to show details of the surface, × 3. Locality P10.

(20) Surface of a fragmentary pedicle valve showing the papillose and costellate ornamentation, × 3, hypotype, U.S.N.M. 125404. Locality S103.

D. *Cleiothyridina attenuata* Cooper, new species....................... 60

(21-25) Respectively anterior, posterior, side, ventral, and dorsal views, × 1, of the holotype, U.S.N.M. 125394a; (26, 27) ventral and dorsal views, × 2, of the holotype. Locality U.O. 2205-5.

E. *Cleiothyridina gerardi* (Diener).................................... 61

(28-31) Respectively dorsal, posterior, ventral, and side views of an imperfect specimen, × 1, beak outline restored, figured specimen, U.S.N.M. 125398. Locality L8.

Plate 12

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A. *Rostranteris sulcatum* Cooper, new species........................... 65

(1-5) Respectively posterior, ventral, side, dorsal, and anterior views of a complete specimen, × 2, paratype, U.S.N.M. 125408. Locality U.O. 2201-2.

(6) Dorsal view of the holotype, × 1, U.S.N.M. 125410; (7-11) respectively ventral, anterior, side, posterior, and dorsal views of the holotype, × 2. Locality S41.

B. *Rostranteris merriami* Cooper, new species........................... 64

(12-16) Respectively anterior, posterior, ventral, side, and dorsal views of the holotype, × 2, U.S.N.M. 125409a; (17, 18) side and dorsal views of the holotype, × 1; (19-23) respectively anterior, ventral, dorsal, posterior, and side views of another perfect specimen, × 2, paratype, U.S.N.M. 125409b; (24, 25) side and dorsal views of the preceding paratype, × 1. Locality S41.

(26) Specimen with brachial valve rubbed away to show loop with its long, longitudinal spine, × 4, paratype, U.S.N.M. 125560. Locality S50. Specimen photographed under water.

C. *Dielasma rectimarginatum* Cooper, new species....................... 67

(27-31) Respectively dorsal, side, anterior, posterior, and ventral views of the holotype, U.S.N.M. 125414. Locality U.O. 2201-1.

D. *Dielasma brevicostatum* Cooper, new species......................... 66

(32-36) Respectively side, posterior, anterior, dorsal, and ventral views, × 1, of the holotype, U.S.N.M. 125413a; (37-39) respectively side, posterior, and dorsal views of a large paratype, × 1, U.S.N.M. 125413b. Locality U.O. 2202-2.

(40, 41) Anterior and ventral views of a large, exfoliated specimen, × 1, paratype, U.S.N.M. 125415. Locality U.O. 2216-2.

E. *Hustedia* sp. 1.. 63

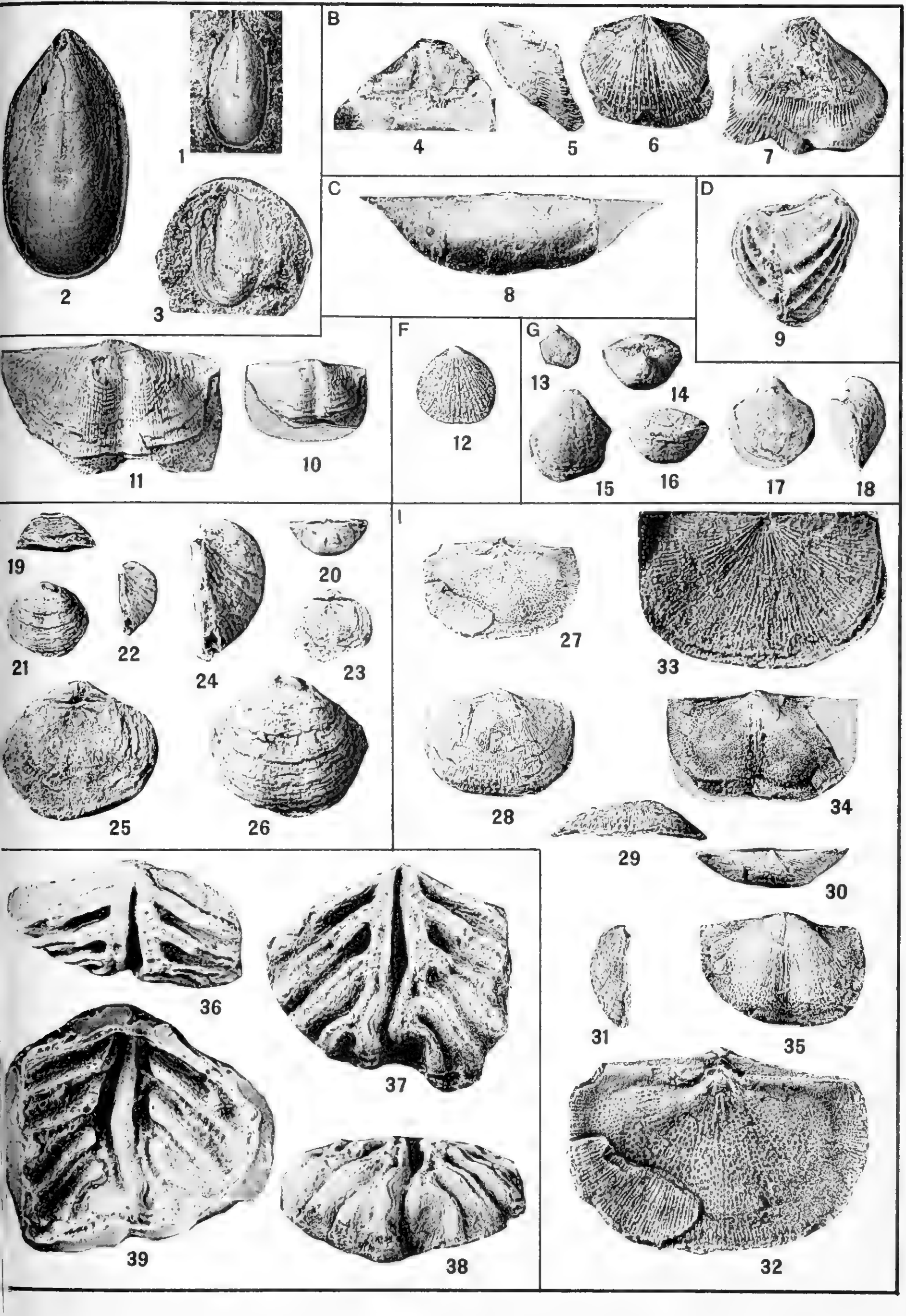
(42) Ventral view of an imperfect specimen, × 1, figured specimen, U.S.N.M. 127578; (43, 44) side and ventral views of the same specimen, × 2. Locality S25.

F. *Spiriferellina pauciplicata* Cooper, new species..................... 62

(45-49) Respectively dorsal, anterior, side, posterior, and ventral views, × 1, of the poorly preserved holotype, U.S.N.M. 125464. Locality S87.

G. *Pseudomartinia berthiaumei* Cooper, new species.................... 58

(50-54) Respectively ventral, anterior, side, posterior, and dorsal views × 1, of the holotype, U.S.N.M. 125395. Locality S12.



Lingula, Derbyia, Paeckelmannia. Meekella, Chonetinella, Rhipidomella, Crurithyris, Chonetes, and Leptodus?

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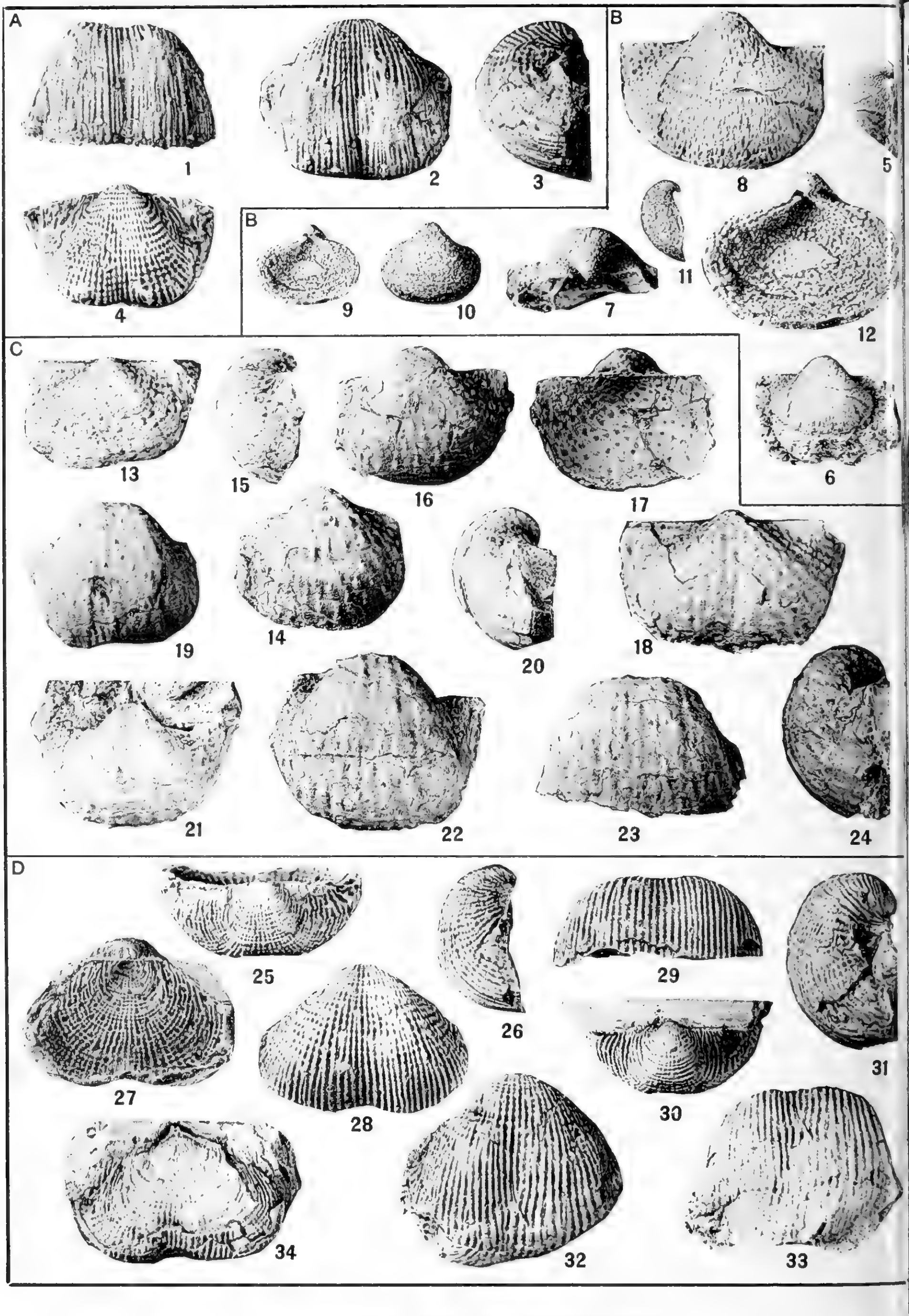

ALEXENIA?, KROTOVIA, AND AVONIA

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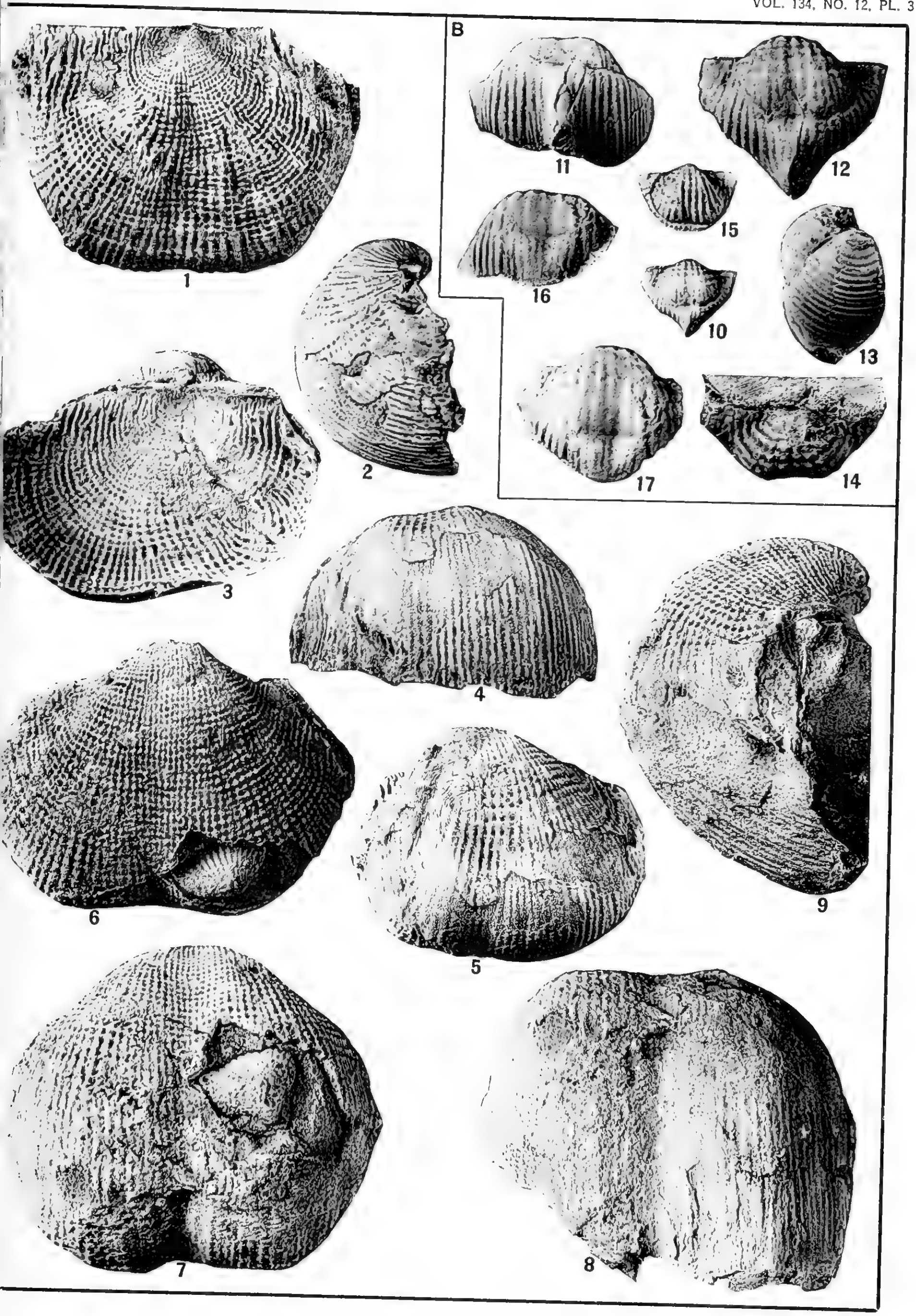

ANTIQUATONIA AND PROBOSCIDELLA?

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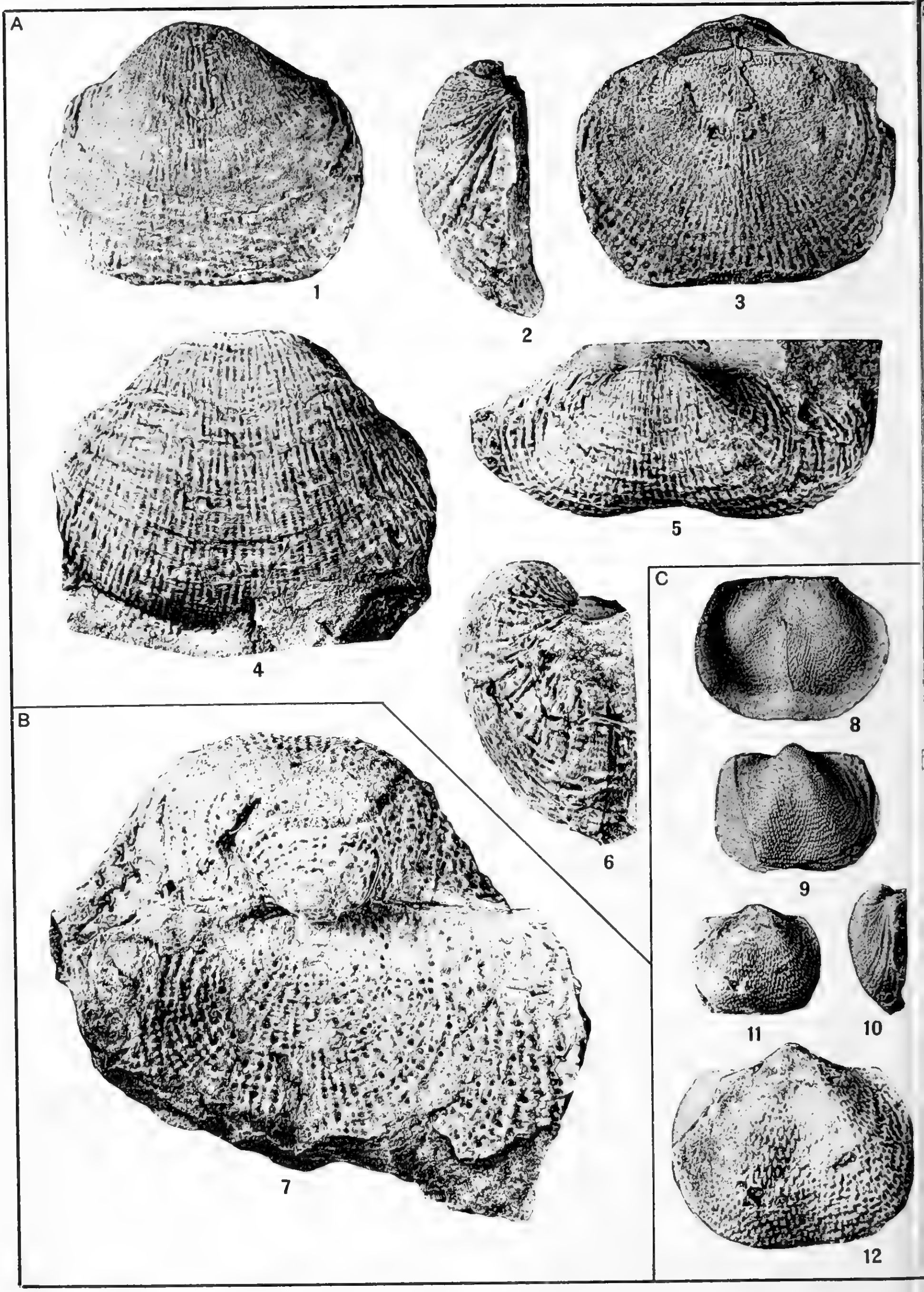

KOCHIPRODUCTUS AND WAAGENOCONCHA

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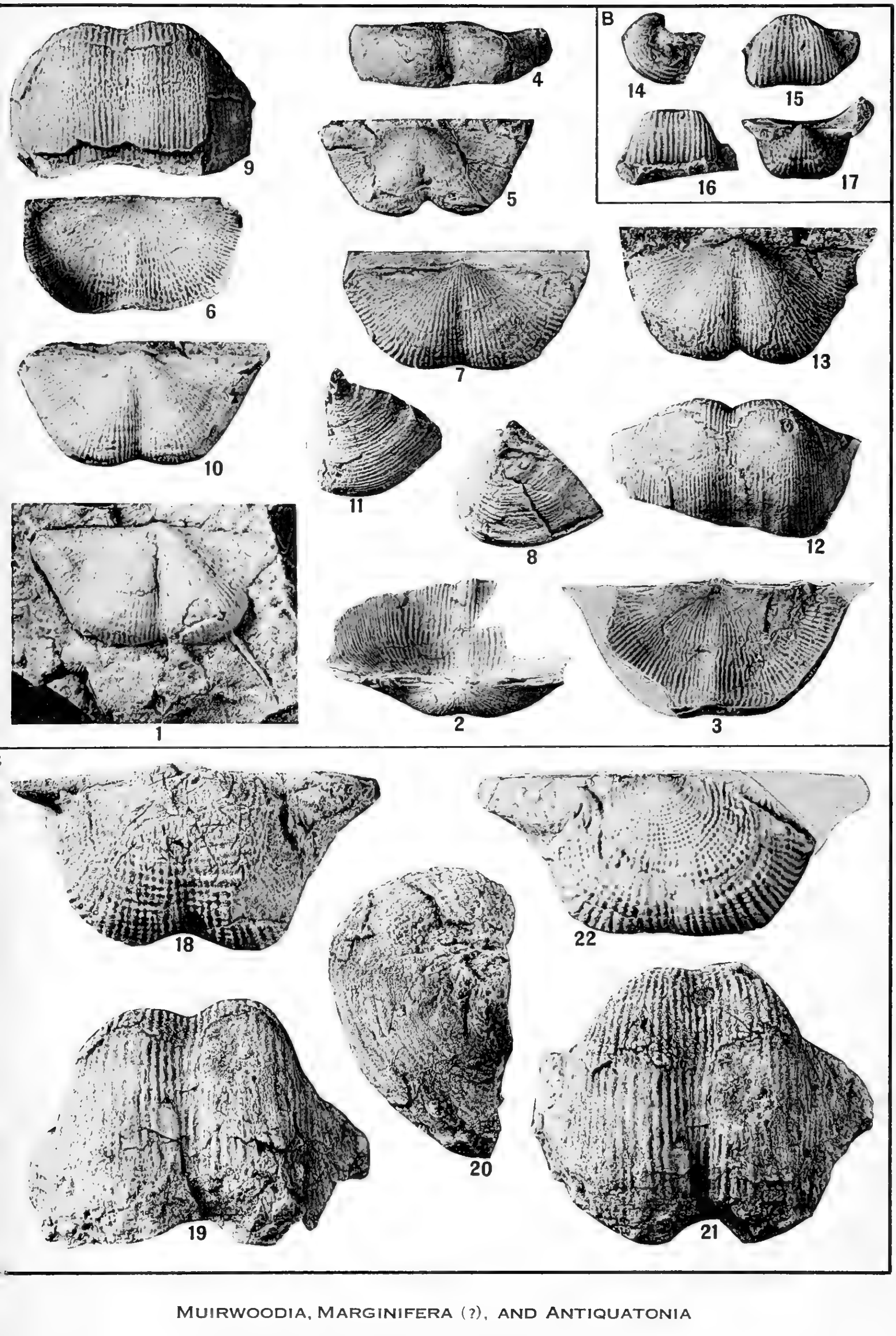

Muirwoodia, Marginifera (?), and Antiquatonia

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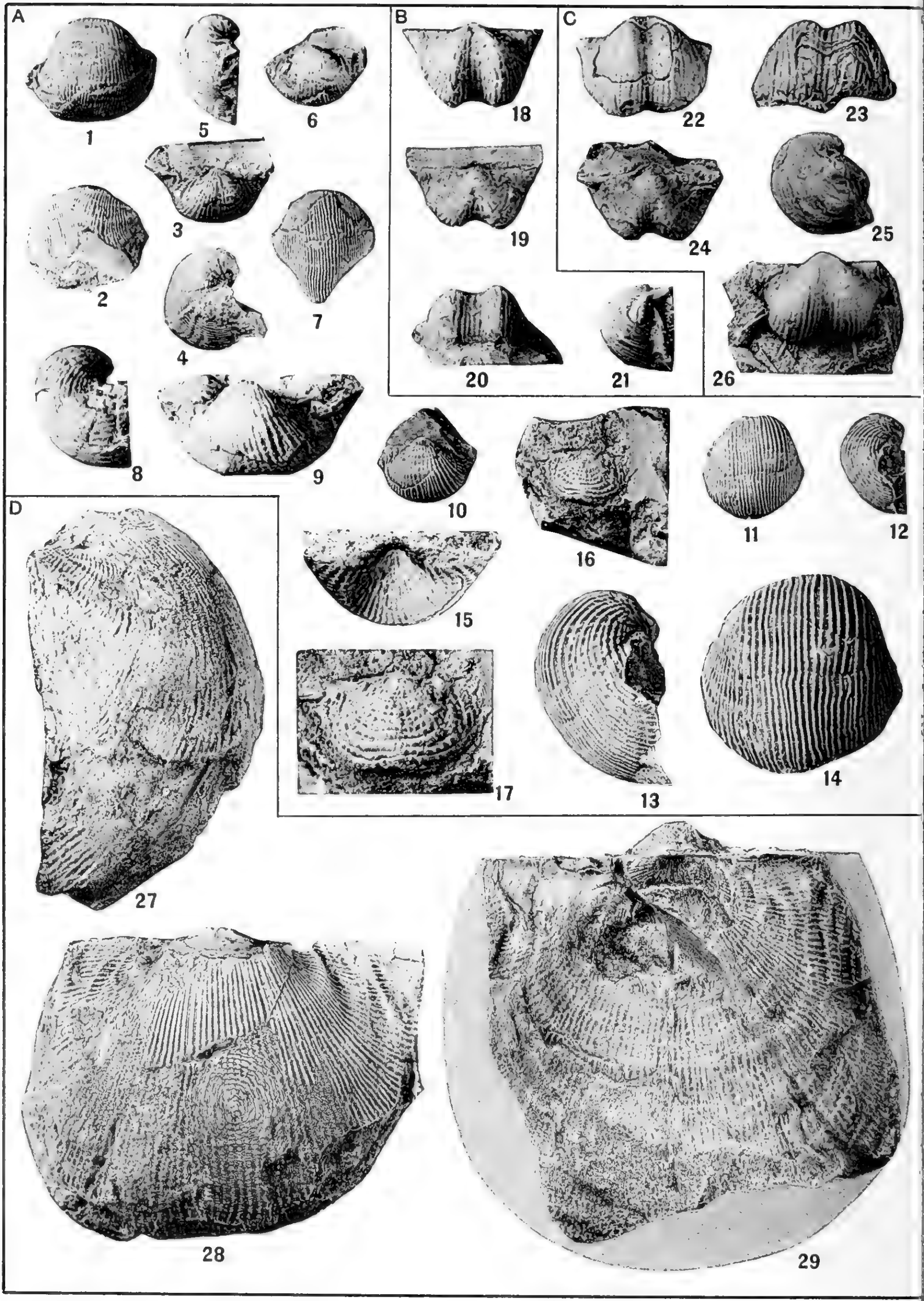

ANIDANTHUS, MARGINIFERA?, AND LINOPRODUCTUS

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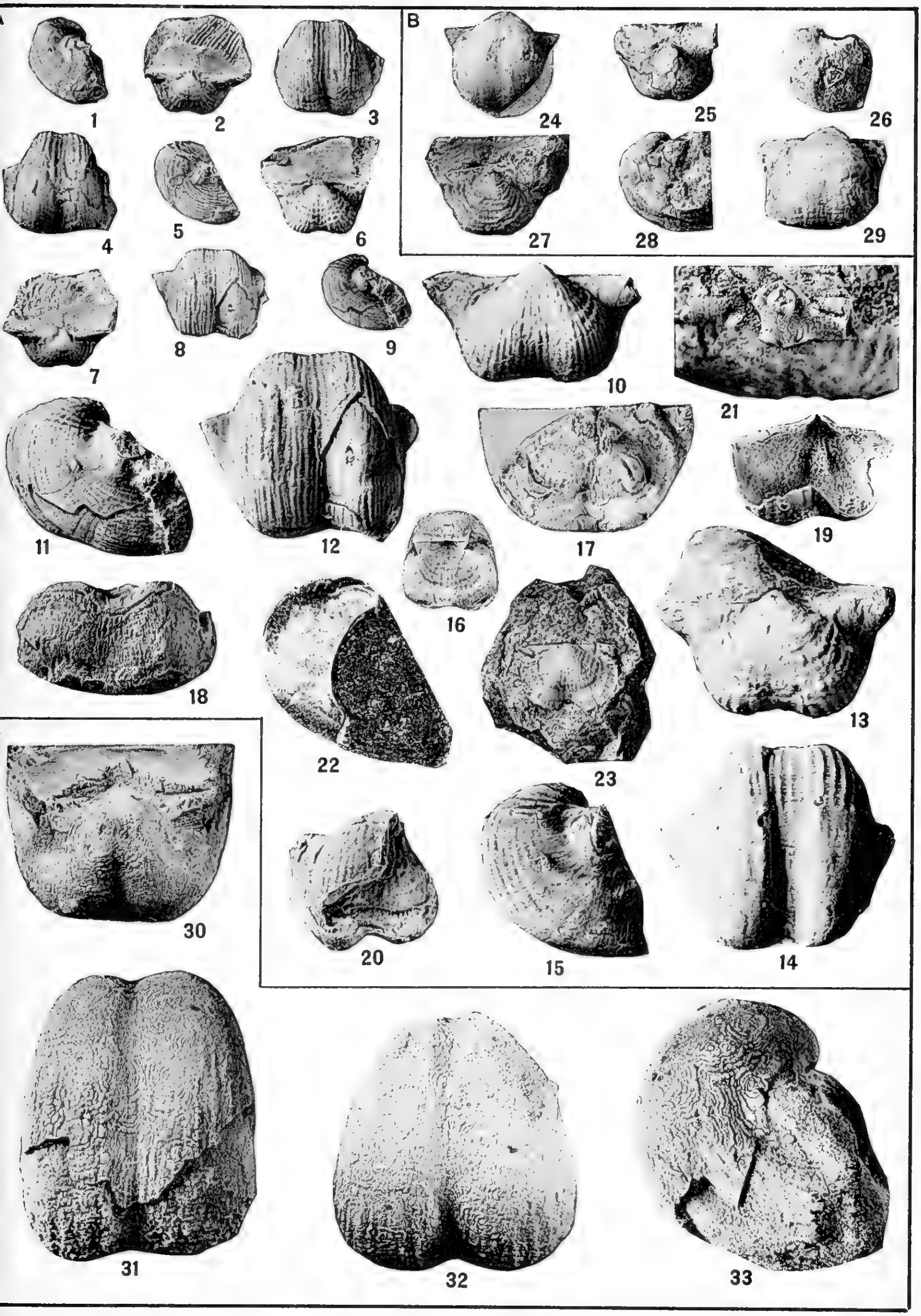

PROBOLIONIA, MARGINIFERA?, AND PLEUROHORRIDONIA?

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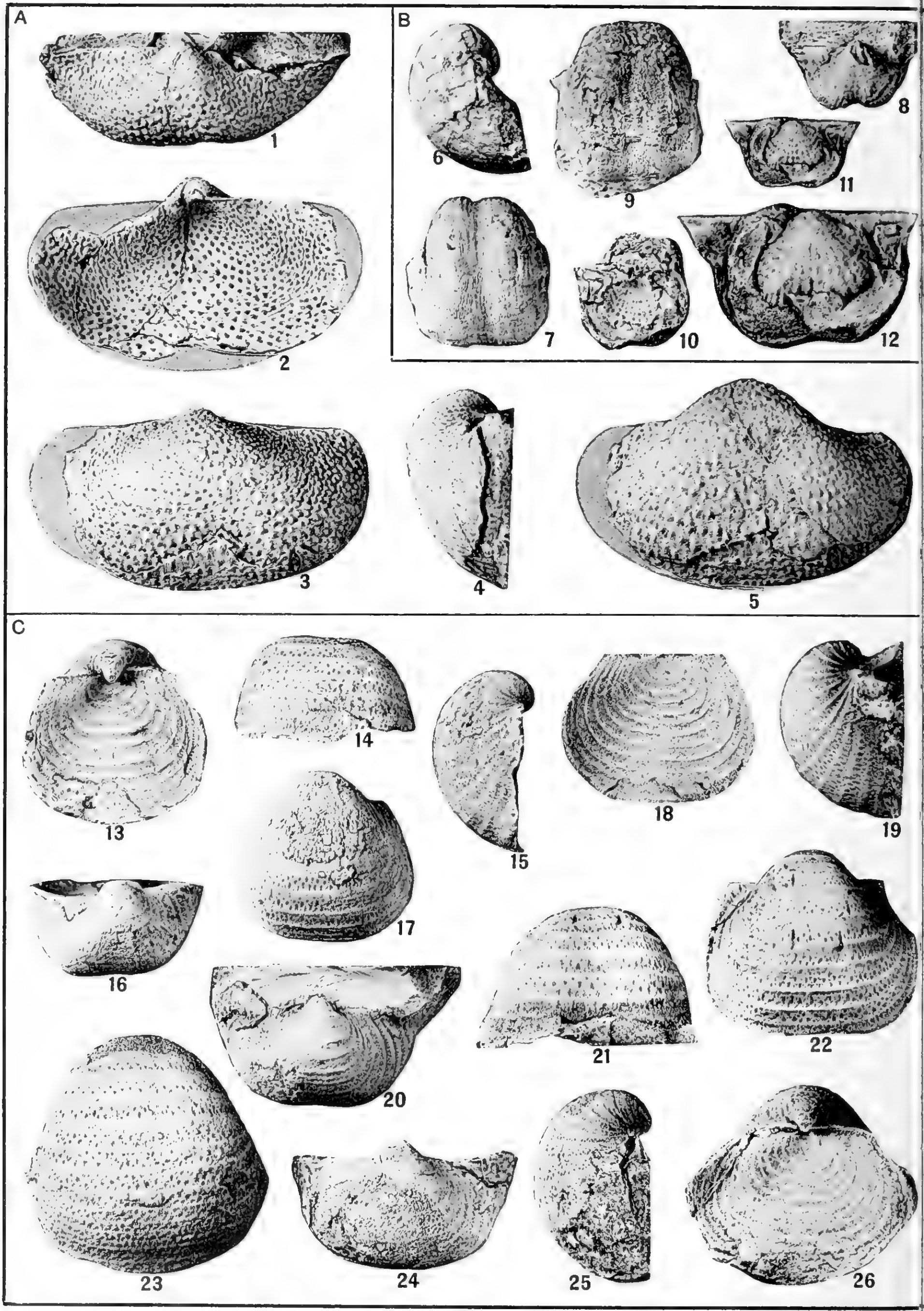
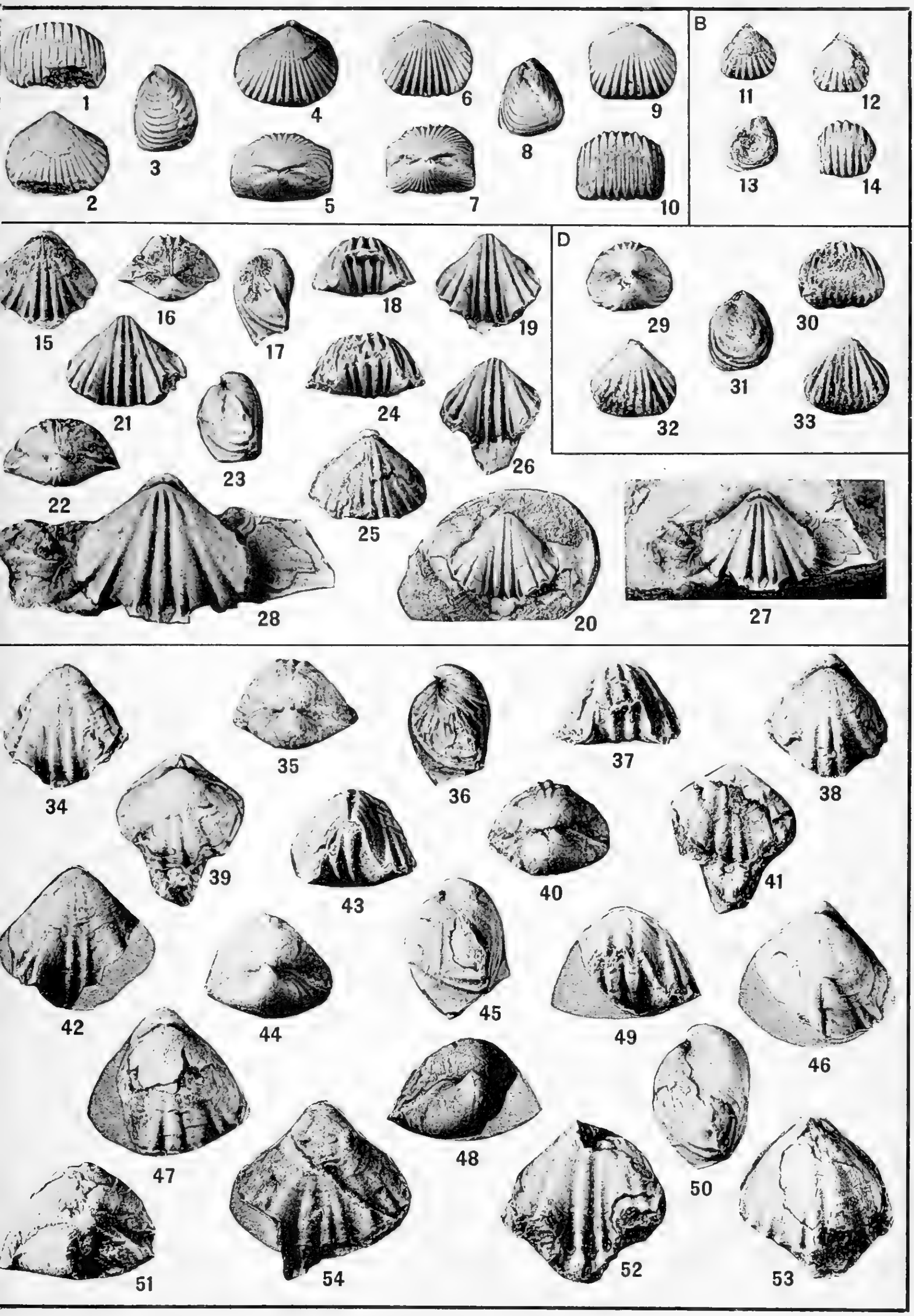


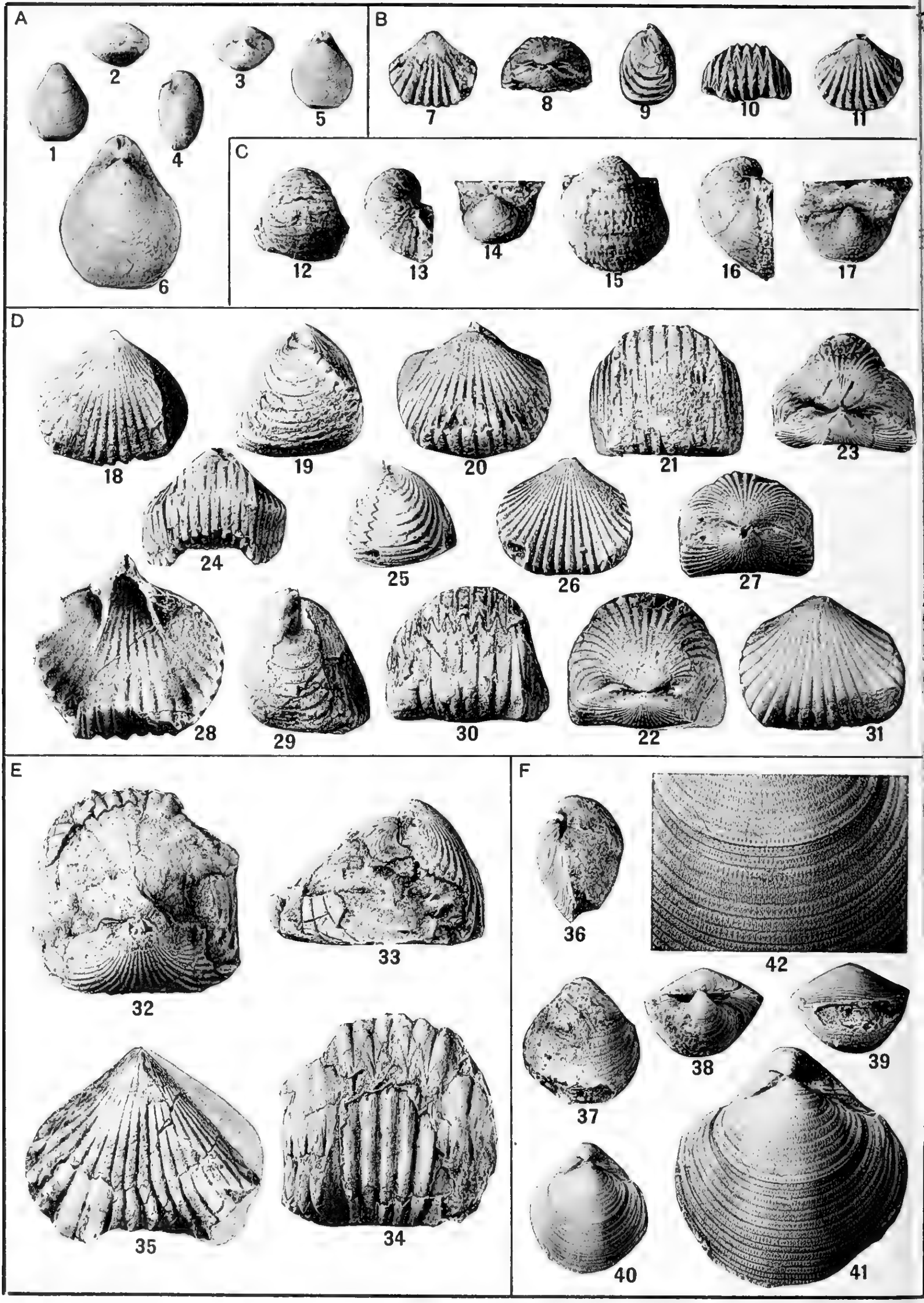
Krotovia, Probolionia, and Echinoconchus

(see explanation of plates at end of text)



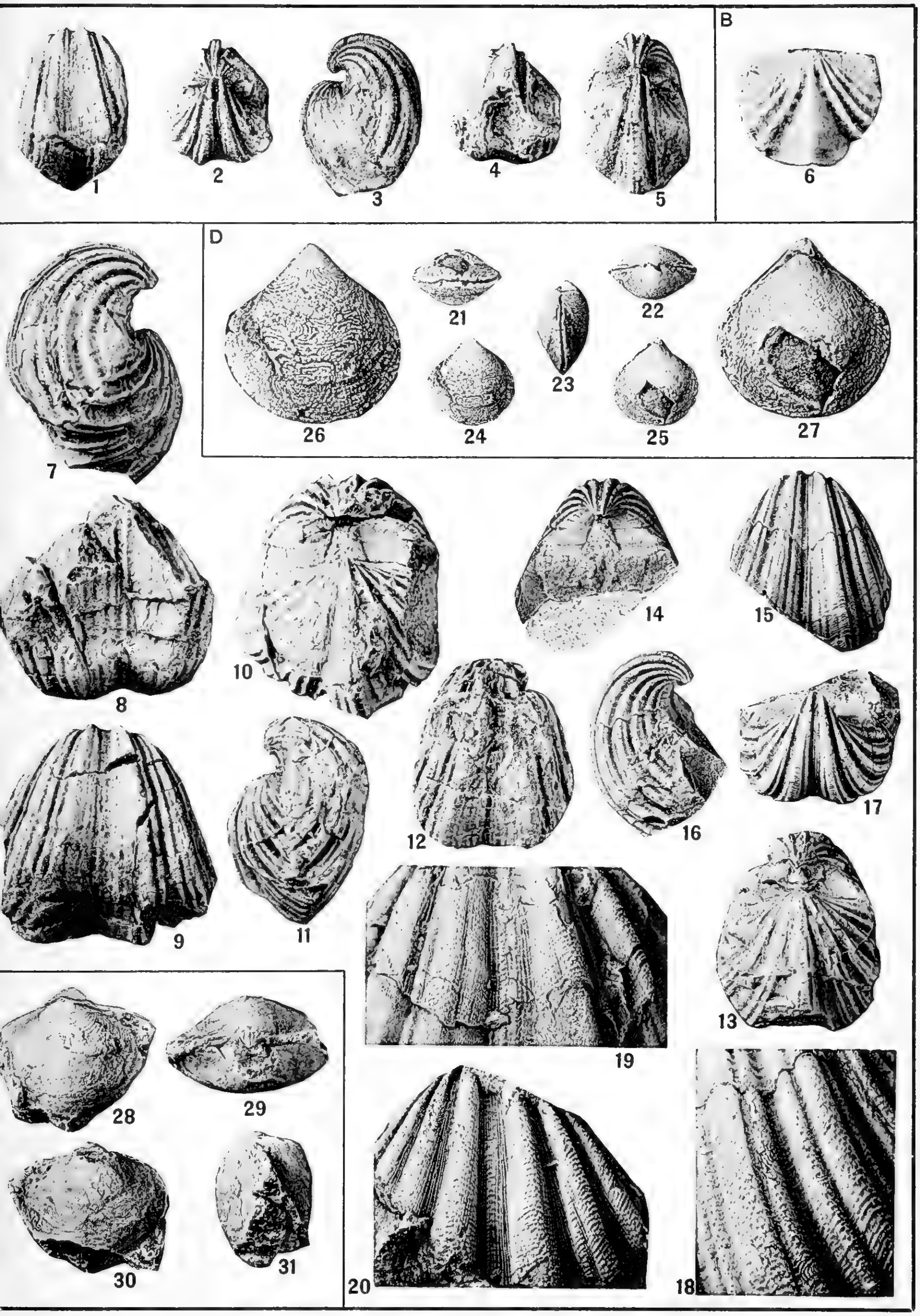
RHYNCHOPORA AND STENOSCISMA

(SEE EXPLANATION OF PLATES AT END OF TEXT)



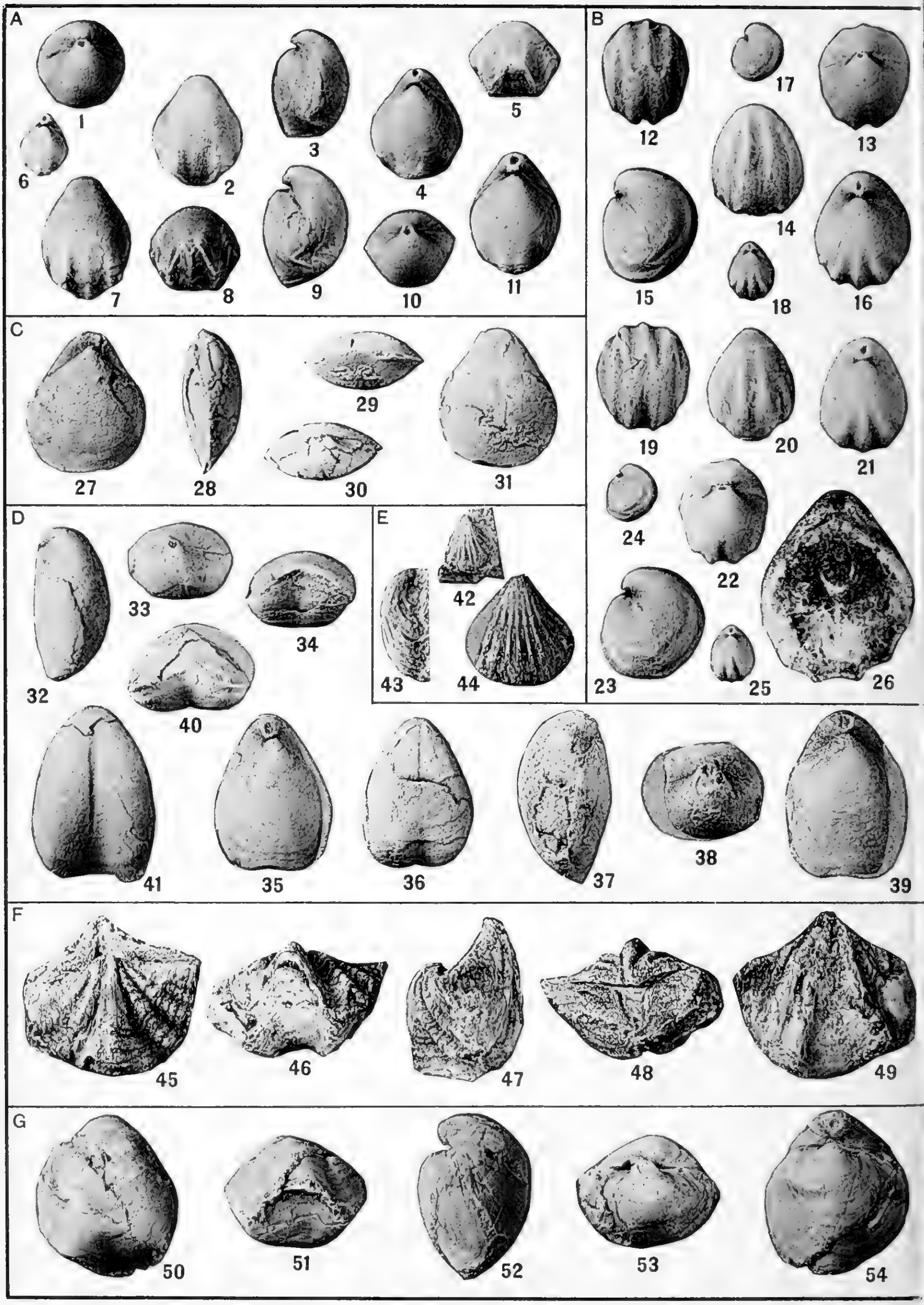
DIELASMA?, WELLERELLA, KROTOVIA, RHYNCHOPORA, STENOSCISMA, AND SQUAMULARIA

(SEE EXPLANATION OF PLATES AT END OF TEXT)



Spiriferella, Punctospirifer, and Cleiothyridina

(see explanation of plates at end of text)



Rostranteris, Dielasma, Hustedia, Spiriferellina, and Pseudomartinia

(see explanation of plates at end of text)